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Chapter 10. North Atlantic Rhodolith Beds

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Abstract

Beds of coralline algal sediment form ecologically and economically important habitats in the North Atlantic. These habitats can occur from the intertidal down to 60 m depth, and they are locally abundant in several countries. Fourteen species of coralline algae form rhodoliths or maerl in this region; *Lithothamnion corallioides*, *L. glaciale*, *L. tophiforme* and *Phymatolithon calcareum* are the most widely recorded. The structure and biodiversity of these habitats is destroyed by dredging and can be degraded by towed demersal fishing gear and by mussel and salmon farming. Legislation has been

passed in the European Union (EU) to protect *P. calcareum* and *L. corallioides* which should be extended to include the other maerl species from the region. Outside the EU there is a lack of baseline information concerning the importance of these habitats: a fuller understanding of their role may lead to protection in Scandinavia, Iceland and the Atlantic coasts of Canada and the United States. The design of such protected areas would need to consider the ongoing effects of invasive species, ocean warming and acidification.

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11.1. Introduction

Aggregations of living unattached corallines, previously often referred to as nodules, were given the name rhodoliths by Bosselini & Ginsberg (1971). Adey & MacIntyre (1973) provided an early discussion of their genesis and distribution. Such aggregations have long been known as maerl in the North East Atlantic, a Breton term for unattached thalli that lack a shell or pebble core (Irvine & Chamberlain 1994). Here, we provide an overview of rhodolith/maerl occurrence in the colder waters of the North Atlantic and summarize the distribution, species composition, biodiversity and ecological importance of these habitats. We include the eastern coasts of Canada and the United States north of Cape Hatteras plus Greenland, Iceland, Europe and Macaronesia (Azores, Madeira and Canary Islands).

11.2. Distribution and species composition

Unattached coralline algal beds occur on open coasts, in tide-swept channels and in sheltered areas with weak currents, from the intertidal to 60 m depth with the deepest records found in Svalbard and Macaronesia (Cabioch 1974, Alfonso-Carrillo & Gil-Rodríguez 1982, Hall-Spencer et al. 2010, Teichert et al. 2012). These habitats are particularly abundant in Scotland, Ireland and Brittany (De Grave et al. 2000, Hall-Spencer et al. 2010) and in Newfoundland and Labrador (Adey & MacIntyre 1973). The more northern beds are less well known but existing literature indicates that these habitats may be important and extensive at high latitudes (Foslie 1895, Adey 1968, Snell 1968, Gunnarsson 1977, Freiwald 1995, Teichert et al. 2012).

Many species of crustose coralline algae can continue to survive unattached in appropriate environmental conditions. However, fewer species commonly form rhodoliths or maerl. For example, *Lithothamnion lemoineae* forms thick crusts in the North Atlantic subarctic that can become detached but rarely survive as rhodoliths.

In contrast, *Clathromorphum compactum* occasionally forms rhodolith beds in the Subarctic coating pebbles in narrow island passages with strong currents.

The North Atlantic harbours fourteen rhodolith/maerl-forming species of coralline algae (Table 11.1; Pardo et al., submitted). The four most widely recorded species are *Lithothamnion corallioides*, *L. glaciale*, *L. tophiforme* and *Phymatolithon calcareum* (Fig. 11.1). These four species have been exhaustively researched in the North Atlantic to find reliable identification features; Adey & McKibbin (1970), Irvine & Chamberlain (1994), Adey et al. (2005) and Teicher et al. (2012). In the northwestern Atlantic, *Lithothamnion glaciale* and *Lithothamnion tophiforme* occupy different, overlapping ecological niches. *L. glaciale* is particularly widespread, ranging from the intertidal pools to moderately deep water and from highly exposed to protected shorelines in Subarctic and Boreal Regions (Adey 1966). In contrast, *L. tophiforme* is more abundant in Arctic and deeper (25-39 m) waters (Adey et al. 2005). On the Labrador Coast, the two species typically occur together at 20-25 m. *Leptophytum foecundum*, in its rhodolith state, is colder Subarctic to

Arctic in distribution and occurs primarily in shell and pebble beds in strong current zones. The cores of this species are usually pebbles or dead mollusc shell.

Currently, efforts are being made to understand the diversity of rhodolith-forming corallines in the North Atlantic area using molecular techniques (Peña et al. 2014). This approach has led to the recent description of *Mesophyllum sphaericum* which forms maerl in the NE Atlantic (Peña et al. 2011). The use of DNA sequences from type material will continue to improve the taxonomy of this group (Peña et al. 2014). Species of North Atlantic *Lithophyllum* will require considerable taxonomic work as there appear to be cryptic species, problems with the features used to separate species and the widespread use of incorrect names (Irvine & Chamberlain 1994). In the north Atlantic *Lithophyllum* rarely contribute to maerl beds but at a few sites, such as Mannin Bay and Kingstown Bay (Ireland) and the Bay of Brest (France), species traditionally called *L. dentatum* and *L. fasciculatum* can be abundant (Cabioch 1968, Hall-Spencer et al. 2010).

The colder parts of the North Atlantic Ocean comprise four biogeographic regions: Arctic; Subarctic; Boreal (Celtic) and Lusitanian (Adey & Steneck, 2001, Adey & Hayek 2011). The Subarctic Region transitions with the Boreal Region primarily in southern Iceland, the Norwegian Coast and to a lesser extent in northwestern Scotland. The North Atlantic Subarctic Region (NW Atlantic, S. Greenland and Spitzbergen and northern Iceland) as a Pleistocene, glacially-restricted outlier of the North Pacific Subarctic is relatively depauperate in seaweeds (Adey et al. 2008, Maggs et al. 2008), while the overlapping Boreal and Lusitanian Regions are relatively rich in seaweed species. Likewise, the number of species of coralline algae forming beds of rhodolith or maerl is higher in European coastal Boreal/Lusitanian regions than the Subarctic Coasts. Further studies to uncover any hidden species diversity are needed to fully clarify these relationships and to understand evolutionary patterns (Aguirre et al. 2000).

11.3. Biodiversity and ecology

Unattached coralline algae produce banks of carbonate rich sediments that trap suspended particulates and infaunal faeces to build complex habitats that can be 1000s of years old (Grall & Hall-Spencer, 2003). They can also provide sediments for current transport to adjacent marine habitats (Farrow et al. 1978, Bosence 1979, 1980) and to coasts where carbonate sand dunes are important habitats for terrestrial organisms (Birkett et al. 1998a).

Rhodoliths and maerl are formed by coralline algae with relatively slow growth rates and a perennial life strategy; some thalli can live >100 years (Bosence 1983, Potin et al. 1990, Foster 2001, Blake & Maggs 2003, Bosence & Wilson 2003, Frantz et al. 2005). Many rhodoliths begin as crusts growing on rock; they break free from the substratum due to invertebrate boring and/or wave action and bioturbation, and continue growing unattached on surrounding or deeper sedimentary bottoms (Adey & MacIntyre 1973, Adey & Hayek 2011). Thallus fragmentation is the major mechanism of propagation of rhodolith beds (Bosence 1976, Johansen 1981). Coralline algae can accumulate in large beds with a three-dimensional matrix that provides a wide range of ecological niches (Bosence 1983, Birkett et

al. 1998a, Hall-Spencer 1998, Barberá et al. 2004, Grall et al. 2006, Hinojosa-Arango et al. 2009).

These habitats have considerable ecological significance due to the high diversity of associated organisms (Fig. 11.2). There have been numerous studies of the associated flora and fauna of NE Atlantic beds (Cabioch, 1969, Keegan 1974, Bosence 1979, 1980, Maggs 1983a,b, Hall-Spencer 1998, BIOMAERL Team 1999, Hall-Spencer & Atkinson 1999, Barbéra et al. (2004), Kamenos et al. 2004a,b,c, Hinojosa-Arango et al. 2009, Peña & Bárbara 2008a,b, 2010a,b, 2013, Peña 2010, Teichert et al. 2012, Scottish MPA Project 2013). In contrast, the number of studies available for the north-western Atlantic is more limited: two studies in Canada include investigations on fish of rhodolith beds by Kulka et al. (2004) and the epi- and in-fauna by Gagnon et al. (2012).

A review of the associated flora of NE Atlantic rhodolith beds (Peña et al. submitted) reported a total of 349 algal species, which is around 30% of the total seaweed diversity in this region. The most diverse beds (150-257 seaweed species) occur in the temperate regions with 25-42% of the total seaweed diversity recorded in the

area. The flora of northern rhodolith beds (Iceland, Scandinavia) is less diverse but has not been studied in detail. The associated flora increases the heterogeneity and complexity of the habitat due to the presence of a wide range of algal morphologies, ranging from endolithic and crustose forms to large kelp. The associated flora of temperate NE Atlantic rhodolith beds is seasonal with a peak of diversity in the spring-summer period (Cabioch 1969, Maggs 1983a, Bárbara et al. 2004, Grall et al. 2006, Peña & Bárbara 2010a). Species with heteromorphic life-histories and crustose sporophyte phases are particularly abundant (Maggs & Guiry 1989, Peña & Bárbara 2010b). The presence of some algal species is largely confined to rhodolith beds, such as the Rhodophyta *Gelidiella calcicola*, *Cruoria cruoriaeformis*, *Gelidium maggsiae* and *Halymenia latifolia* and the Chlorophyta *Cladophora rhodolithicola* (Cabioch 1969, Maggs 1983, Maggs & Guiry 1987, 1989, Rico & Guiry 1997, Bárbara et al. 2004, Grall et al. 2006, Leliaert et al. 2009, Peña & Bárbara 2010a,b, 2013).

The BIOMAERL project revealed 556 animal taxa associated with NE Atlantic maerl beds: 10 Porifera, 35 Cnidaria, 174 Annelida, 137

Crustacea, 138 Mollusca, 26 Echinodermata, 22 Bryozoa, 11 Ascidiacea, and 32 Pisces taxa (Barberá et al. 2004). A ten year survey of nine maerl beds in Brittany lists 1,204 fauna species, including 295 Annelida, 290 Arthropoda, 207 Mollusca, 35 Echinodermata, and 377 species of other phyla (Grall unpublished).

The three-dimensional matrix of coralline algal sediments enhances their biodiversity (Bosence 1979); this is evident when their diversity is compared with surrounding habitats; kelp forests harbour around 10% fewer species of the NE Atlantic flora, seagrasses host around 5% fewer species, and muddy and sand banks harbour 30 to 50% fewer species than adjacent maerl beds (Whelan & Cullinane 1985, Shultze et al. 1990, Davison & Hughes 1998, Birkett et al. 1998b, Grall 2002, Otero-Schmitt & Pérez-Cirera 2002, Johnson et al. 2005). Maerl beds also provide brood stock areas for commercially important bivalves, such as scallops, as well as nursery areas for juvenile fish such as cod (Hall-Spencer et al. 2003, Kamenos & Moore 2004, Kamenos et al. 2004a,b,c). In the northwestern Atlantic, rhodolith beds of *Lithothamnion* typically support abundant scallops, (*Aequipecten irradians*) which are commercially harvested.

11.4. Conservation status

In the North Atlantic, coralline algal sediments are dredged for use as a fertilizer on acidic soils, as a food additive for animals and humans, in water treatment filters and in cosmetics (Blunden et al. 1981, De Grave & Whitaker 1999, Foster 2001, Grall & Hall-Spencer 2003, Emerton & Choi 2008). This dredging of biodiverse nursery grounds is widely considered to be environmentally unsustainable (Barberá et al. 2003) and has ceased in the United Kingdom.

Although not as devastating as dredging, European maerl beds have also been impacted by aquaculture (Hall-Spencer et al. 2006, Hall-Spencer & Bamber 2007, Peña & Bárbara 2008a, Peña 2010), changes in current patterns associated with construction (Birkett et al. 1998a, Grall & Hall-Spencer 2003), dredge fisheries (Hall-Spencer 1998, Hall-Spencer & Moore 2000, Hall-Spencer et al. 2003, Hauton et al. 2003, Kamenos et al. 2003), as well as increased sedimentation and eutrophication (Hily et al. 1992, Grall & Glemarec 1997). There is also a growing realisation that these habitats may be especially vulnerable to ocean acidification since the high Mg-calcite skeletons of coralline algae dissolve easily as CO₂ levels

rise (Nelson 2009, Büdenbender et al. 2011, Porzio et al. 2011, Díaz-Pulido et al. 2012, Noisette et al. 2013, see Chapter XX by Martin & Hall-Spencer).

Indirect effects to NE Atlantic maerl beds arise due to the spread of invasive species such as the gastropod *Crepidula fornicata* the Rhodophyta *Antithamnionella spirographidis*, *A. ternifolia*, *Bonnemaisonia hamifera*, *Dasya sessilis*, *Grateloupia turuturu*, *Heterosiphonia japonica* and *Neosiphonia harveyi*, the Heterokontophyta *Colpomenia peregrina*, *Sargassum muticum* and *Undaria pinnatifida*, and the Chlorophyta *Codium fragile* (Grall & Hall-Spencer 2003, Pena et al. submitted).. Only through monitoring will we be able to detect ecological changes to these habitats (BIOMAERL Team 1999, Birkett et al. 1998a).

Research efforts have been made to understand the effects of physical factors on rhodolith-forming species in the North Atlantic, including the effect of temperature (Adey & McKibbin 1970, Blake & Maggs 2003, Wilson et al. 2004, Kamenos et al. 2008, Kamenos 2010, Kamenos & Law 2010); the influence of light (Adey 1970, Adey & McKibbin 1970, Adey & Macintyre 1973, Wilson et al.

2004, Rix et al. 2012, Teichert et al 2013); the biological response of organic matter/burial (Wilson et al. 2004, Blake et al. 2007, Rix et al. 2012); the response of heavy metal contamination (Wilson et al. 2004) and the influence of ocean acidification (Hall-Spencer et al. 2006, Büdenbender et al. 2011, Burdett et al. 2012, Ragazzola et al. 2013, Noisette et al. 2013).

Many of these studies confirmed the negative effect of ocean acidification, rise of temperature and burial on the physiology of rhodolith-forming species, suggesting that a combination of physical stressors can affect coralline species and the flora and fauna assemblages associated with them. Also, the negative effects on the rhodolith bed structure and disturbance and loss of diversity of the associated flora and fauna has been documented, mostly due to anthropogenic activities such as bivalve fishing and aquaculture (BIOMAERL Team 1999, Bárbera et al. 2003, Hall-Spencer et al. 2003, 2006, Hall-Spencer & Bamber 2007, Peña & Bárbara 2008a, Peña 2010). Apart from the decrease in the cover and thickness of the living maerl layer, a decrease in maerl size was observed in Galician beds impacted by mussel aquaculture (Peña 2010).

The EU Habitats Directive (92/43/EEC) includes maerl and lists *Lithothamnion corallioides* and *Phymatolithon calcareum* for protection. Maerl beds are also included in the list of threatened habitats within the NE Atlantic due to multiple threats from anthropogenic activities, high sensitivity and low recovery capacity (OSPAR 2006).

Many areas of maerl are now included within areas that are listed as protected areas; in NW Spain for example 28% of known maerl beds are located within protected areas with another 19 unprotected maerl beds proposed for future conservation actions (Peña & Bárbara 2006, 2009).

There are still information gaps concerning the biological and ecological characteristics of maerl assemblages in Europe. Information on reproduction, size, distribution and diversity of coralline algae forming maerl beds is necessary to improve management of these habitats (OSPAR 2006). Barberá et al. (2004) suggested that maerl beds should be recognized as a specific habitat in the EU Habitats Directive and that the full range of maerl-forming species should be listed for conservation purposes otherwise the rarest types

of maerl bed may not be given the high conservation status they require.

The development of newer methodologies for the characterization of maerl beds was also recommended by the Census of Marine Life project Natural Geography In Shore Areas (NaGISA, www.coml.org). A standardized methodology is required to monitor maerl beds in space and time for features such as reproductive effort, kind of reproduction, size, distribution, and diversity of coralline algae forming the habitat (Steller et al. 2007). Examination of these features can help to assess patterns typical of “pristine” vs “impacted” maerl beds in time (past vs present) and space (different beds located at distance of km, tens of km or hundreds of km) and can be used to evaluate the health of the habitats.

11.5 Conclusion

The four coralline algal species that most commonly grow unattached in the North Atlantic have been studied intensively in Europe but detailed information on the status and ecology of these habitats is lacking from the USA, Canada, Greenland and Iceland. There

is a lack of long-term monitoring of these wonderful habitats throughout the North Atlantic which is a priority for management of these productive coastal systems. The activities that are most damaging for these habitats are now well known; the next steps are to raise awareness, enforce conservation legislation and promote sensible stewardship of these highly diverse habitats.

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Figure legends

Fig. 11.1. Distribution map and regions of interaction for unattached species of coralline algae in the North Atlantic. Eight species are represented; *Lithothamnion glaciale* and *Phymatolithon calcareum* are the most widespread. Interrupted lines indicate that the abundance is lower than in other areas represented. Arrows indicate possible direction of distribution (information requires future verification).

Fig. 11.2. North Atlantic beds of maerl and rhodoliths. a) Mannin Bay, Ireland, pale pink *Lithophyllum fasciculatum*, vivid red/pink *Phymatolithon calcareum*. b) Iceland dredge sample, *Lithothamnion glaciale*. c) Galicia, Spain, *Mesophyllum sphaericum*. d) Dog Island, Northern Labrador, Canada, mix of *L. glaciale* and *L. tophiforme*.

Table 11.1. Rhodolith/maerl-forming species of coralline algae in the Northern Atlantic. Information on classification, type locality and distribution are presented. Unverified records are not included (see Pardo et al. submitted).

Order/Family/Species	Type locality	Distribution in the NE Atlantic
Corallinales		
Corallinaceae		
Lithophylloideae		
<i>Lithophyllum crouaniorum</i> Foslie	Berwick-upon Tweed, Northumberland, Eng- land	Azores (as <i>L. crouanii</i>) ¹

<i>Lithophyllum dentatum</i> (Kützing) Foslie	Naples, Italy	Ireland ²
<i>Lithophyllum duckerae</i> Woelker- ling	Sicily, Italy	Cornwall, England ²
<i>Lithophyllum fasciculatum</i> (La- marck) Foslie	Unknown*	Ireland ^{2,3} , France ⁴
<i>Lithophyllum hibernicum</i> Foslie	Ballynakill Harbour, Galway, Ireland	Ireland ²

Mastophoroideae

Neogoniolithon brassica-florida Algoa Bay, Cape Azores¹
 (Harvey) Setchell & L.R. Ma- Province, South Africa
 son

Spongites fruticulosa Kützing Mediterranean Sea Madeira⁵

Hapalidiaceae

Melobesioideae

Leptophytum foecundum (Kjell- Kara Sea, Russia. Newfoundland and Labrador Canada (Adey
 man) Adey pers. comm.)

Lithothamnion corallioides Rade de Brest, Finis- France^{2,5,6}, Ireland^{2,7,8}, England², Spain⁹, Ma-
 (P.L.Crouan & H.M.Crouan) tère, France deira⁵, Canary Islands¹⁰
 P.L.Crouan & H.M.Crouan

<i>Lithothamnion glaciale</i> Kjellman	Spitzbergen, Svalbard, Norway.	North Atlantic Arctic and Subarctic ^{11,12,13,14} , Svalbard ¹⁵ , Iceland ^{16,17,18} , Scandinavia ¹⁹ , Norway ^{17,20} , Britain ^{2,21} , Ireland ^{2,21}
<i>Lithothamnion tophiforme</i> (Esper) Unger	Julianehaab, Green- land	Canada ^{11,12} , Greenland ¹² , Iceland ^{17,18,22} , Nor- way ^{12,17,20}
<i>Phymatolithon calcareum</i> (Pallas) Adey & McKibbin	Falmouth, England	Sweden ²³ , Norway ¹⁷ , British Isles ² , Ire- land ^{24,25,26} , France ^{27,28,29} , Spain ^{9,30} , Azores ⁴
<i>Phymatolithon purpureum</i> (P.L.Crouan & H.M.Crouan) Woelkerling & L.M. Irvine	Mingant, Brest, France	Norway ²¹ , Britain and Ireland ⁸

Mesophyllum sphaericum V. Peña, Benencia Island, Ria Spain³¹

I. Bárbara, W.H. Adey, R. Rios- de Arousa, Galicia,
mena-Rodriguez & H.G. Choi Spain

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