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54 Abstract

Maerl beds worldwide face habitat destruction (e.g. from dredging, fishing gear and fish farms), the combined pressures of ocean warming and acidification, and the spread of invasive species. Maerl beds have high conservation status in European legislation, yet their associated flora is poorly known. Here, we evaluate the known macroalgal diversity of NE Atlantic maerl beds from Svalbard to Portugal. Maerl beds occur from the low intertidal down to 51 m in the clearest waters. To date, 350 macroalgal species have been recorded on maerl in the NE Atlantic (67 % are Rhodophyta), a remarkable 30 % of the total seaweed diversity in this region. Eleven non-native species have been recorded on Atlantic European maerl beds, the most widely distributed being phases of *Bonnemaisonia hamifera* ("*Trailliella intricata*"), *Asparagopsis armata* ("*Falkenbergia rufolanosa*"), *Antithamnionella*

		spirographidis and *Heterosiphonia japonica*. The flora of maerl beds off Iceland and Norway is poorly known, but maerl beds off Britain, Ireland, France and Spain have been surveyed extensively and support several species that are maerl specialists (i.e. *Cruoria cruoriaeformis, Cladophora rhodolithicola, Gelidiella calcicola*). Our observations of *G. calcicola* and *Gelidium maggsiae* are new records for Portugal. Maerl beds in the Algarve have many of the same macroalgal species as Mediterranean maerl beds, but they are not as floristically diverse as those in Spain because they are confined to deeper water. Our census provides a baseline that can be used to assess changes to these habitats over the coming years.
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The diversity of seaweeds on maerl in the NE Atlantic

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Abstract Maerl beds worldwide face habitat destruction (e.g. from dredging, fishing gear and fish farms), the combined pressures of ocean warming and acidification, and the spread of invasive species. Maerl beds have high conservation status in European legislation, yet their associated flora is poorly known. Here, we evaluate the known macroalgal diversity of NE Atlantic maerl beds from Svalbard to Portugal. Maerl beds occur from the low intertidal down to 51 m in the clearest waters. To date, 350 macroalgal species have been recorded on maerl in the NE Atlantic (67 % are Rhodophyta), a remarkable 30 % of the total seaweed diversity in this region. Eleven non-native species have been recorded on Atlantic European maerl beds, the most widely distributed being phases of *Bonnemaisonia hamifera* ("*Trailliella intricata*"), *Asparagopsis armata* ("*Falkenbergia rufolanosa*"), *Antithamnionella spirographidis* and *Heterosiphonia japonica*. The flora of maerl beds off Iceland and Norway is poorly known, but maerl beds off Britain, Ireland, France and Spain have been surveyed extensively and support several species that are maerl specialists (i.e. *Cruoria cruoriaeformis, Cladophora rhodolithicola, Gelidiella calcicola*). Our observations of *G. calcicola* and *Gelidium maggsiae* are new records for Portugal. Maerl beds in the Algarve have many of the same macroalgal species as Mediterranean maerl beds, but they are not as floristically diverse as those in Spain because they are confined to deeper water. Our census provides a baseline that can be used to assess changes to these habitats over the coming years.

Keywords NE Atlantic · Biodiversity · Maerl · Macroalgae · Invasive species

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Introduction

Maerl beds are formed by unattached non-geniculate coralline algae that build up over thousands of years to form intricate coastal marine habitats (Blake and Maggs 2003; Bosence and Wilson 2003). In the NE Atlantic, maerl beds are concentrated on the westernmost coasts of Europe, being rare in the eastern English Channel, Irish Sea, North Sea and Baltic (Hall-Spencer 1998). European maerl beds are afforded conservation protection since their three-dimensional carbonate matrix provides a wide range of ecological niches for associated flora and fauna (Barberá et al. 2003). They are also productive ecosystems due to their associated flora (Martin et al. 2005). Activities such as dredging (e.g. for soil conditioner or shipping channels), destructive fishing (e.g. with dredges or trawls) and fish farming can reduce the complexity and biodiversity of these habitats, as can the spread of invasive

species such as the gastropod *Crepidula fornicata* (Barberá et al. 2003; Grall and Hall-Spencer 2003; Hall-Spencer et al. 2006; Peña and Bárbara 2008a). As well as these direct impacts, maerl beds face pressures from ocean warming and acidification: coralline algae are thought to be highly vulnerable to anthropogenic CO_2 emissions (Nelson 2009; Büdenbender et al. 2011; Porzio et al. 2011; Díaz Pulido et al. 2012; Noisette et al. 2013).

In the NE Atlantic, maerl beds occur from Svalbard to the Iberian Peninsula (Hall-Spencer et al. 2010; Teichert et al. 2012). They can be found in a wide variety of hydrodynamic conditions which have a strong influence on maerl morphology and associated biodiversity (Bosence 1976; Hall-Spencer and Atkinson 1999). This morphological variability can lead to difficulties in identification, since different species can look the same and the same species can look very different depending upon depth and water movement. For this reason, there are many descriptions of the varieties of widespread maerl-forming species such as *Phymatolithon calcareum* and *Lithothamnion corallioides* (Foslie 1895; Lemoine 1910; Adey and McKibbin 1970). Variations in form and habitat stability contribute to the variety of ecological niches available to seaweeds that live on maerl (Hinojosa et al. 2009; Pascelli et al. 2013).

Previous studies of NE Atlantic maerl beds show a latitudinal replacement in the composition of the maerl-forming species from the subarctic beds of Iceland and Norway to warm-temperate beds of the Iberian Peninsula (Irvine and Chamberlain 1994). Data on the flora of NE Atlantic maerl beds are dispersed and often restricted to grey literature reports. Nevertheless, these data show that maerl beds can be very rich floristically and include species such as *Cruoria cruoriaeformis* and *Cladophora rhodolithicola* that are seldom or never found in other habitats (Maggs and Guiry 1987; Barberá et al. 2003; Leliaert et al. 2009; Peña and Bárbara 2010a). Here, we provide a catalogue and an overview of the associated maerl flora recorded in the NE Atlantic regions, including new data from southern Portugal, to draw attention to information gaps and provide a baseline against which future changes can be assessed.

Methods

We used published and unpublished studies to extract lists of the macroalgae recorded from maerl beds in Iceland, Norway, Britain, Ireland, France (Brittany), Spain (Galicia) and Portugal (the Algarve) (Table 1). For species with heteromorphic life histories, both morphological phases are included and our nomenclature follows Guiry and Guiry (2013). We reviewed approximately 54 studies as follows: Svalbard (1), Iceland (3), Norway (4), Sweden (1), Britain (11, from Scotland, Wales and Cornwall), Ireland (14, mainly from west and northeast coasts), France (15, from Brittany and Bay of Biscay), Spain (22, from Galicia) and Portugal (2, from the Algarve). Additional survey data were obtained by V.P. off Iceland (Hvalfjördur, at 3–10 m depth), Norway (Skarsundet, 11 m depth), Ireland (Strangford Lough, Northern Ireland, 10 m depth), Britain (Dorset, 12 m depth) and France (Brittany, REBENT survey) during 2003–2005, and by I.B. and V.P. off Galicia and the Algarve. Photographs showing characteristic features of NE Atlantic maerl beds are also provided, taken on diving and dredging surveys by the authors between 2002 and 2012.

Results

In the NE Atlantic, most maerl beds occur in areas <30 m depth but in very clear waters live maerl can occur to 51 m depth (Fig. 1). Wave action can arrange living maerl in the furrows of sediment megaripples (Figs. 2 and 3). Maerl occurs intertidally in Ireland, France and Spain, in some cases with adjacent beaches composed of dead maerl (Fig. 3). By contrast, maerl beds in the Algarve have only been found at 13–23 m depth.

Our literature search has shown that in the NE Atlantic maerl beds harbour at least 350 associated algal species (excluding the maerl-forming species themselves; Table 2): 233 Rhodophyta, 72 Heterokontophyta and 45 Chlorophyta. This is around 30 % of the total seaweed diversity recorded in the NE Atlantic (Table 2). The diversity of the associated flora is especially high in the waters off Iberia to Britain and Ireland (25–42 % of the total seaweed diversity recorded in these regions; Table 2; Fig. 4). Maerl-associated flora range from crustose forms to large brown algae such as *Laminaria hyperborea, L. ochroleuca, Saccharina latissima* and *Saccorhiza polyschides* (Table 3). For ten species of red algae and two browns, both gametangial and sporangial life history phases have been found on maerl. Two red algae and one brown have been recorded only as their crustose sporophytic stage.

The maerl-associated flora recorded in Iceland and Norway is low (8 and 14 species, respectively) and is undoubtedly underestimated. Our surveys conducted on two subtidal maerl beds in Iceland and Norway in June and July 2004 recorded few algal species, although some were abundant (*Desmarestia viridis* and the non-native *Heterosiphonia japonica* in Norway; Table 3; Fig. 4). At lower latitudes, the associated flora of maerl beds of Britain, Ireland, France and Spain is very diverse, especially in Spain where >250 species are reported. In the Algarve, 60 species of seaweeds have been found on maerl. The occurrence of *Gelidiella calcicola* and *Gelidium maggsiae* constitute new records for Portugal, increasing their known southern distribution (Guiry and Guiry 2013). Eleven species have not previously been reported on NE Atlantic beds (i.e. the red algae *G. bipectinatum,*

t1.1 **Table 1** Chronological list of NE Atlantic maerl studies used in our analyses of associated flora, showing the regions covered

t1.2		Svalbard	Iceland	Norway	Sweden	Britain	Ireland	France (Atlantic)	Spain (Atlantic)	Portugal
t1.3	Foslie 1895			+						
t1.4	Lemoine 1910							+		
t1.5	Cotton 1912						+			
t1.6	Hamel 1928								+	
t1.7	Miranda 1934								+	
t1.8	Miranda 1936								+	
t1.9	Suneson 1958				+					
t1.10	Seoane-Camba 1960								+	
t1.11	Jacquotte 1962							+		
t1.12	Adey 1968		+							
t1.13	Donze 1968								+	
t1.14	Seoane-Camba and Campo Sancho 1968								+	
t1.15	Sneli 1968			+						
t1.16	Cabioch 1969							+		
t1.17	Adey and McKibbin 1970								+	
t1.18	Niell 1970								+	
t1.19	L'Hardy-Halos et al. 1973							+		
t1.20	Blunden et al. 1977							+		
t1.21	Farnham and Jephson 1977					+				
t1.22	Gunnarsson 1977		+							
t1.23	Blunden et al. 1981					+	+	+		
t1.24	Maggs 1983						+			
t1.25	Maggs and Irvine 1983					+	+	+		
t1.26	Maggs et al. 1983						+			
t1.27	Maggs and Guiry 1987					+	+	+		
t1.28	Maggs and Guiry 1989					+	+	+		
t1.29	Hily et al. 1992							+		
t1.30	Otero-Schmitt 1993								+	
t1.31	Bárbara et al. 1996								+	
t1.32	Rico and Guiry 1997						+			
t1.33	Birkett et al. 1998a					+	+			
t1.34	Bárbara et al. 1999								+	
t1.35	BIOMAERL Team 1999					+		+	+	
t1.36	De Grave and Whitaker 1999						+			
t1.37	Valenzuela 2001								+	
t1.38	Bárbara et al. 2002								+	
t1.39	Otero-Schmitt and Pérez-Cirera 2002								+	
t1.40	Bárbara et al. 2004								+	
t1.41	Husa et al. 2004			+						
t1.42	Sjøtun et al. 2008			+		+	+	+		
t1.43	Hinojosa et al. 2009						+			
t1.44	Leliaert et al. 2009					+	+	+		
t1.45	Peña and Bárbara 2008a								+	
t1.46	Peña and Bárbara 2008b								+	
t1.47	Peña et al. 2009									+
t1.48	Destombe et al. 2010								+	
t1.49	Hall-Spencer et al. 2010		+			+	+	+		
t1.50	Peña 2010								+	
t1.51	Peña and Bárbara 2010a								+	

t1.52 **Table 1** (continued)

	Svalbard	Iceland	Norway	Sweden	Britain	Ireland	France (Atlantic)	Spain (Atlantic)	Portugal
t1.53 Peña and Bárbara 2010b								+	
t1.54 Bunker 2011					+				
t1.55 Sauriau et al. 2012							+		
t1.56 Teichert et al. 2012	+								
t1.57 Peña and Bárbara 2013									+
t1.58 Present study		+	+		+	+	+	+	+

Peyssonnelia bornetii, *P. coriacea, Predaea ollivieri, P. pusilla,* the browns *Cutleria adspersa* "*Aglaozonia melanoidea*" phase*, Dictyota cyanoloma, Phyllariopsis purpurascens* and *Zonaria tournefortii*, and the greens *Cladophora prolifera* and *Codium bursa*; Table 3; Fig. 4). All except *Peyssonnelia coriacea*, *Predaea pusilla* and *P. purpurascens* have also been recorded on Mediterranean maerl beds (Peña and Bárbara 2008a).

Similarities of NE Atlantic maerl bed flora

Many species (72 Rhodophyta, 11 Heterokontophyta, 4 Chlorophyta) are widely distributed, being recorded on maerl beds in at least four regions (Table 3). A total of 45 species (37 Rhodophyta, 6 Heterokontophyta, 2 Chlorophyta) occur on maerl beds off Britain, Ireland, France and Spain. The most widely distributed are the "*Trailliella intricata*" sporophyte phase of *Bonnemaisonia hamifera* and *Polysiphonia stricta* which occur on maerl from Iceland to Spain, and *Pterothamnion plumula* and *Rhodophyllis divaricata* which occur on maerl from Norway to south Portugal (Table 3). *Saccharina latissima* is also widespread on maerl beds from Iceland to Spain and *Brongniartella byssoides, Phyllophora crispa,* and *Spermothamnion repens* have been recorded on maerl beds from Norway to Spain. Twenty-five other species were also reported from Britain/Ireland to south Portugal: the Rhodophyta *Apoglossum ruscifolium, Asparagopsis armata* sporophyte "*Falkenbergia rufolanosa*", *Atractophora hypnoides* sporophyte "*Rhododiscus pulcherrimus*", *Bonnemaisonia asparagoides, Callophyllis laciniata, Compsothamnion thuyoides, Cruoria cruoriaeformis, Cryptopleura ramosa, Dudresnaya verticillata, Gelidiella calcicola, Gelidium spinosum, Gracilaria gracilis, Halarachnion ligulatum* (both stages)*, Halymenia latifolia, Hildenbrandia rubra, Hypoglossum hypoglossoides, Jania rubens, Lomentaria clavellosa, Peyssonnelia dubyi, Plocamium cartilagineum, Pterosiphonia parasitica* and *Stenogramma interruptum*, and the brown seaweed *Halopteris filicina*. Of the green seaweeds, only four species were reported in maerl beds of four different regions: *Cladophora rhodolithicola* and *Rhizoclonium tortuosum* from Britain–Ireland to Spain, and *Bryopsis plumosa* and *Cladophora hutchinsiae* from Britain–Ireland to south Portugal (excluding France).

Eleven non-native species have so far been recorded on NE Atlantic maerl beds (Table 3): the Rhodophyta *Antithamnionella spirographidis, A. ternifolia, Bonnemaisonia hamifera* (both stages), *Dasya sessilis, Grateloupia turuturu, Heterosiphonia japonica* and *Neosiphonia harveyi*, the Heterokontophyta *Colpomenia peregrina, Sargassum muticum* and *Undaria pinnatifida*, and the Chlorophyta *Codium fragile*. The sporophytic stage of *Bonnemaisonia hamifera* ("*Trailliella intricata*") was recorded in maerl beds of six different regions whereas the sporophytic stage of *Asparagopsis armata* ("*Falkenbergia rufolanosa*"), *Antithamnionella spirographidis* and *Heterosiphonia japonica* were reported in four different regions.

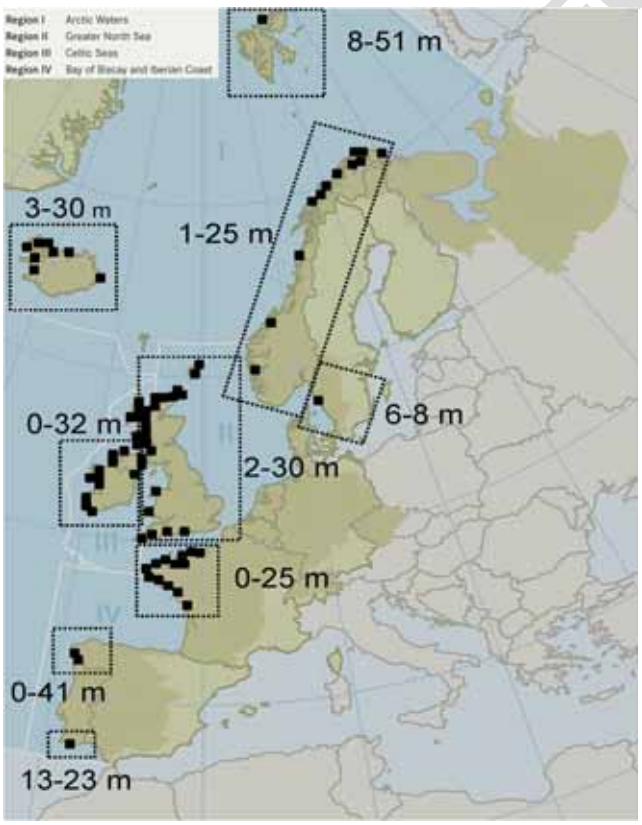

Fig. 1 Location and depth range of maerl beds in the OSPAR. Data from Hall-Spencer et al. (2010), and the present study

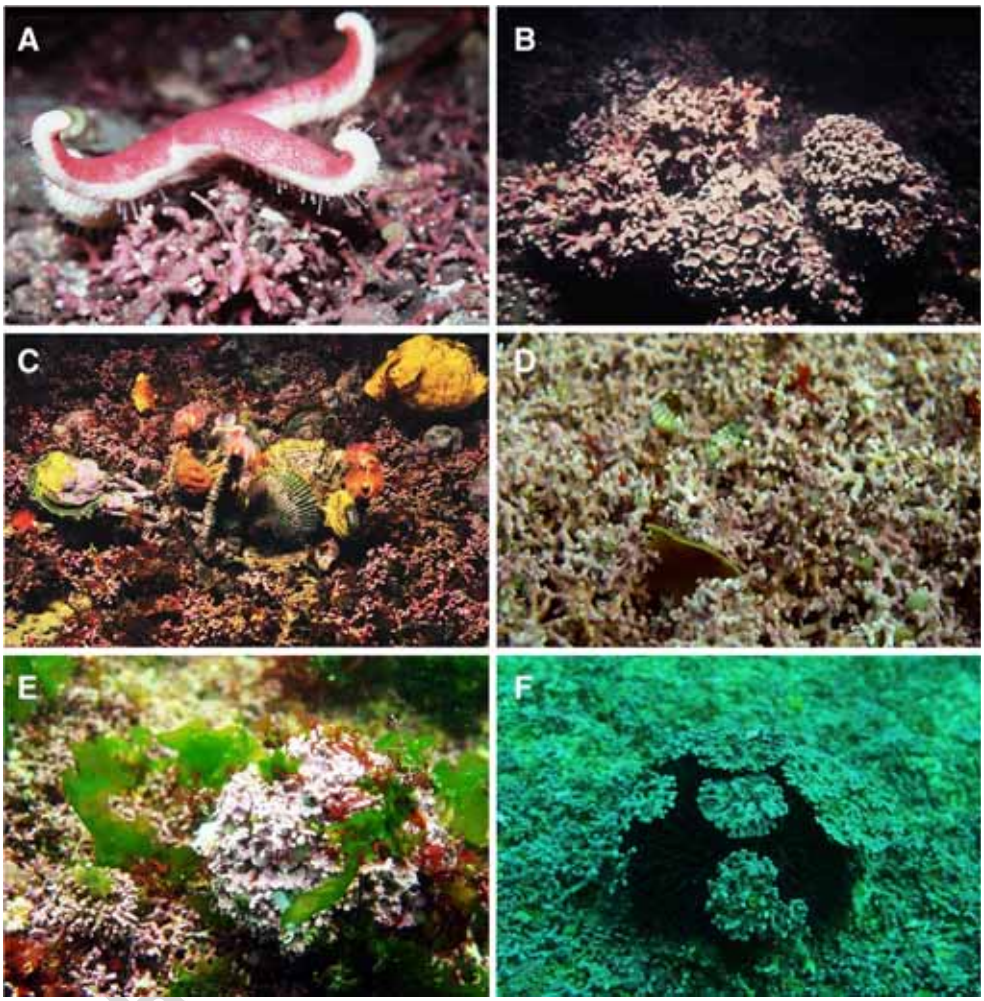

Fig. 2 A range of maerl morphologies on subtidal beds off Scotland (**a** *Lithothamnion glaciale*), Ireland (**b** *Lithophyllum* sp.), Brittany (**c** *Lithothamnion corallioides*), Galicia (**d** *Phymatolithon calcareum* and *L. corallioides*, **e** *Mesophyllum sphaericum*) and in South Portugal (**f** *Phymatolithon* sp.)

Some seaweeds are maerl specialists, in that they are usually only found in this habitat. These include the red algal species *Cruoria cruoriaeformis, Halymenia latifolia, Gelidiella calcicola and Gelidium maggsiae* which have been recorded from Britain–Ireland to south Portugal (Table 3). The chlorophyte *Cladophora rhodolithicola* has been found on maerl from Britain- Ireland to Galicia; in the literature, this species was erroneously referred to *C. rupestris* (Leliaert et al. 2009).

Regional differences in NE Atlantic maerl associated flora

As expected, there are clear biogeographic trends in our catalogue of maerl-associated flora. For example, *Scagelothamnion pusillum* and *Turnerella pennyi* have a northern distribution and have only been recorded on maerl beds in Iceland (Table 3). Britain also has some species not recorded on maerl in other regions (12 Rhodophyta, two Heterokontophyta and one Chlorophyta) with *Schmitzia hiscockiana* and *Scinaia turgida* only recorded on Scottish maerl beds. In Brittany, 26 seaweed species have not been recorded on other NE Atlantic maerl beds (13 Rhodophyta, 12 Heterokontophyta and 1 Chlorophyta); the Galician beds have 83 algal species not recorded on maerl in other regions (56 Rhodophyta, 15 Heterokontophyta and 12 Chlorophyta) whereas maerl off south Portugal has eight species (3 Rhodophyta, 3 Heterokontophyta and 2 Chlorophyta) which extend into the Mediterranean. Maerl beds off Galicia and south Portugal harbour nine species that have not been recorded further north (i.e. the Rhodophyta *Anotrichium furcellatum, Contarinia peyssonneliaeformis, Erythroglossum lusitanicum, Hildenbrandia crouaniorum* and *Mesophyllum lichenoides,* the Heterokontophyta *Cystoseira usneoides* and *Stypocaulon scoparium* and the Chlorophyta *Codium tomentosum* and *C. vermilara*).

Discussion

Maerl beds are patchily distributed on the westernmost coasts of Europe from the Algarve to Svalbard where they are the deepest habitat-forming algae in the NE Atlantic. They occur

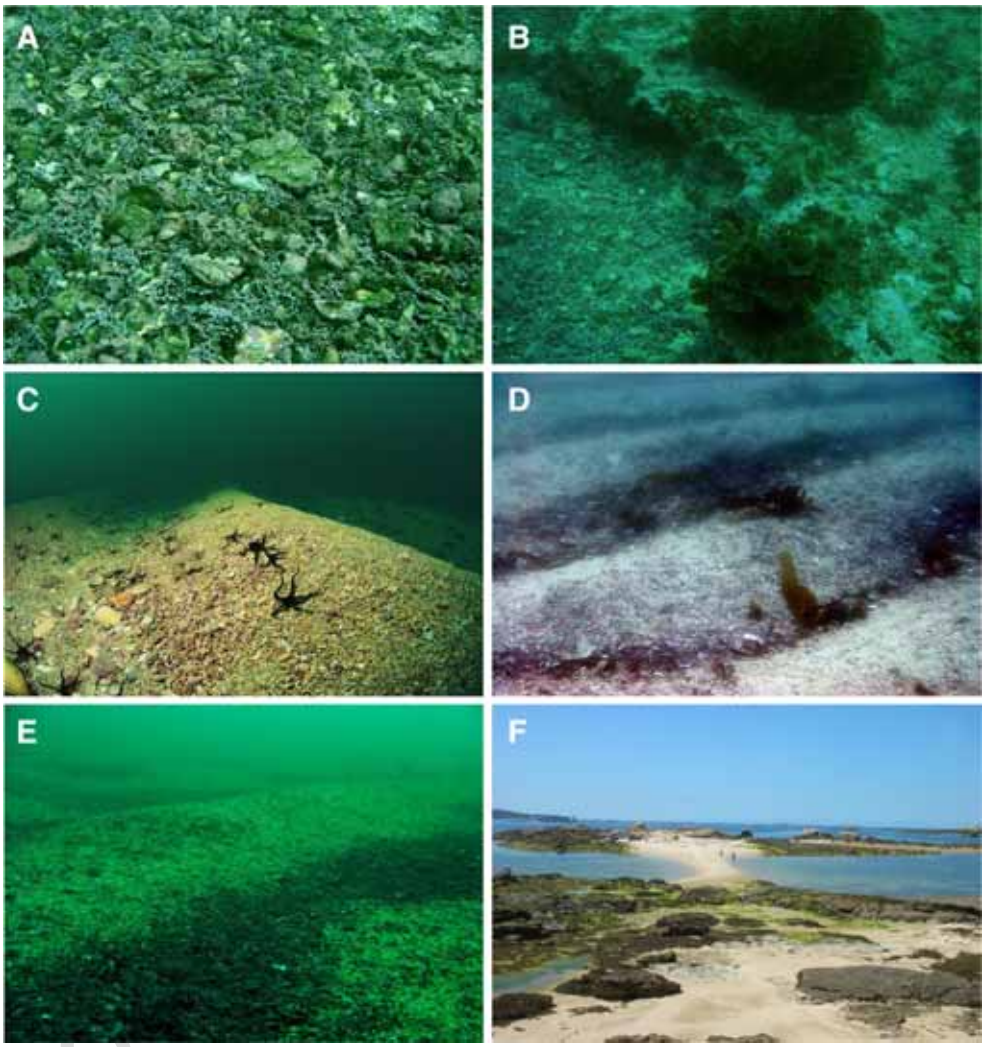

Fig. 3 **a**, **b** Subtidal maerl beds in South Portugal. Maerl bed mixed with cobbles (**a**), sometimes occurring between rocky outcrops (**b**). **c**–**e** Maerl beds with ripples and megaripples in Brittany (**c**), Galicia (**d**) and South Portugal (**e**). **f** Maerl beach with intertidal bed in Galicia

t2.1 **Table 2** Number of algal species recorded on maerl beds in each Atlantic region according to the literature (Table 1), and previously unpublished data (see "Methods")

t2.2		Rhodophyta	Heterokontophyta	Chlorophyta	Maerl flora	Total seaweed diversity by region	Maerl flora/total seaweed diversity (%)
t2.3	Iceland	5	3	0	8	269	2.97
t2.4	Norway	10	3	1	14	314	4.45
t2.5	Britain	127	26	21	174	687	25.32
t2.6	Ireland	112	20	18	150	570	26.31
t2.7	France (Atlantic)	118	42	14	174	416	41.82
t2.8	Spain (Atlantic)	183	43	31	257	649	39.59
t2.9	Portugal	44	10	6	60	537	11.17
t2.10	NE Atlantic	233	72	45	350	1232	28.40

The percentage of maerl associated flora compared with the total seaweed diversity recorded in each region is shown. Total seaweed diversity was obtained according to these references: Iceland (Gunnarsson and Jonsson 2002), Norway (Guiry and Guiry 2013), Ireland (Guiry 2012), Britain (Hardy and Guiry 2003; Leliaert et al. 2009), France (Atlantic coast: Dizerbo and Herpe 2007; Leliaert et al. 2009; Bárbara and Díaz-Tapia 2012), Spain (Atlantic coast: Gorostiaga et al. 2004; Bárbara et al. 2005, 2008, 2012, 2013a, b; Peña and Bárbara 2006, 2010a; Leliaert et al. 2009; Cires-Rodríguez and Cuesta-Moliner 2010; Peña et al. 2011; Secilla 2012; Díaz-Tapia et al. 2013a, b) and Portugal (Araújo et al. 2009; Tronholm et al. 2010; Berecibar 2011; Peña and Bárbara 2013; present study). The total seaweed diversity reported in the NE Atlantic coasts is provided according to Tittley (2002), Guiry and Guiry (2013) and the present study

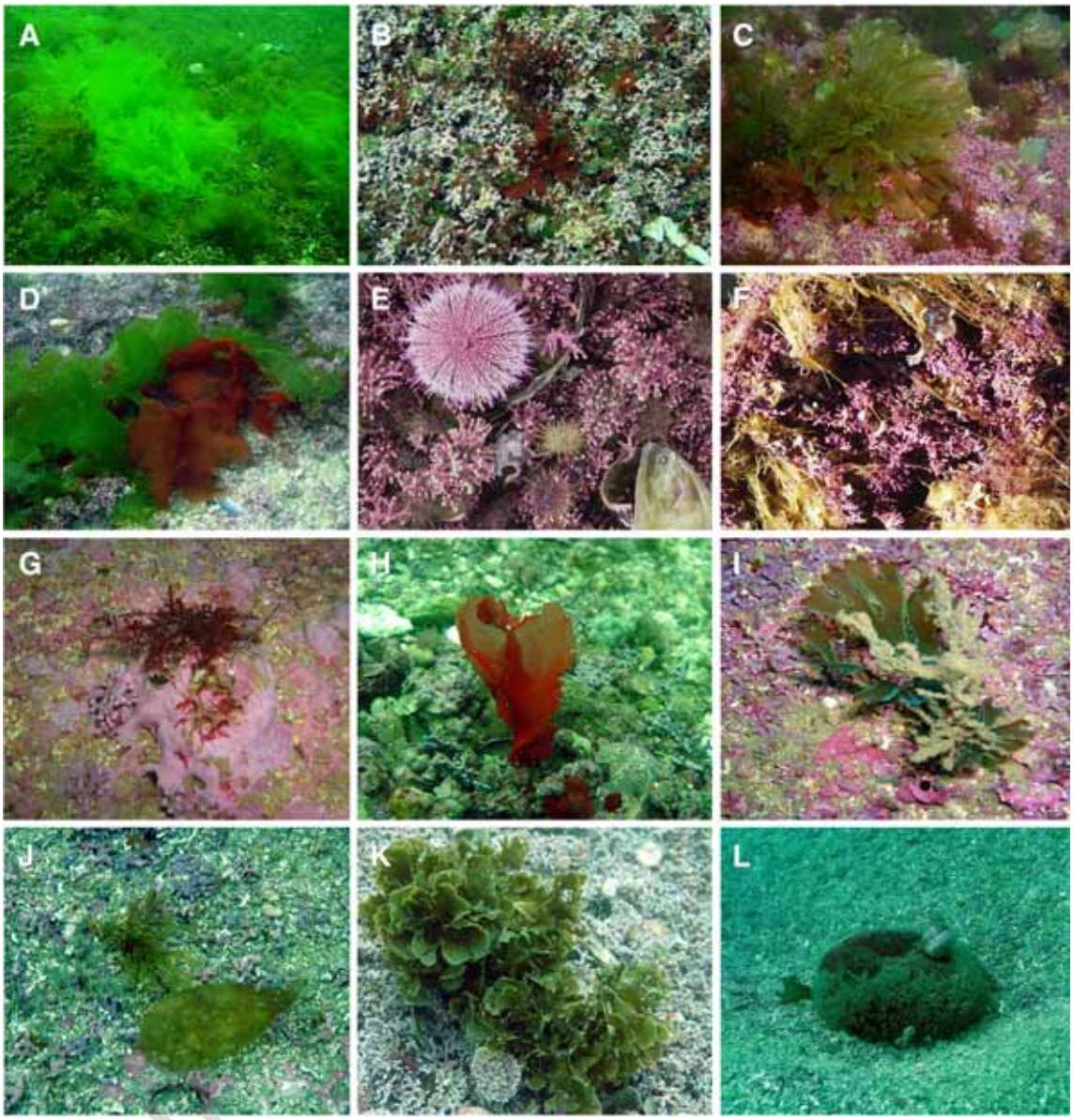

Fig. 4 **a**–**d** High seaweed diversity in temperate maerl beds (Galicia, 3–11 m, May 2005, and May and September 2007). **e** Maerl sample collected in Iceland almost devoid of associated flora (Hvalfjördur, dredge at 4–10 m, July 2004). **f** Large specimens of *Desmarestia viridis* on maerl in Norway (Skärsundet, dredge at 11 m, June 2004). **g**–**l** Portuguese maerl beds with *Gelidium bipectinatum* (**g**), *Predaea pusilla* (**h**), *Dictyota cyanoloma* (**i**), *Phyllariopsis purpurascens* (**j**), *Zonaria tournefortii* (**k**), and *Codium bursa* (**l**)

from the low intertidal to 51 m depth, compared with 60 m in Macaronesia (Cabioch 1974; Afonso-Carrillo and Gil-Rodríguez 1982), and 100 m in the exceptionally clear waters of the Mediterranean (Jacquotte 1962; Ballesteros 1988; BIOMAERL Team 1999). Maerl can live down to depths with ca. 1 % surface illumination where they do not need to compete with fast-growing, non-coralline species that occupy shallower areas (Teichert et al. 2012).

Our catalogue shows that NE Atlantic maerl beds harbour at least 350 macroalgal species, which is a staggering 30 % of the NE Atlantic seaweed diversity and includes several new regional records. The heterogeneous structure of maerl beds provides a wide range of niches (e.g. cobbles, shells and maerl thalli with patches of muddy, sandy and gravelly sediments) that allow a wide range of algal morphologies to co-occur, from endolithic and crustose forms to large kelps. Varing levels of disturbance within maerl habitats also promote diversity, in line with the intermediate disturbance hypothesis (Connell 1978). For comparison, kelp forests are thought to harbour around 10 % of the NE Atlantic flora and seagrasses around 5 % (Birkett et al. 1998b; Davison and Hughes 1998).

The diversity of the associated flora of the NE Atlantic maerl beds is especially high around Britain–Ireland and the Iberian Peninsula with 150–257 associated species. The high

t3.1 **Table 3** List of macroalgal species (and life cycle phases) recorded on NE Atlantic maerl for Iceland, Norway, Britain, Ireland, France, Spain and Portugal

t3.2	Division	Species	ATLANTIC	> 4 regions	Iceland	Norway	Britain	Ireland	France	Spain	Portugal
t3.3	H	*Acinetospora crinita* (Carmichael) Sauvageau	+							+	
t3.4	H	*Arthrocladia villosa* (Hudson) Duby	+				+		+		
t3.5	H	*Asperococcus bullosus* J.V. Lamouroux	+						+	+	
t3.6	H	*Asperococcus ensiformis* (Delle Chiaje) M.J. Wynne	+							+	
t3.7	H	*Asperococcus fistulosus* (Hudson) W.J. Hooker	+				+	+			
t3.8	H	*Carpomitra costata* (Stackhouse) Batters	+						+	+	
t3.9	H	*Chorda filum* (Linnaeus) Stackhouse	+			+	+		+		
t3.10	H	*Cladosiphon zosterae* (J. Agardh) Kylin	+						+		
t3.11	H	*Cladostephus spongiosus* (Hudson) C. Agardh	+	+			+	+	+	+	
t3.12	H	*Colpomenia peregrina* Sauvageau	N						N	N	
t3.13	H	*Cutleria adspersa* (Mertens ex Roth) De Notaris *stadium* "*Aglaozonia melanoidea*" Sauvageau	*								*
t3.14	H	*Cutleria multifida* (Turner) Greville	+				+		+	+	
t3.15	H	*Cutleria multifida stadium* "*Aglaozonia parvula*" (Greville) Zanardini	+	+			+	+	+	+	
t3.16	H	*Cystoseira baccata* (S.G. Gmelin) P.C. Silva	+							+	
t3.17	H	*Cystoseira nodicaulis* (Withering) M. Roberts	+						+	+	
t3.18	H	*Cystoseira usneoides* (Linnaeus) M. Roberts	+							+	+
t3.19	H	*Desmarestia aculeata* (Linnaeus) J.V. Lamouroux	+				+		+		
t3.20	H	*Desmarestia dudresnayi* J.V. Lamouroux *ex* Leman	+							+	
t3.21	H	*Desmarestia ligulata* (Stackhouse) J.V. Lamouroux	+						+	+	
t3.22	H	*Desmarestia viridis* (Müller) Lamouroux	+	+	+	+		+	+		
t3.23	H	*Dictyopteris lucida* Ribera Siguán, Gómez Garreta, Pérez Ruzafa, Barceló Martí *et* Rull Lluch	+							+	
t3.24	H	*Dictyopteris polypodioides* (A.P. De Candolle) J.V. Lamouroux	+						+	+	
t3.25	H	*Dictyota cyanoloma* Tronholm, De Clerck, Gómez Garreta *et* Rull LLuch									*
t3.26	H	*Dictyota dichotoma* (Hudson) J.V. Lamouroux	+	+		+	+	+	+	+	+
t3.27	H	*Ectocarpus fasciculatus* Harvey	+	+	+		+		+	+	
t3.28	H	*Ectocarpus siliculosus* (Dillwyn) Lyngbye	+	+				+	+	+	
t3.29	H	*Elachista scutulata* (J.E. Smith) Areschoug	+						+		
t3.30	H	*Feldmannia irregularis* (Kützing) G. Hamel	+						+		
t3.31	H	*Feldmannia paradoxa* (Montagne) G. Hamel	+						+		
t3.32	H	*Feldmannia* sp.	+				+	+			
t3.33	H	*Halidrys siliquosa* (Linnaeus) Lyngbye	+						+		
t3.34	H	*Halopteris filicina* (Grateloup) Kützing	+	+			+	+	+	+	+
t3.35	H	*Hincksia granulosa* (J.E. Smith) P.C. Silva	+						+	+	
t3.36	H	*Hincksia hincksiae* (Harvey) P.C. Silva	+						+		
t3.37	H	*Hincksia ovata* (Kjellman) P.C. Silva	+						+		
t3.38	H	*Hincksia sandriana* (Zanardini) P.C. Silva	+						+		
t3.39	H	*Hincksia secunda* (Kützing) P.C. Silva	+	+			+	+	+	+	
t3.40	H	*Kuckuckia kylinii* Cardinal	+						+		
t3.41	H	*Laminaria hyperborea* (Gunnerus) Foslie	+							+	
t3.42	H	*Laminaria ochroleuca* Bachelot de la Pylaie	+							+	
t3.43	H	*Liebmannia leveillei* J. Agardh	+						+	+	
t3.44	H	*Litosiphon laminariae* (Lyngbye) Harvey	+							+	
t3.45	H	*Mesogloia vermiculata* (J.E. Smith) S.F. Gray	+				+	+	+		
t3.46	H	*Myrionema strangulans* Greville	+						+	+	

t3.47 **Table 3** (continued)

	Division	Species	ATLANTIC	> 4 regions	Iceland	Norway	Britain	Ireland	France	Spain	Portugal
t3.48	H	*Padina pavonica* (Linnaeus) Thivy	+							+	
t3.49	H	*Petroderma maculiforme* (Wollny) Kuckuck	+							+	
t3.50	H	*Phycocelis foecunda* Strömfelt	+							+	
t3.51	H	*Phyllariopsis purpurascens* (C.Agardh) Henry *et* South	*								+
t3.52	H	*Pseudolithoderma extensum* (P.L. Crouan *et* H.M. Crouan) S. Lund	+				+		+		
t3.53	H	*Pseudolithoderma roscoffense* Loiseaux	+							+	
t3.54	H	*Punctaria latifolia* Greville	+							+	
t3.55	H	*Punctaria plantaginea* (Roth) Greville	+						+		
t3.56	H	*Pylaiella littoralis* (Linnaeus) Kjellman	+					+	+		
t3.57	H	*Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes, Druehl *et* G.W. Saunders	+	+	+		+	+	+	+	
t3.58	H	*Saccorhiza polyschides* (Lightfoot) Batters	+						+	+	+
t3.59	H	*Sargassum muticum* (Yendo) Fensholt	N					N		N	
t3.60	H	*Sauvageaugloia griffithsiana* (Griffiths *ex* Harvey) Hamel *ex* Kylin	+						+		
t3.61	H	*Scytosiphon lomentaria* (Lyngnbye) Link	+				+		+	+	
t3.62	H	*Scytosiphon lomentaria* stadium "*Microspongium gelatinosum*" Reinke	+							+	
t3.63	H	*Spatoglossum solierii* (Chauvin *ex* Montagne) Kützing	+				+				
t3.64	H	*Sphacelaria caespitula* Lyngbye	+				+	+			
t3.65	H	*Sphacelaria cirrosa* (Roth) C. Agardh	+	+			+	+	+	+	
t3.66	H	*Sphacelaria plumula* Zanardini	+	+			+	+	+	+	
t3.67	H	*Sphacelaria rigidula* Kützing	+				+			+	
t3.68	H	*Sporochnus pedunculatus* (Hudson) C. Agardh	+	+			+	+	+		+
t3.69	H	*Stilophora tenella* (Esper) P.C. Silva	+						+		
t3.70	H	*Stragularia clavata* (Harvey) G. Hamel	+				+	+		+	
t3.71	H	*Striaria attenuata* (Greville) Greville	+				+	+			
t3.72	H	*Stypocaulon scoparium* (Linnaeus) Kützing	+							+	+
t3.73	H	*Symphyocarpus strangulans* Rosenvinge	+				+	+		+	
t3.74	H	*Taonia atomaria* (Woodward) J. Agardh	+						+	+	+
t3.75	H	*Tilopteris mertensi* (Turner) Kützing	+				+				
t3.76	H	*Undaria pinnatifida* (Harvey) Suringar	N							N	
t3.77	H	*Zonaria tournefortii* (Lamouroux) Montagne	*								+
t3.78	R	*Acrochaetium savianum* (Meneghini) Nägeli	+						+		
t3.79	R	*Acrochaetium virgatulum* (Harvey) Batters	+							+	
t3.80	R	*Acrosorium ciliolatum* (Harvey) Kylin	+	+				+	+	+	+
t3.81	R	*Aglaothamnion bipinnatum* (P.L. Crouan *et* H.M. Crouan) J. Feldmann *et* Feldmann Mazoyer	+				+	+		+	
t3.82	R	*Aglaothamnion feldmanniae* Halos	+							+	
t3.83	R	*Aglaothamnion hookeri* (Dillwyn) Maggs *et* Hommersand	+	+			+	+	+	+	
t3.84	R	*Aglaothamnion pseudobyssoides* (P.L. Crouan *et* H.M. Crouan) Halos	+				+	+		+	
t3.85	R	*Aglaothamnion tenuissimum* (Bonnemaison) Feldmann Mazoyer	+	+			+	+	+	+	
t3.86	R	*Aglaothamnion tripinnatum* (C. Agardh) Feldmann Mazoyer	+						+	+	
t3.87	R	*Ahnfeltia plicata* (Hudson) E.M. Fries	+				+	+		+	
t3.88	R	*Ahnfeltia plicata stadium* "*Porphyrodiscus simulans*" Batters	+				+	+			

t3.89 **Table 3** (continued)

	Division	Species	ATLANTIC	> 4 regions	Iceland	Norway	Britain	Ireland	France	Spain	Portugal
t3.90	R	*Ahnfeltiopsis devoniensis* (Greville) P.C. Silva *et* DeCew	+							+	
t3.91	R	*Anotrichium furcellatum* (J. Agardh) Baldock	+							+	+
t3.92	R	*Antithamnion cruciatum* (C. Agardh) Nägeli	+	+			+	+	+	+	
t3.93	R	*Antithamnion densum* (Suhr) M.A. Howe	+							+	
t3.94	R	*Antithamnion villosum* (Kützing) Athanasiadis	+							+	
t3.95	R	*Antithamnionella spirographidis* (Schiffner) E.M. Wollaston	N	N			N	N	N	N	
t3.96	R	*Antithamnionella ternifolia* (J.D. Hooker *et* Harvey) Lyle	N				+		N	N	N
t3.97	R	*Apoglossum ruscifolium* (Turner) J. Agardh	+	+			+	+	+	+	+
t3.98	R	*Asparagopsis armata* Harvey	+						+	+	
t3.99	R	*Asparagopsis armata* Harvey *stadium* "*Falkenbergia rufolanosa*" (Harvey) F. Schmitz	+	+			+	+	+	+	+
t3.100	R	*Atractophora hypnoides* P.L. Crouan *et* H.M. Crouan	+				+	+	+		
t3.101	R	*Atractophora hypnoides* stadium "*Rhododiscus pulcherrimus*" P.L.Crouan *et* H.M.Crouan	+	+			+	+	+	+	*
t3.102	R	*Bangia fuscopurpurea* (Dillwyn) Lyngbye	+				+	+			
t3.103	R	*Bangia stadium Conchocelis rosea* Batters	+						+		
t3.104	R	*Boergeseniella fruticulosa* (Wulfen) Kylin	+	+			+	+	+	+	
t3.105	R	*Boergeseniella thuyoides* (Harvey) Kylin	+							+	
t3.106	R	*Bonnemaisonia asparagoides* (Woodward) C. Agardh	+	+			+	+	+	+	+
t3.107	R	*Bonnemaisonia asparagoides* stadium "*Hymenoclonium serpens*" (P.L. Crouan *et* H.M. Crouan) Batters	+				+	+		+	
t3.108	R	*Bonnemaisonia clavata* G. Hamel	+							+	
t3.109	R	*Bonnemaisonia hamifera* Hariot	+				+	+			
t3.110	R	*Bonnemaisonia hamifera* stadium "*Trailliella intricata*" Batters	+	+	+	+	+	+	+	+	
t3.111	R	*Bornetia secundiflora* (J. Agardh) Thuret	+							+	
t3.112	R	*Brongniartella byssoides* (Goodenough *et* Woodward) F. Schmitz	+	+		+	+	+	+	+	
t3.113	R	*Calliblepharis ciliata* (Hudson) Kützing	+	+			+	+	+	+	
t3.114	R	*Calliblepharis jubata* (Goodenough *et* Woodward) Kützing	+	+			+	+	+	+	
t3.115	R	*Callithamnion corymbosum* (J.E. Smith) Lyngbye	+				+	+		+	
t3.116	R	*Callithamnion tetragonum* (Withering) S.F. Gray	+						+	+	
t3.117	R	*Callithamnion tetricum* (Dillwyn) S.F. Gray	+							+	
t3.118	R	*Callocolax neglectus* F. Schmitz *ex* Batters	+						+		
t3.119	R	*Callophyllis cristata* (C. Agardh) Kützing	+				+				
t3.120	R	*Callophyllis laciniata* (Hudson) Kützing	+	+			+	+	+	+	+
t3.121	R	*Calosiphonia vermicularis* (J.Agardh) F.Schmitz	+							+	
t3.122	R	*Ceramium callipterum* Feldmann Mazoyer	+							+	
t3.123	R	*Ceramium ciliatum* (J. Ellis) Ducluzeau	+	+			+	+	+	+	
t3.124	R	*Ceramium cimbricum* H.E. Petersen	+	+			+	+	+	+	
t3.125	R	*Ceramium comptum* Børgesen	+						+		
t3.126	R	*Ceramium deslongchampsii* Chauvin *ex* Duby	+				+	+			
t3.127	R	*Ceramium diaphanum* (Lightfoot) Roth	+				+		+	+	
t3.128	R	*Ceramium echionotum* J. Agardh	+	+			+	+	+	+	
t3.129	R	*Ceramium secundatum* Lyngbye	+				+	+	+	+	
t3.130	R	*Ceramium tenuicorne* (Kützing) Waern	+							+	
t3.131	R	*Ceramium virgatum* Roth	+	+			+	+	+	+	

t3.132 **Table 3** (continued)

	Division	Species	ATLANTIC	> 4 regions	Iceland	Norway	Britain	Ireland	France	Spain	Portugal
t3.133	R	*Champia parvula* (C. Agardh) Harvey	+	+			+	+	+	+	
t3.134	R	*Chondracanthus acicularis* (Roth) Fredericq	+	+				+	+	+	+
t3.135	R	*Chondracanthus teedei* (Mertens *ex* Roth) Kützing	+						+	+	
t3.136	R	*Chondracanthus teedei* var. *lusitanicus* (J.E. De Mesquita Rodrigues) Bárbara *et* Cremades	+							+	
t3.137	R	*Chondria capillaris* (Hudson) M.J. Wynne	+				+	+		+	
t3.138	R	*Chondria coerulescens* (J. Agardh) Falkenberg	+							+	
t3.139	R	*Chondria dasyphylla* (Woodward) C. Agardh	+	+			+	+	+	+	
t3.140	R	*Chondria scintillans* Feldmann Mazoyer	+							+	
t3.141	R	*Chondrus crispus* Stackhouse	+				+	+		+	
t3.142	R	*Chylocladia verticillata* (Lightfoot) Bliding	+	+			+	+	+	+	
t3.143	R	*Coccotylus truncatus* (Pallas) M.J. Wynne *et* J.N. Heine	+				+				
t3.144	R	*Colacodictyon reticulatum* (Batters) J. Feldmann	+							+	
t3.145	R	*Colaconema caespitosum* (J. Agardh) Jackelman, Stegenga *et* Bolton	+					+		+	
t3.146	R	*Colaconema daviesii* (Dillwyn) Stegenga	+					+	+	+	
t3.147	R	*Compsothamnion thuyoides* (J.E. Smith) Nägeli	+	+			+	+	+	+	+
t3.148	R	*Contarinia peyssonneliaeformis* Zanardini	+							+	*
t3.149	R	*Corallina officinalis* Linnaeus	+	+		+	+	+		+	
t3.150	R	*Cordylecladia erecta* (Greville) J. Agardh	+	+			+	+	+	+	
t3.151	R	*Crouania attenuata* (C. Agardh) J. Agardh	+							+	
t3.152	R	*Cruoria cruoriaeformis* (P.L. Crouan *et* H.M. Crouan) Denizot	+	+			+	+	+	+	*
t3.153	R	*Cruoria pellita* (Lyngbye) Fries	+	+			+	+	+	+	
t3.154	R	*Cruoriopsis hauckii* Batters	+						+		
t3.155	R	*Cryptonemia lomation* (Bertoloni) J. Agardh	+							+	
t3.156	R	*Cryptopleura ramosa* (Hudson) L. Newton	+	+			+	+	+	+	+
t3.157	R	*Cystoclonium purpureum* (Hudson) Batters	+				+	+			
t3.158	R	*Dasya corymbifera* J. Agardh	+				+	+	+		
t3.159	R	*Dasya hutchinsiae* Harvey	+							+	
t3.160	R	*Dasya ocellata* (Grateloup) Harvey	+						+	+	+
t3.161	R	*Dasya rigidula* (Kützing) Ardissone	+							+	
t3.162	R	*Dasya sessilis* Yamada	N							N	
t3.163	R	*Dasya* sp.	+				+	+			
t3.164	R	*Delesseria sanguinea* (Hudson) J.V. Lamouroux	+				+	+			
t3.165	R	*Dermocorynus montagnei* P.L. Crouan *et* H.M. Crouan	+				+	+			
t3.166	R	*Dilsea carnosa* (Schmidel) Kuntze	+					+		+	
t3.167	R	*Drachiella spectabilis* J. Ernst *et* J. Feldmann	+							+	
t3.168	R	*Dudresnaya verticillata* (Withering) Le Jolis	+	+			+	+	+	+	+
t3.169	R	*Dumontia contorta* (S.G. Gmelin) Ruprecht	+				+				
t3.170	R	*Ellisolandia elongata* (Ellis *et* Solander) Hind *et* Saunders	+							+	
t3.171	R	*Erythrodermis traillii* (Holmes *ex* Batters) Guiry *et* Garbary	+				+				
t3.172	R	*Erythroglossum laciniatum* (Lightfoot) Maggs *et* Hommersand	+				+	+		+	
t3.173	R	*Erythroglossum lusitanicum* Ardré	+							+	+
t3.174	R	*Erythroglossum sandrianum* (Zanardini) Kylin	+						+		
t3.175	R	*Erythrotrichia carnea* (Dillwyn) J. Agardh	+	+			+	+	+	+	

t3.176 **Table 3** (continued)

	Division	Species	ATLANTIC	> 4 regions	Iceland	Norway	Britain	Ireland	France	Spain	Portugal
t3.177	R	*Furcellaria lumbricalis* (Hudson) Lamouroux	+				+	+			
t3.178	R	*Gastroclonium ovatum* (Hudson) Papenfuss	+						+	+	
t3.179	R	*Gastroclonium reflexum* (Chauvin) Kützing	+	+			+	+		+	+
t3.180	R	*Gayliella flaccida* (Harvey ex Kützing) T.O. Cho *et* L.J. McIvor	+							+	
t3.181	R	*Gelidiella calcicola* Maggs *et* Guiry	+	+			+	+	+	+	*
t3.182	R	*Gelidiocolax margaritoides* (Martin *et* Pocock) Fan *et* Papenfuss	+							+	
t3.183	R	*Gelidium bipectinatum* Furnari in Furnari, Cormaci *et* Serio	*								+
t3.184	R	*Gelidium crinale* (Hare *ex* Turner) Gaillon	+							+	
t3.185	R	*Gelidium maggsiae* Rico *et* Guiry	+					+		+	*
t3.186	R	*Gelidium pulchellum* (Turner) Kützing	+						+	+	
t3.187	R	*Gelidium pusillum* (Stackhouse) Le Jolis	+				+		+	+	
t3.188	R	*Gelidium spinosum* (S.G. Gmelin) P.C. Silva	+	+			+	+	+	+	+
t3.189	R	*Gigartina pistillata* (S.G. Gmelin) Stackhouse	+							+	
t3.190	R	*Gloiocladia repens* (C.Agardh) Sánchez *et* Rodríguez Prieto	+							+	
t3.191	R	*Gonimophyllum buffhamii* Batters	+				+	+			
t3.192	R	*Gracilaria bursa pastoris* (Gmelin) Silva	+						+		
t3.193	R	*Gracilaria dura* (C.Agardh) J.Agardh	+							+	
t3.194	R	*Gracilaria gracilis* (Stackhouse) M. Steentoft, L.M. Irvine *et* W.F. Farnham	+	+			+	+	+	+	+
t3.195	R	*Gracilaria multipartita* (Clemente) Harvey	+						+	+	
t3.196	R	*Grateloupia turuturu* Yamada	N							N	
t3.197	R	*Griffithsia corallinoides* (Linnaeus) Trevisan	+				+	+			
t3.198	R	*Griffithsia schousboei* Montagne	+							+	
t3.199	R	*Gymnogongrus crenulatus* (Turner) J.Agardh	+						+	+	
t3.200	R	*Gymnogongrus griffithsiae* (Turner) Martius	+						+	+	
t3.201	R	*Halarachnion ligulatum* (Woodward) Kützing	+	+			+	+	+	+	+
t3.202	R	*Halarachnion ligulatum* stadium "*Cruoria rosea*" (P.L. Crouan *et* H.M. Crouan) P.L. Crouan *et* H.M. Crouan	+	+			+	+	+	+	*
t3.203	R	*Halopithys incurva* (Hudson) Batters	+				+	+	+		
t3.204	R	*Halurus flosculosus* (J. Ellis) Maggs *et* Hommersand	+	+			+	+	+	+	
t3.205	R	*Halymenia latifolia* P.L. Crouan *et* H.M. Crouan *ex* Kützing	+	+			+	+	+	+	+
t3.206	R	*Haraldia lenormandii* (Derbès *et* Solier) J. Feldmann	+							+	
t3.207	R	*Haraldiophyllum bonnemaisonii* (Kylin) A.D. Zinova	+					+		+	
t3.208	R	*Herposiphonia secunda* (C. Agardh) Ambronn	+							+	
t3.209	R	*Herposiphonia tenella* (C. Agardh) Ambronn	+							+	
t3.210	R	*Heterosiphonia japonica* Yendo	N	N		N	N		N	N	
t3.211	R	*Heterosiphonia plumosa* (J. Ellis) Batters	+	+			+	+	+	+	
t3.212	r	*Hildenbrandia crouaniorum* J. Agardh	+							+	*
t3.213	R	*Hildenbrandia rubra* (Sommerfelt) Meneghini	+				+	+	+	+	*
t3.214	R	*Holmsella pachyderma* (Reinsch) Sturch	+				+	+		+	
t3.215	R	*Hydrolithon farinosum* (Lamouroux) Penrose *et* Chamberlain	+							+	
t3.216	R	*Hypnea musciformis* (Wulfen) J.V. Lamouroux	+							+	
t3.217	R	*Hypoglossum hypoglossoides* (Stackhouse) F.S. Collins *et* Hervey	+	+			+	+	+	+	+
t3.218	R	*Jania longifurca* Zanardini	+							+	

t3.219 **Table 3** (continued)

	Division	Species	ATLANTIC	> 4 regions	Iceland	Norway	Britain	Ireland	France	Spain	Portugal
t3.220	R	*Jania rubens* (Linnaeus) J.V. Lamouroux	+	+			+	+	+	+	+
t3.221	R	*Jania rubens* var. *corniculata* (Linnaeus) Yendo	+						+	+	
t3.222	R	*Kallymenia reniformis* (Turner) J. Agardh	+						+	+	
t3.223	R	*Laurencia obtusa* (Hudson) J.V. Lamouroux	+						+	+	
t3.224	R	*Laurencia pyramidalis* Bory de Saint Vincent *ex* Kützing	+							+	
t3.225	R	*Liagora viscida* (Forsskål) C. Agardh	+						+	+	
t3.226	R	*Lithophyllum incrustans* Philippi	+	+				+	+	+	+
t3.227	R	*Lomentaria articulata* (Hudson) Lyngbye	+	+			+	+	+	+	
t3.228	R	*Lomentaria clavellosa* (Turner) Gaillon	+	+		+	+	+	+	+	+
t3.229	R	*Mastocarpus stellatus* (Stackhouse) Guiry	+				+				
t3.230	R	*Mastocarpus stellatus* stadium "*Petrocelis cruenta*" J. Agardh	+							+	
t3.231	R	*Melobesia membranacea* (Esper) J.V. Lamouroux	+				+	+		+	
t3.232	R	*Membranoptera alata* (Hudson) Stackhouse	+				+	+			
t3.233	R	*Mesophyllum lichenoides* (J. Ellis) M. Lemoine	+							+	+
t3.234	R	*Microcladia glandulosa* (Solander *ex* Turner) Greville	+				+		+	+	
t3.235	R	*Monosporus pedicellatus* (J.E. Smith) Solier	+	+			+	+	+	+	
t3.236	R	*Myriogramme minuta* Kylin	+							+	
t3.237	R	*Naccaria wiggii* (Turner) Endlicher	+				+	+	+		
t3.238	R	*Neosiphonia harveyi* (J.W. Bailey) M. S. Kim, H. G. Choi, Guiry *et* G.W. Saunders	N						N	N	
t3.239	R	*Nitophyllum punctatum*(Stackhouse) Greville	+	+			+	+	+	+	
t3.240	R	*Odonthalia dentata* (Linnaeus) Lyngbye	+				+				
t3.241	R	*Ophidocladus simpliciusculus* (P.L. Crouan *et* H.M. Crouan) Falkenberg	+							+	
t3.242	R	*Osmundea pinnatifida* (Hudson) Stackhouse	+	+			+	+	+	+	
t3.243	R	*Peyssonnelia armorica* (P.L.Crouan *et* H.M.Crouan) Weber van Bosse	+				+			+	*
t3.244	R	*Peyssonnelia atropurpurea* P.L. Crouan *et* H.M. Crouan	+							+	
t3.245	R	*Peyssonnelia bornetii* Boudouresque et Denizot	*								*
t3.246	R	*Peyssonnelia coriacea* J. Feldmann	*								*
t3.247	R	*Peyssonnelia dubyi* P.L. Crouan *et* H.M. Crouan	+	+			+	+	+	+	*
t3.248	R	*Peyssonnelia harveyana* P.L. Crouan *et* H.M. Crouan *ex* J. Agardh	+	+			+	+		+	*
t3.249	R	*Peyssonnelia immersa* Maggs *et* Irvine	+	+			+	+	+	+	
t3.250	R	*Phycodrys rubens* (Linnaeus) Batters	+				+	+	+		
t3.251	R	*Phyllophora crispa* (Hudson) P.S. Dixon	+	+		+	+	+	+	+	
t3.252	R	*Phyllophora pseudoceranoides* (Gmelin) Newroth *et* Taylor	+				+	+	+		
t3.253	R	*Phymatolithon laevigatum* (Foslie) Foslie	+				+				
t3.254	R	*Phymatolithon lenormandii* (Areschoug) Adey	+				+				
t3.255	R	*Pleonosporium borreri* (J.E. Smith) Nägeli	+	+			+	+	+	+	
t3.256	R	*Pleonosporium flexuosum* (C. Agardh) Bornet *ex* De Toni	+							+	
t3.257	R	*Plocamium cartilagineum* (Linnaeus) Dixon	+	+			+	+	+	+	+
t3.258	R	*Plocamium raphelisianum* Dangeard	+							+	
t3.259	R	*Plumaria plumosa* (Hudson) O. Küntze	+				+	+			
t3.260	R	*Pneophyllum confervicola* (Kützing) Chamberlain	+						+		
t3.261	R	*Pneophyllum fragile* Kützing	+						+		
t3.262	R	*Polyides rotundus* (Hudson) Gaillon	+				+	+			

t3.263 **Table 3** (continued)

	Division	Species	ATLANTIC	> 4 regions	Iceland	Norway	Britain	Ireland	France	Spain	Portugal
t3.264	R	*Polyneura bonnemaisonii* (C. Agardh) Maggs *et* Hommersand	+	+			+	+	+	+	
t3.265	R	*Polysiphonia atlantica* Kapraun *et* J.N. Norris	+						+	+	
t3.266	R	*Polysiphonia brodiaei*(Dillwyn) Sprengel	+							+	
t3.267	R	*Polysiphonia caespitosa* (Pocock) Hollenberg	+							+	
t3.268	R	*Polysiphonia denudata* (Dillwyn) Greville *ex* Harvey	+							+	
t3.269	R	*Polysiphonia elongata* (Hudson) Sprengel	+	+			+	+	+	+	
t3.270	R	*Polysiphonia fibrillosa* (Dillwyn) Sprengel	+				+	+	+		
t3.271	R	*Polysiphonia foetidissima* Cocks ex Bornet	+							+	
t3.272	R	*Polysiphonia fucoides* (Hudson) Greville	+				+	+		+	
t3.273	R	*Polysiphonia furcellata* (C. Agardh) Harvey	+				+	+			
t3.274	R	*Polysiphonia nigra* (Hudson) Batters	+	+			+	+	+	+	
t3.275	R	*Polysiphonia stricta* (Dillwyn) Greville	+	+	+	+	+	+	+	+	
t3.276	R	*Polysiphonia subulifera* (C. Agardh) Harvey	+				+	+	+		
t3.277	R	*Porphyropsis coccinea* (J. Agardh *ex* Areschoug) Rosenvinge	+						+		
t3.278	R	*Porphyrostromium boryanum* (Montagne) P.C. Silva	+						+	+	
t3.279	R	*Porphyrostromium ciliare* (Carmichael) M.J. Wynne	+							+	
t3.280	R	*Predaea pusilla* (Berthold) Feldmann	*								+
t3.281	R	*Predaea ollivieri* Feldmann	*								+
t3.282	R	*Pterocladiella capillacea* (S.G. Gmelin) Santelices *et* Hommersand	+				+	+		+	+
t3.283	R	*Pterosiphonia ardreana* Maggs *et* Hommersand	+						+	+	
t3.284	R	*Pterosiphonia complanata* (Clemente) Falkenberg	+				+		+	+	
t3.285	R	*Pterosiphonia parasitica* (Hudson) Falkenberg	+	+			+	+	+	+	+
t3.286	R	*Pterosiphonia pennata* (C. Agardh) Sauvageau	+	+			+	+	+	+	
t3.287	R	*Pterosiphonia pinnulata*(Kützing) Maggs *et* Hommersand	+				+		+		
t3.288	R	*Pterothamnion crispum* (Ducluzeau) Nägeli	+				+	+		+	
t3.289	R	*Pterothamnion plumula* (J. Ellis) Nägeli	+	+		+	+	+	+	+	+
t3.290	R	*Ptilota gunneri* Silva, Maggs *et* Irvine	+				+				
t3.291	R	*Ptilothamnion sphaericum* (P.L. Crouan *et* H.M. Crouan *ex* J. Agardh) Maggs *et* Hommersand	+						+	+	
t3.292	R	*Radicilingua thysanorhizans*(Holmes) Papenfuss	+	+			+	+	+	+	
t3.293	R	*Rhodomela confervoides* (Hudson) P.C. Silva	+				+	+			
t3.294	R	*Rhodophyllis divaricata* (Stackhouse) Papenfuss	+	+		+	+	+	+	+	+
t3.295	R	*Rhodophysema elegans* (P.L. Crouan *et* H.M. Crouan *ex* J. Agardh) Dixon	+				+	+			
t3.296	R	*Rhodothamniella floridula* (Dillwyn) J. Feldmann	+	+			+	+	+	+	
t3.297	R	*Rhodymenia ardissonei* Feldmann	+						+		
t3.298	R	*Rhodymenia delicatula* P. Dangeard	+				+	+			
t3.299	R	*Rhodymenia pseudopalmata* (J.V. Lamouroux) P.C. Silva	+						+	+	
t3.300	R	*Rytiphlaea tinctoria* (Clemente y Rubio) C. Agardh	+						+		
t3.301	R	*Sahlingia subintegra*(Rosenvinge) Kornmann	+							+	
t3.302	R	*Scagelothamnion pusillum* (Ruprecht) Athanasiadis	+		+						
t3.303	R	*Schizymenia dubyi* (Chauvin ex Duby) J. Agardh	+						+		
t3.304	R	*Schizymenia dubyi* stadium "*Haematocelis rubens*" J. Agardh	+							+	
t3.305	R	*Schmitzia hiscockiana* Maggs & Guiry					+				
t3.306	R		+							+	

t3.307 **Table 3** (continued)

	Division	Species	ATLANTIC	> 4 regions	Iceland	Norway	Britain	Ireland	France	Spain	Portugal
		Schottera nicaeensis (J.V. Lamouroux *ex* Duby) Guiry *et* Hollenberg									
t3.307	R	*Scinaia furcellata* (Turner) J. Agardh	+						+	+	
t3.308	R	*Scinaia interrupta* (De Candolle) M.J. Wynne	+	+			+	+	+	+	
t3.309	R	*Scinaia turgida* Chemin	+				+				
t3.310	R	*Seirospora interrupta* (J.E. Smith) F. Schmitz	+				+	+			
t3.311	R	*Solieria chordalis* (C. Agardh) J. Agardh	+				+		+		
t3.312	R	*Spermothamnion repens* (Dillwyn) Rosenvinge	+	+		+	+	+	+	+	
t3.313	R	*Spermothamnion strictum* (C. Agardh) Ardissone					+				
t3.314	R	*Sphaeroccus coronopifolius* Stackhouse					+				
t3.315	R	*Sphaerococcus coronopifolius* stadium "*Haematocelis fissurata*" P.L. Crouan *et* H.M. Crouan	+						+	+	
t3.316	R	*Sphondylothamnion multifidum* (Hudson) Nägeli	+	+			+	+	+	+	
t3.317	R	*Spyridia griffithsiana*(J.E. Smith) G.C. Zuccarello, Prud'homme van Reine *et* Stegenga	+	+			+	+	+	+	
t3.318	R	*Stenogramma interruptum* (C. Agardh) Montagne *ex* Harvey	+	+			+	+	+	+	+
t3.319	R	*Streblocladia collabens* (C.Agardh) Falkenberg	+							+	
t3.320	R	*Stylonema alsidii* (Zanardini) K.M. Drew	+				+	+		+	
t3.321	R	*Stylonema cornu cervi* Reinsch	+							+	
t3.322	R	*Tiffaniella capitata* (Schousboe *ex* Bornet) Doty *et* Meñez	+							+	
t3.323	R	*Titanoderma pustulatum*(J.V. Lamouroux) Nägeli	+				+	+		+	
t3.324	R	*Turnerella pennyi* (Harvey) F. Schmitz	+		+						
t3.325	R	*Turnerella pennyi* stadium "*Cruoria arctica*" Schmitz	+		+						
t3.326	R	*Wildemania miniata* (C. Agardh) Foslie	+				+		+		
t3.327	C	*Acrochaete viridis*(Reinke) Nielsen	+							+	
t3.328	C	*Acrochaete wittrockii* (Wille) Nielsen	+				+	+			
t3.329	C	*Bryopsis hypnoides* J.V. Lamouroux	+						+	+	
t3.330	C	*Bryopsis plumosa*(Hudson) C. Agardh	+	+			+	+		+	+
t3.331	C	*Chaetomorpha aerea*(Dillwyn) Kützing	+							+	
t3.332	C	*Chaetomorpha ligustica* (Kützing) Kützing	+							+	
t3.333	C	*Chaetomorpha linum* (O.F. Müller) Kützing	+				+		+	+	
t3.334	C	*Cladophora albida* (Nees) Kützing	+				+	+		+	
t3.335	C	*Cladophora battersii* Hoek	+				+	+			
t3.336	C	*Cladophora hutchinsiae* (Dillwyn) Kützing	+	+			+	+		+	+
t3.337	C	*Cladophora laetevirens* (Dillwyn) Kützing	+							+	
t3.338	C	*Cladophora lehmanniana* (Lindenberg) Kützing	+							+	
t3.339	C	*Cladophora pellucida* (Hudson) Kützing	+						+	+	
t3.340	C	*Cladophora prolifera* (Roth) Kützing	*								+
t3.341	C	*Cladophora pygmaea* Reinke	+				+	+	+		
t3.342	C	*Cladophora retroflexa* (Bonnemaison *ex* P.L. Crouan *et* H.M. Crouan) Hoek	+				+	+	+		
t3.343	C	*Cladophora rhodolithicola* Leliaert	+	+			+	+	+	+	
t3.344	C	*Cladophora sericea*(Hudson) Kützing	+					+		+	
t3.345	C	*Codiolum* sp. Braun	+				+	+			
t3.346	C	*Codium bursa* (Linnaeus) C. Agardh	*								+
t3.347	C	*Codium fragile*(Suringar) Hariot	N							N	
t3.348	C	*Codium tomentosum* Stackhouse	+							+	+
t3.349	C	*Codium vermilara*(Olivi) Delle Chiaje	+							+	+

t3.350 **Table 3** (continued)

	Division	Species	ATLANTIC	> 4 regions	Iceland	Norway	Britain	Ireland	France	Spain	Portugal
t3.351	C	*Derbesia marina* (Lyngbye) Solier	+				+	+		+	
t3.352	C	*Derbesia tenuissima* (Moris *et* De Notaris) P.L.Crouan *et* H.M.Crouan	+							+	
t3.353	C	*Gomontia polyrhiza* (Lagerheim) Bornet *et* Flahault	+						+	+	
t3.354	C	*Ostreobium quekettii* Bornet *et* Flahault	+				+		+	+	
t3.355	C	*Phaeophila* sp. Hauck	+				+	+			
t3.356	C	*Pirula salina* (Dangeard) Printz	+				+	+			
t3.357	C	*Pringsheimiella scutata* (Reinke) Marchewianka	+				+	+			
t3.358	C	*Rhizoclonium tortuosum*(Dillwyn) Kützing	+	+			+	+	+	+	
t3.359	C	*Ulothrix subflaccida* Wille	+							+	
t3.360	C	*Ulva clathrata*(Roth) C. Agardh	+				+	+		+	
t3.361	C	*Ulva compressa* Linnaeus	+				+		+	+	
t3.362	C	*Ulva lactuca* Linnaeus	+					+	+		
t3.363	C	*Ulva pseudocurvata* Koeman *et* Hoek	+							+	
t3.364	C	*Ulva rigida* C. Agardh	+					+	+	+	
t3.365	C	*Ulva rotundata* Bliding	+							+	
t3.366	C	*Ulva scandinavica*Bliding	+							+	
t3.367	C	Ulva sp.	+			+	+				
t3.368	C	*Ulvaria obscura* (Kützing) P. Gayral ex C. Bliding	+				+			+	
t3.369	C	*Ulvella lens* P.L. Crouan *et* H.M. Crouan	+							+	
t3.370	C	*Ulvella setchellii* P.J.L. Dangeard	+						+		
t3.371	C	*Umbraulva olivascens* (P.J.L. Dangeard) G. Furnari	+						+	+	
t3.372	C	*Uronema marinum* Womersley	+				+				

The species are listed in alphabetical order within the divisions Rhodophyta (*R*), Heterokontophyta (*H*) and Chlorophyta (C). New records are marked with an asterisk. Species occurring in more than four different regions are also detailed in a separate column. Non-native species are marked with *N*

diversity of these temperate maerl beds is in line with Tittley (2002) who suggested that the area comprising Ireland, southern England, Atlantic France and Spain may be considered a "hot-spot" of macroalgal species richness. The low diversity of associated maerl flora in Iceland and Norway is partly due to lack of sampling effort, although Teichert et al. (2012) and our own surveys of maerl in these regions show that they are genuinely depauperate. The high diversity found in Galicia reflects intensive sampling efforts (Peña 2010), whereas the relatively low diversity found on maerl beds off Armação de Pera and Lagos in the Algarve (60 species) relates to the fact that these beds are relatively small (*ca*. 3 km^2) and are confined to deeper waters (13–23 m depth, Peña et al. 2009). The maerl beds off Galicia, Brittany and Ireland are larger (ca. 22 km^2, Peña and Bárbara 2009; ca. 97 km^2, J. Grall, personal communication; and ca. 60 km^2, De Grave et al. 2000, respectively) and extend into shallower waters than those off the Algarve. Monitoring of NE Atlantic maerl beds shows that the associated flora is strongly seasonal with peak diversity in spring–summer (Cabioch 1969; Maggs 1983; Bárbara et al. 2004; Peña and Bárbara 2010b), similar to the pattern seen in the SW Atlantic (Pascelli et al. 2013).

Approximately 67 % of the associated flora of NE Atlantic maerl beds is Rhodophyta. Some species with heteromorphic life histories have both stages recorded on maerl (i.e. *Halarachnion ligulatum, Cutleria multifida*). The composition of seaweed communities living on maerl is influenced by latitude, with warm-tolerant species gradually replaced by cold-tolerant species further north, where a lack of light must further restrict the diversity of seaweeds able to cope with subpolar winters. Climate change will almost certainly alter the biogeographic distributions of maerl-associated seaweeds in the coming decades, as will the ongoing spread of invasive species, 11 of which already pervade NE Atlantic beds. The most widely distributed species are *Polysiphonia stricta, Pterothamnion plumula* and *Rhodophyllis divaricata*, and the non-native species *Bonnemaisonia hamifera* stadium "*Trailliella intricata*". Species that can be thought of as maerl specialists, since they are mainly confined to maerl beds (*Cladophora rhodolithicola, Cruoria cruoriaeformis, Gelidiella calcicola, Halymenia latifolia*) are mostly distributed in temperate areas where maerl beds are more biodiverse. The recent detection of cryptic species supported by molecular data (i.e. *C. rhodolithicola*) has revealed misidentifications in

the literature. Investigations of this sort are likely to reveal even greater seaweed diversity on the NE Atlantic maerl beds.

The occurrence of maerl beds from the Arctic to temperate areas together with their wide bathymetric range confirm the significant ecological contribution of maerl beds as ecosystem engineers and productive habitats in our coasts. The flora of southern maerl beds in the NE Atlantic is well documented, strongly seasonal and diverse. The maerl bed flora north of Britain is, however, poorly known and warrants targeted research. Our census of maerl beds provides a baseline that can be used to assess the impacts of changes that are expected to take place due to the combined effects of sea surface warming, acidification, spreading invasive species and habitat degradation.

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