

Coastal Research Library 15

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Rhodolith/ Maërl Beds: A Global Perspective

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Tribute to Rafael Riosmena-Rodríguez

In Memoriam

On March 15th 2016 we heard the sad news that our colleague and friend Rafael Riosmena-Rodríguez passed away suddenly as a result of heart failure. Rafael Riosmena, Rafa, was an internationally renowned scientist who dedicated 25 years working on many different aspects of marine biology, but particularly on the taxonomy and biology of red coralline algae.

Rafael was born in 1966 in León, Guanajuato. He began his degree in marine biology at the Universidad Autónoma de Baja California Sur (UABCS), in La Paz (México), then a Master's degree from San Jose State University (SJSU) in the United States, and a Ph.D. degree in marine botany at La Trobe University in Australia. He was currently a professor and researcher at UABCS, level III member of the National Research System of México (SNI).

He focused his work on the taxonomy of rhodolith-forming coralline red algae and the ecological significance of rhodolith beds. Rafa has left behind a valuable scientific legacy of more than 100 scientific papers published in peer-reviewed journals. He also edited many books on different aspects of the marine biology of the Gulf of California. Rafael was the driving force behind this book, his latest contribution to the knowledge of rhodoliths and rhodolith beds.

One of his most important contributions to science was to build a consolidated group of many young people, that now are spread in respected institutions all over the world, continuing his studies. His enthusiasm, generosity, and friendly behaviour facilitated an excellent atmosphere in which to work, and great collegiality with scientists internationally. Thanks to this tireless work training good researchers, Rafa's scientific school is now continuing his legacy.

Rafa wasn't only a highly regarded phycologist. He was also deeply committed to the defence and protection of the environment, also denouncing corrupt activities in México. His wide knowledge of the marine environments of the Gulf of California and his untiring work trying to unravel the mechanisms behind ecological interactions led him into contact with institutions trying to find the way to manage and protect these environments. We all depend upon marine ecosystems, so we have to learn how to interact with wildlife maintaining the equilibrium and seeking

sustainable approaches. Rafa provided scientific data to guide non-scientists at different levels in the protection of these precious environments.

In addition to all his scientific accomplishments and contributions, Rafa was a good friend, with kind words and always willing to help anyone. Our memories will be of Rafa smiling. We are indebted to him because, thanks to his constancy and firm conviction, he established a group of active scientists researching rhodoliths that share more than scientific results. We will miss him, but we know that his legacy will live in his lovely family and in all his students around the world. Nada nos detiene! Thanks Rafa!

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Part I
The Role of Rhodolith/Maërl Beds
in Modern Oceans

Chapter 1

Natural History of Rhodolith/Maërl Beds: Their Role in Near-Shore Biodiversity and Management

Rafael Riosmena-Rodríguez

Abstract Rhodolith/maërl beds are living and dead aggregations of free-living non-geniculate coralline algae that cover extensive benthic areas in recent oceans and are common in fossil deposits. They are slow growing organisms and can be long-lived (>100 years), distributed over a wide depth range from intertidal sites to 270 m. Rhodolith/maërl beds are a common feature of modern and ancient carbonate shelves worldwide that represent a sedimentary transition from sandy/muddy areas to the rocky substrate. They are bioengineers and provide a three-dimensional habitat for associated species. It has been demonstrated that rhodolith/maërl grounds are a suitable habitat for multispecies recruitment and provide refuge for juvenile life stages of commercially important shellfish species. Rhodoliths are resilient to a variety of environmental disturbances, but can be severely impacted by harvesting these commercial species, ocean acidification or global warming. The value of rhodoliths as a unique biotope around the world is under threat from different kinds of human activities. Despite the importance of rhodolith/maërl beds in the marine environment, a major limitation for protection is the lack of a clear definition of an ecosystem. A thorough review of the literature revealed a total of 12 vernacular/scientific terms that have been applied to free-living coralline red algae and these should be treated as synonyms. The Challenger Expedition (1872–1876) was one of the first voyages that promoted the understanding of the rich flora and fauna associated with coralline deposits. During the nineteenth century additional surveys in other areas of the world have confirmed the value of this ecosystem. During twentieth and twenty-first centuries many researchers have produced a vast scientific literature, documenting the importance of rhodolith/maërl, to understand their relevance regarding biodiversity in nearshore habitats. The relevance includes the description of new species or where the distribution of poorly known species has been extended, but more importantly the high number of associated species which

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includes species under protection, species ecologically relevant or species which are part of a formal fisheries. As a consequence of the concern about the state of the ecosystems in Europe at the end of the twentieth century, the EU developed a network of protected areas known as Natura 2000 sites. A series of publications on the conservation status of the maërl/rhodoliths in Atlantic and Mediterranean waters, Brittany, Gulf of California, and their relationship with fisheries, stated clearly that the health of rhodolith habitats in some areas of the world is decreasing, and there is an urgent need for management strategies. The combination of the interest in developing rhodolith/maërl conservation in other countries, the decline of the French Atlantic maërl deposits, and the correlation of rhodolith/maërl presence in or near oil deposits has motivated the exploration of rhodoliths in other areas such as Brazil, México, Australia and New Zealand. Understanding is increasing about the ecological role of rhodoliths in nearshore environments worldwide, the biodiversity associated with rhodoliths, and how human activities are having an increasing impact. The recognition of the importance of rhodolith beds as biodiversity centers has increased with the number of published papers and the growth in knowledge about the taxonomic status of the associated species.

1.1 Introduction

Rhodolith/maërl beds are living and dead aggregations of free-living non-geniculate coralline algae that cover extensive benthic areas in recent oceans and are common in fossil deposits. They are distributed worldwide, with a wide depth range from intertidal sites to 270 m, the deepest known record for a marine plant (Littler and Littler 1984). Individual rhodolith/maërl can be monospecific or multispecific (Riosmena-Rodríguez et al. 2010; Fig. 1.1a, see Villas-Bôas et al. 2014). Rhodoliths develop around skeletal and non-skeletal nuclei (Fig. 1.1b) although they can also grow without any material in the center, usually producing a concentric arrangement of the algal thalli (Rivera et al. 2004, Fig. 1.1c). Rhodoliths have a wide variety of growth forms ranging from fruticose to lumpy, and they can be discoid or irregularly shaped (Fig. 1.1d) averaging approximately 6 cm in diameter (Foster 2001).

Rhodoliths are slow growing and can be long-lived (>100 years), being resilient to varying environmental disturbances (Bosence 1983a, b, c; Steller et al. 2003). The growth, distribution and survivorship of rhodoliths are regulated by many factors, of which light, temperature, and sedimentation are considered the main ones (Wilson et al. 2004). Occasional rotation is necessary but does not need to be frequent, to prevent sedimentation and to allow light to reach all surfaces of the thalli. This rotation is the result of natural disturbances, stochastic phenomena recognized as important determinants of the presence and abundance of associated species. However, Marrack (1999) has shown that bioturbation is more relevant for rhodolith movement than currents. Steller (2003) documented the disturbance caused by fisheries to rhodolith beds and the associated community in Bahía Concepción

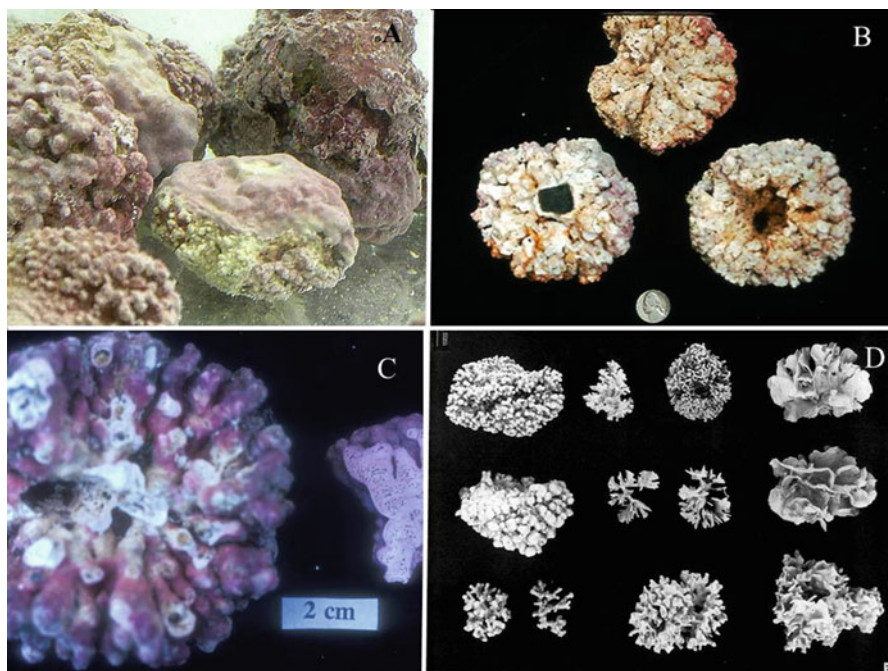


Fig. 1.1 (a) Several species growing on a single rhodolith. (b) Central core made from different materials (Photo courtesy MS Foster). (c) Rhodolith plant in which growth bands can be observed (*right*). (d) Range of growth forms present in rhodolith beds

(México). She forecast the recovery process that might eventually return it to its original state, and this process can take from days up to years.

Rhodolith/maërl beds are common features of modern and ancient carbonate shelves worldwide (Nelson 2009) that represent a sedimentary transition from sandy/muddy areas to the rocky substrate (Foster 2001). They can be very extensive, with typically 30–100% cover, mostly in coarse gravel and clean sands, or in muddy mixed sediments, which occur either on the open coast or in tide-swept channels of marine inlets (Foster et al. 1997). Bosence (1983a, b) outlined the relevance of rhodolith/maërl deposits around the world, initially describing a detailed morphological classification system (Bosence 1976, 1983a), probably the first attempt before the excellent system proposed by Woelkerling et al. (1993). Bosence (1983b) described the ecological settings where rhodolith/maërl are distributed based on a review of the literature (Bosence 1983b – Figs. 1.2 and 1.3), and this set the standard for the map in Foster (2001). Bosence (1983b) stated that rhodolith beds can be present in (1) tropical reefs in tropical areas, (2) seagrass meadows in both tropical and temperate areas, (3) kelp forests in temperate areas, and, (4) forming large beds themselves in both temperate and tropical areas. Freiwald et al. (1991) supported this classification, and Kendrick and Brearley (1997) and Foster et al. (2007) described the same relationship with *Sargassum* forests in subtropical and tropical



Fig. 1.2 (a) Rhodolith bed associated with seagrasses. (b) Rhodolith bed in a coral reef (part known as rubble). (c) Holdfast of *Undaria* attached to rhodoliths in Korea (Photo courtesy SM Boo)

zones. Bosence (1983b) also noted the strong influence of water depth and geographic distribution on bed composition.

Rhodolith beds are bioengineers and provide a three-dimensional habitat for associated species (review by Nelson 2009). Rhodoliths harbor distinctive high-diversity faunal and floral assemblages by virtue of their branching and interlocking nature (Steller et al. 2003; Teichert 2013). Rhodoliths also provide stable habitats onto which a variety of species can attach, including other algae, commercial species such as clams, pen shells and corals. Rhodoliths are resilient to a variety of environmental disturbances, but can be severely impacted by harvesting these commercial species (Steller et al. 2003; Hall-Spencer et al. 2010), ocean acidification or global warming (Martin and Gattuso 2009).

Rhodoliths have been used to obtain recent paleoecological and paleoclimatic information (Kamenos et al. 2008) but also deep-time paleoecological-paleoclimatological inferences (Aguirre et al. this volume). Rhodolith communities contribute significantly to the global calcium carbonate budget (Nelson 2009; Amado-Filho et al. 2012a, b). Rhodoliths can be the main carbonate sediment producers, often forming extensive deposits such as beaches or sand dunes (Sewell et al. 2007; Johnson et al. 2012). They have been exploited as a source of calcium carbonate and used for a wide variety of applications including as fertilizer and soil

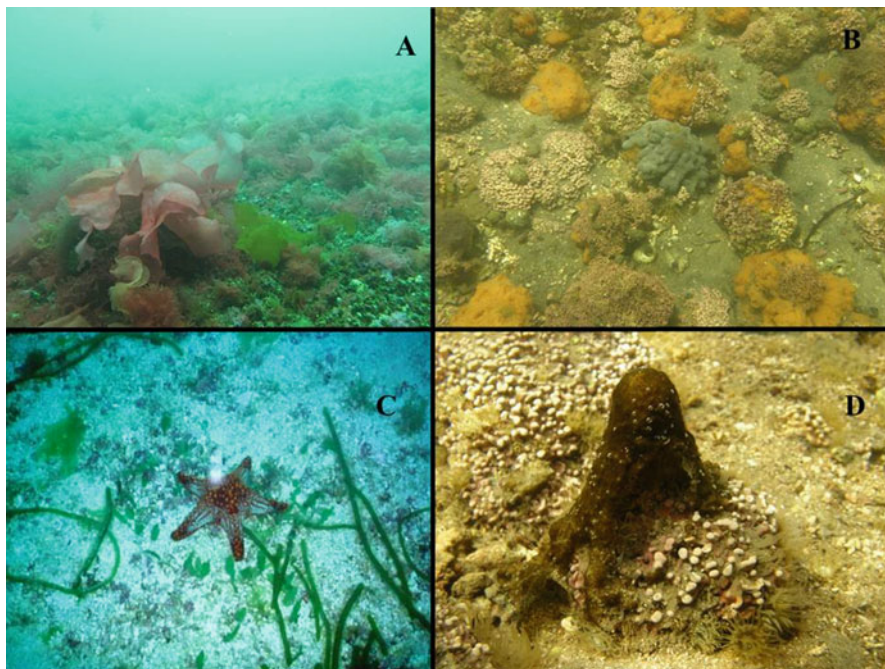


Fig. 1.3 (a) Subtidal bed with high diversity of red algae (Photo taken by AN Suárez-Castillo). (b) Rich sponge-rhodolith assemblage. (c) High biomass producers such as *Caulerpa* and *Codium* along with a seastar (Photo courtesy MS Foster). (d) Rich cyanobacteria gas producer associated with rhodolith beds

ameliorator, biological denitrifier, drinking water potabilizer, toxin eliminator, as an animal fodder additive, in pharmaceuticals, cosmetics, bone surgery, and even in the nuclear industry (López-Benito 1963; Blunden et al. 1980, 1997; Gray et al. 2000; Barbera et al. 2003; Grall and Hall-Spencer 2003; Riul et al. 2008).

The value of rhodoliths as a unique biotope around the world is under threat from different kinds of human activities. The lack of regulation of small and large-scale trawling, reduction of water quality, modification of water circulation, and any other activities that affect rhodolith stability and disturbance are of particular concern (Hall-Spencer et al. 2010; Figueiredo et al. 2012, 2015).

In several parts of the world rhodolith beds and rhodolith-forming species have been recognised as important to conserve, for example as Special Areas of Conservation (UK and Europe), or are considered in the development of Marine Parks (BIOMAËRL 1999, 2003) under the European Community Habitats Directive (Annex V) (Hall-Spencer et al. 2007). Maërl beds have also been included in the UK Biodiversity Action Plan (Anon 1995; Birkett et al. 1998), the Natura 2000 sites, in the OSPAR list, and in the Mediterranean Red Book of threatened habitats (Boudouresque et al. 1990; Hall-Spencer et al. 2010). These management strategies led to the prohibition of their commercial exploitation across Europe, and ultimately

rhodolith beds have been proposed as critical marine habitats for conservation in several areas of the world (IBAMA 1996; Birkett et al. 1998; De Grave 1999; De Grave and Whitaker 1999; Hall-Spencer 2005; Metri 2006; Metri and Rocha 2008; Rocha et al. 2006; Hall-Spencer et al. 2010; Sanchez-Ibarra et al. 2013; Peña et al. 2014; as well as the links <http://www.petronoticias.com.br/archives/62197>; <http://www.europapress.es/illes-balears/noticia-oceana-celebra-proteccion-contra-pesca-arrastre-dos-montanas-sumergidas-canal-mallorca-20140811143359.html>). It is necessary to take into consideration the response of these assemblages to both natural and artificial disturbances in the development and implementation of coastal management plans around the world and develop monitoring activities in marine protected areas.

In New Zealand and Australia, rhodolith beds have also been recognized as important biogenic habitats for fishery productivity and different monitoring programs are currently being developed to integrate these habitats into management systems, which will help resource users and managers strike a better balance between resource extraction and ecosystem integrity and resilience. It is also known that rhodolith forming-species have been included in the New Zealand list of “sensitive marine habitats” by the Ministry for the Environment (MacDiarmid et al. 2013).

Despite the importance of rhodolith/maërl beds in the marine environment, a major limitation to protection is the lack of a clear definition of an ecosystem. There have been proposed some vernacular and scientific names used for the same or similar concepts, and there is confusion about the meaning of these terms. Some names have been used for living material only, based on their form, shape or origin, whereas other names have been applied to the sediment produced by the organisms, and additional names have been applied to the environment in general. Without a detailed analysis of the all possible vernacular names, the understanding of their role in coastal ecosystems is limited: reliable nomenclature is necessary for their inclusion in legislation or to enable them to be protected.

1.2 Vernacular and Scientific Names

Understanding vernacular/scientific names applied to rhodoliths is relevant to appreciating the natural history of rhodolith/maërl beds, their historical context and how people have recognized this habitat, and also how to correctly define and interpret what is a rhodolith, and how they are distributed in the world oceans. A thorough review of the literature revealed a total of 12 vernacular/scientific terms that have been applied to free-living coralline red algae (Table 1.1). Rhodolith and maërl are the most common terms used for free-living coralline red algae that live on sediments. These names are synonyms (Steller et al. 2003) because they represent the same ecological function. There are other ten names that have been used for the same concept and should be treated as orthographic synonyms.

The term “maërl” was documented by Crouan and Crouan (1867) as a Breton word for unattached, branched corallines, living or dead, loose-lying, often occurring

Table 1.1 An exhaustive list of terms and definitions that have been used for free-living coralline red algae in scientific literature

Scientific term	References
1. Boxwork rhodolith	Basso (1998)
2. Coating	Bressan and Babbini (2003)
3. Coralline algal nodules	Siesser (1972)
4. Maërl	Crouan and Crouan (1867), Lemoine (1910), Cabioch (1969), Bosence (1983a, b), Steneck (1986), Irvine and Chamberlain (1994), Freiwald (1995), Cabioch in Dauvin (1997), Atabey (1998), Birkett et al. (1998), and Hall-Spencer et al. (2010)
5. Nucleated rhodoliths	Lemoine (1910)
6. Nodules	Steneck (1986)
7. Prâlines	Basso (1998)
8. Oncolith/onkoid	Steneck (1986)
9. Rhodoid	Steneck (1986)
10. Rhodolith	Bosellini and Ginsburg (1971), Siesser (1972) Bates and Jackson (1983), Bosence (1983a, b), Steneck (1986), Irvine and Chamberlain (1994), Freiwald (1995), Foster et al. (1997), Atabey (1998), Birkett et al. (1998), Foster (2001), Bressan and Babbini (2003), and Hall-Spencer et al. (2010)
11. Rubble	Steneck (1986)
12. Unattached branches	Steneck (1986)

in extensive deposits or algal gravels found off the northwest coast of France (maërl beds or banks). Cabioch (in Dauvin 1997), described that the name came from “marga” (calcareous sedimentary outcrops), “marle” or “marne”, and that it is used generally for non-algal calcareous sedimentary lacustrine deposits. This name is probably based on the latin word “margella” (= coral). Modern definitions for Maërl include: (1) Cabioch (1969) – as Corallinacées arbusculaires; (2) Steneck (1986) – as free-living corallines composed of loose-lying branches of a single species, and, (3) Hall-Spencer et al. (2010) – a collective term for various species of non-jointed coralline red algae (Corallinaceae) that live unattached.

The etymological meaning of rhodolith is “red stone” (Bosence 1983a), derived from the Greek words rose-like (ρόδειος) and stone (λίθος). Rhodoliths, described as nodules and unattached branched growths with a nodular form composed principally of coralline algae (Bosence 1983a), are often restricted to structures with a nonalgal core (Irvine and Chamberlain 1994). Those coralline algal nodules with a nucleus have been referred to as nucleated rhodoliths by Lemoine (1910). In addition, the term rhodolith is used for nodules composed of a single species of coralline alga or multiple species or boxwork (Basso 1998, Fig. 1.1). Due to fragmentation of branched rhodoliths, their occurrences are generally linked with maërl-type (algal gravel) carbonate deposits (Freiwald 1995).

Rubble is a term commonly used in coral reef ecology to describe broken pieces of coral reefs (Shannon et al. 2013) that are covered with coralline and noncoralline algal species. However, after some time these pieces become covered with coralline algae and thus might be considered equivalent to rhodoliths, as they form beds from these broken pieces (Guzman et al. 2004).

The remaining nine terms that have been used in the literature are defined and discussed in great detail by Aguirre et al. ([this volume](#)). Evaluating these terms about their ecological significance is necessary.

1.3 Relevance to Nearshore Biodiversity

The Challenger Expedition (1872–1876) was one of the first voyages that promoted the understanding of the rich flora and fauna associated with coralline deposits. Kjellman (1883: 96) was the first researcher to discover the maërl beds in the Arctic Ocean and Gran (1893) described the associated flora and fauna. Later, Pruvot (1897) described the diverse fauna in La Mancha Occidentale. In the Indian Ocean, three major expeditions (German Tiefsee- Expedition -1898–1899, Siboga Expedition -1899–1900, and Percy Sladen Trust Expedition -1905) investigated not only the coralline algal flora, but also the associated biota. As part of these cruises the flora and fauna were studied by scientists documenting and describing new species including Weber van Bosse and Foslie (1904), Weber van Bosse (1913), and Gardiner (1920). Miranda (1934) provided the first account about the maërl and associated biodiversity in the Galician Rias, and Feldmann (1943) described the flora associated with deep maërl banks in Algeria, one of the few studies about this specific habitat worldwide in war time. In the Pacific Ocean, the studies of Dawson (1944, 1960) in Baja California Peninsula and Segawa (1959) for Japan reported the presence of beds and described the rhodolith species composition.

The discovery and description of the kelp species *Laminaria rodriguezii* in the Mediterranean associated with maërl beds triggered interest in improving understanding of the flora associated with this system. Pérès and Piccard (1955) sketched the spatial organization of marine communities based on the diversity of benthic habitats in the Mediterranean. They used the term “binominia” for each benthic habitat (Pérès and Piccard 1955) and maërl was considered a type of ecosystem. Jacoutte (1962) provided the first description of the flora and invertebrate fauna associated with maërl beds in the Mediterranean, showing the biodiversity of the beds. In this study, 64 seaweed species were determined, and the Rhodophyta reported as the most diverse group.

The best represented invertebrate phyla in rhodolith beds are crustaceans, echinoderms, molluscs and polychaetes. In maërl beds in the Atlantic Ocean, Donze (1968) reported a few subtidal species, but this work was a starting point to understand the rich underwater flora: the habitat produced by rhodolith beds is not only the area supporting biodiversity but also the sediment produced from the rhodoliths. This realization led researchers to describe and analyze the fauna and flora in the

sediments derived from maërl/rhodoliths in different regions, such as Algeria (Falconetti 1970), Ireland (Bosence 1979; Keegan 1974), Britain (Hardiman et al. 1976), and France (Augier and Boudouresque 1978). Blunden et al. (1977) proposed the use of maërl commercially not only to promote the use of maërl but also to highlight the need to understand the associated species.

As part of the characterization of the benthic communities along the Brazilian coastal shelf, Kempf et al. (1968), Kempf (1970) stated the “remarkable predominance of coralline algae” in areas not dominated by riverine sediments. The relevance of Kempf’s (1970) observations was in relation to the spatial description of the beds, that reached 100 m in depth but also 120 nautical miles off shore, as the dominant habitat along the Brazilian continental shelf. In addition to the physical characterization of the ecosystem, considerable efforts were made to understand the rich flora and fauna (Lavradoi and Ignacio 2006).

Rhodolith/maërl deposits were clearly recognized as important ecosystems in Europe in the late 1970s, and the inventory efforts showed their importance as highly biodiverse habitats. Mora-Bemúdez (1980) documented the distribution of carbonate deposits with high diversity of infauna in Galician Rias. Later, Myers and McGrath (1980, 1983) described new amphipod species associated with maërl beds in several areas of the world. At the same time, studies on molluscs from Mulroy Bay (Nunn 1993) documented the presence of species that were also part of fisheries. Maggs (1983) continued with the description of the flora associated with maërl beds in Irish waters. In this study, two different types of beds were determined based on wave exposure. This was the first example of a quantitative sampling study using SCUBA to determine rhodolith abundance. Strong seasonal changes were found rather than spatial changes. Bosence (1985) carried out the first comparison of the fauna in dead and living maërl, finding strong differences in species composition and density.

A similar situation was found in the Central Pacific nearby Penguin Bank, where Agegian and Abbott (1985) described three slightly different mesophotic algal zones based on submersible surveys. The shallow zone (45–70 m) contained a diverse assemblage of algae (*Lobophora variegata*, *Dictyota friabilis*, *Halimeda* spp., coralline algal rhodoliths, *Mesophyllum mesomorphum*, and *Peyssonnelia rubra*). The mid-depth zone (90–110 m) was characterized by *Codium mamillosum* and crustose coralline algae (CCA), while the deep zone (110–182 m) was composed primarily of CCA. Ballesteros (1989) also studied this kind of banding in the Mediterranean seaweed assemblages in maërl, concluding that spatial differences are more important than temporal changes.

Rowe et al. (1990) documented the infauna associated with maërl beds in southwest England. They found higher richness in the maërl beds than in surrounding areas. Basso (1992) recognized 93 species in the phytobenthic communities in circalittoral soft bottoms. Using Bray Curtis analyses (to evaluate compositional dissimilarity between two different sites), Rowe et al. (1990) found that all sites dominated by rhodolith beds were closely related, and were very different from the other substrates. Therefore, the presence of rhodoliths was a factor controlling the distribution of associated species. Ramos-Esplá (1992) developed an extensive taxonomic analysis of the

ascidians in Spain and found a high diversity of species associated with maërl/rhodolith beds.

Freiwald (1993) described the close relationship of small gastropods, foraminifera, diatoms, ostracods and bacteria associated with rhodolith beds and their trophic relationships with sea urchins and their impacts on kelp populations. Freiwald (1995) found that the surface of rhodoliths are dominated by vagile herbivores and stimulate metamorphosis of echinoderm species. Later, Friewald (1998) illustrated that fleshy macroalgae are involved in the inshore and offshore sediment transportation by kelp drafting, and Freiwald and Mostafawi (1998) described a close relationship of an ostracod community to sediment type, being the most diverse community that associated with rhodolith beds.

Grall and Glémarec (1997a, b) have evaluated the overall biodiversity value of maërl/rhodolith beds in Bretagne, and have used these communities to calculate indices of perturbation (Grall and Glémarec 1997a). Their contribution was to use these indices to evaluate impacted (where exploitation of maërl was happening) versus unimpacted (control) sites (Grall and Glémarec 1997b). Their functional approach provided a strong baseline for future impact analysis. Hall-Spencer (1998) further demonstrated the relevance of maërl as critical habitats for associated molluscs in Scotland, and Basso and Brusoni (2004) in the Mediterranean.

Hall-Spencer et al. (1998) have shown the impact of Rapido trawling on scallops in benthic habitats and on the abundance of slow moving benthos. Hall-Spencer and Atkinson (1999) have shown the relevance of the maërl for one species (*Upgebia deltaura*) in most of its geographical distribution. They also found that this species functions ecologically as a bioturbator in the sediment removal for the development of their deep holes that may survive storms. The architecture of maërl habitats also provides good shelter for invertebrate predators from larger predators. De Grave (1999) found that 75 % of all macrobenthic species within specific maërl beds are crustaceans, the majority of which are amphipoda. Hall-Spencer (2001) has documented the maërl in the Firth of Clyde, suggesting that this site is well preserved for investigations into process and function of the habitat demonstrating the value of maërl. De Grave and Whitaker (1999) have documented high species richness associated with high functional diversity that shifts from omnivorous crustaceans to filter feeders after dredging. Veale et al. (1999) have documented a direct relationship between the number of individuals in the community in relation to the increase of fishing effort on selective removal of species. Hall-Spencer and Moore (2000a, b) have shown that scallop fishing impacted 70 % of maërl habitats and no signs of recovery were evident in the following years, providing further evidence of the vulnerability of this habitat to specific demersal fishing practices.

During the 1990s research about rhodolith beds started in the Gulf of California as part of an international collaboration between USA and México, and was funded by a series of agencies (InterAmerican Global Change Agency, National Geography, Packard Foundation, Consejo Nacional de Ciencia y Tecnología México, Comisión Nacional para el uso y estudio de la Biodiversidad, National Science Foundation). Studies in Western Australia yielded a series of critical papers about this habitat: Kendrick and Brearley (1997) demonstrated the relevance of rhodolith beds for

Sargassum species demography and dispersal; Collins (1988) and James et al. (1999) documented their distribution between 35 and 60 m depth in the Rottnef Shelf; while Sim and Townsend (1999) documented their presence around Rottnef Island. Steller and Foster (1995) have shown the value of measuring branch density in relation to wave action and how this is independent of species. Foster et al. (1997) reinforced the idea that rhodolith beds develop in two type of environments, wave and current beds, and this information might be able to be used to interpret paleoenvironments.

A regional workshop in La Paz in 1998 led to increasing collaboration between México and USA. It was also the starting point for establishing a new collaborative link with Brazil. Derived from these collaborations, several papers were produced showing the relevance of rhodolith beds in the nearshores of the Gulf of California. Reyes-Bonilla et al. (1998) showed that rhodolith beds also might be a habitat for the rich coral fauna in the Gulf of California as described for free living corals in the Western Pacific by Scoffin et al. (1985). In addition, these rhodolith beds are a feeding ground for sea urchins (James 2000). Studies of rhodolith beds in deeper waters have yielded new species of chitons (Clark 2000), as well as new records and new species of seaweeds (Cho and Riosmena-Rodríguez 2008; Cho et al. 2003; Leon-Cisneros et al. 2009; Hernández-Kantun et al. 2010). The value of rhodoliths as fish habitat was clearly presented by Aburto-Oropeza and Balart-Paez (2001) and was used to delimit Marine Protected Areas by Sala et al. (2002).

The first International Workshop on ‘The Conservation and Management of Maërl’, 23–27 February, 2001 at University Marine Biological Station, Millport (Isle of Cumbrae, Scotland), was dedicated to (1) exchange ideas produced as part of the BIOMAËRL Project among the European countries (Barbera et al. 2003), (2) evaluate the conservation status in relation to fisheries (Grall and Hall-Spencer 2003; Hall-Spencer et al. 2003), (3) evaluate carbonate production and accumulation (Bosence and Wilson 2003), and, (4) evaluate for the first time the impact of trawling over maërl beds in the Mediterranean (Bordehore et al. 2003).

In the second rhodolith workshop in La Paz BCS, in 2006, seven papers were produced as special section of the journal *Ciencias Marinas* (Riosmena-Rodríguez et al. 2007). Later, the meeting was held in Buzios, Brazil, in 2009 and 12 papers were published in a special section of the *Journal of Coastal Research*. Finally, the meeting in Granada, Spain, in 2012 promoted a special issue of *Cryptogamie Algologie* (Aguirre and Peña 2014) with six papers. In addition to the monographs derived from these international meetings, papers on the systematics of coralline algae were published in a special issue of *Phytotaxa* about the *Corallinophyceae* of the Atlantic Ocean (Riosmena-Rodríguez et al. 2015). All of the above efforts have promoted and encouraged more work on recognizing the biodiversity associated with maërl beds and their role in ecological processes.

Steller et al. (2003) compared the species richness and density between rhodolith beds and the surrounding sandflats and demonstrated strong differences between the two habitats but also the value of rhodolith beds in terms of biodiversity. A complementary analysis was presented by Hinojosa-Arango and Riosmena-Rodríguez (2004) who found that faunal abundance differed significantly in relation

to rhodolith-forming species, but no significant differences were observed between different growth-forms in the Gulf of California. Crustaceans, polychaetes and molluscs were the most important taxa in all three rhodolith beds studied. Konar et al. (2006) reported that rhodolith beds in the North Pacific seem to be dominated by chitons instead of any other fauna described in previous studies. Gherardi (2004) determined the high contribution of carbonate sand from rhodolith beds in the Southwestern Atlantic in relation to the associated community structure. Perry (2005) has established the role of rhodolith beds in carbonate production in a reef environment at the Indian Ocean. Castriota et al. (2005) documented the dominance of molluscs in maërl beds in the Mediterranean, and Mathis et al. (2005) described the relevance of this habitat in Australian waters.

It has been demonstrated that maërl grounds provide refuge for juvenile life stages of commercially important shellfish species such as the queen scallop, *Aequipecten opercularis* (Kamenos et al. 2004a, b) and *Agropecten ventricosus* (Steller and Caceres 2009). Maërl has also been found to be important for the juvenile gadoid fish: Atlantic Cod (*Gadus morhua*), Saithe (*Pollachius virens*) and Pollack (*Pollachius pollachius*). These species have all been found to use maërl grounds during their juvenile life stages due to the availability of food and refuge from predators (Hall-Spencer et al. 2003; Kamenos et al. 2004c). Riosmena-Rodríguez and Medina (2011) have demonstrated that rhodolith beds are a relevant habitat for multispecies recruitment.

In the case of seaweeds associated with rhodoliths, a series of papers have been produced over the last 10 years that have shown the biodiversity, seasonal and spatial variation of the flora and their ecological interactions. Amado-Filho et al. (2007) compared the epibenthic macroalgal biomass and composition of rhodolith beds from zone 1 (4–18 m depth) surveyed in two seasons. They showed that samples from summer possessed up to twice as much biomass and species as those from winter. These results can be explained by the high instability of the beds along the southeastern Brazilian coast, caused by frequent storm disturbances, which are higher in winter than in summer (Soares-Gomes and Pires-Vanin 2003; Amado-Filho et al. 2007).

Peña and Bárbara (2008) developed a comprehensive literature review of all Galician studies and produced a list of 198 maërl-associated species (204 infraspecific taxa including life history stages) recorded from a total of 111 maërl beds. The survey (2003–2006) increased the Galician maërl epiflora records to 226 species, highlighting the occurrence of 10 non-native species. An a posteriori review was presented by Peña et al. (2014) in relation to the known seaweeds associated with maërl/rhodolith beds in the NE Atlantic from Svalbard to Portugal. A total of 350 macroalgal species has been recorded in this region, including 11 non-native species. The flora of maërl beds off Iceland and Norway is poorly known, but maërl beds off Britain, Ireland, France and Spain have been surveyed extensively and support several species that are maërl specialists (i.e. *Cruoria cruoriaeformis*, *Cladophora rhodolithicola*, *Gelidiella calcicola*).

Amado-Filho et al. (2010) studied seaweed populations growing on rhodoliths between 4 and 18 m water depth in the southern part of Espírito Santo State (Brazil).

They determined that 167 species are present in the flora with three new records for Brazil. Marked seasonal differences in fleshy algal species composition and abundance were related to seasonal instabilities caused by winter-storm disturbance over the rhodolith beds that were found to be supporting 25 % of the known macroalgal species richness along the Brazilian coast. Pascheli et al. (2013) showed that rhodolith density decreases with increasing depth and during winter. They found that turf-forming seaweeds accounted for 60 % of the biomass growing on rhodoliths and temporal variations were observed in species composition and rhodolith density.

In the case of invertebrates, Figueiredo et al. (2007) made an evaluation of rhodolith/maërl as living substrate for invertebrates comparing the proportion of invertebrates between live and dead at different seasons in a deep bank. They found a general seasonal trend of a reduction in invertebrate abundance from autumn/winter to spring. Amphipods were dominant in autumn (70 % of sample) but half as abundant in winter and spring when their population density was similar to that of polychaetes (49 %). Polychaete abundance was significantly lower in live than in dead transplanted rhodoliths, whereas amphipods showed no difference. Variation in infaunal abundances was related to variability in habitat heterogeneity due to changes in rhodolith size and shape resulting from changes in water turbulence.

In the case of amphipods, there are a series of papers dealing with new records (Bakalem et al. 2014, Algeria; Riera et al. 2014, Canary Islands) and new species (Carvalho et al. 2012, Portugal; Lowry and Stoddart 2012, Australia; Souto et al. 2014, Brazil; Sturaro and Guerra García 2012, Mediterranean).

In other areas of the world polychaetes contribute significantly to diversity present in rhodolith beds. Harvey and Bird (2008) found that polychaetes are dominant taxa in temperate Australian waters. Dos Santos et al. (2011) found four new records and a new species of the genus *Sabellaria* collected in rhodolith beds along the subtidal zone of the coast of João Pessoa and Cabedelo, Paraíba. Later, Berlandi et al. (2012) reviewed the polychaetes associated with several sites along the Brazilian coast. They found a significant difference between Espírito Santo and the Abrolhos, reflected in the polychaete assemblages, with 26 families identified, 4 exclusive to Espírito Santo and 9 in the Abrolhos. The most common families registered different species composition in both rhodolith beds, except for *Eunice multicylindris* and *Arabella mutans* found in both regions. Rhodoliths on the Abrolhos hosted polychaetes dominated by carnivorous or herbivorous families, such as the Syllidae, the most abundant and species-rich family. Rhodoliths found off Espírito Santo hosted polychaetes dominated by burrowers, such as the Lumbrineridae, which were favored by their boxwork structure, built of invertebrates and inorganic material.

In New Zealand, Dewas and O'Shea (2012) found that the large dog cockle, *Tucetona laticostata*, is widely but sporadically distributed throughout coastal waters of the Hauraki Gulf, where it resides partially buried in gravel and rhodoliths in shallow water, at 5–15 m depth. Avila et al. (2013) were the first to evaluate the relationship between sponges and the stability of rhodolith beds. This relationship has been documented for the Mediterranean at 88 m (Calcinai et al. 2013), and

Pereira-Filho et al. (2015) documented, in more detail, the close relationship between sponges and rhodolith/maërl beds in relation to reef formation in the Southwestern Atlantic.

Rhodolith beds are habitats in which new species have been discovered or where the distribution of poorly known species has been extended, such as for echinoderms (Gondim et al. 2014; Granja-Fernandez et al. 2014), octocorals (Bridge et al. 2011; Brice and Polisenio 2014), and sponges (Sitja and Maldonado 2014). Calcavanti et al. (2014) found differences in bacterial assemblages between rhodolith beds and other habitats.

More integrated studies, started by Foster et al. (2007), have documented the benthic macroalgae, benthic epifauna, fish fauna, and cryptofauna linked to a rhodolith bed mixed with *Sargassum* forest at Cabo Los Machos, where a total of 216 taxa were found. There were some large changes in abundance between sampling times, especially in *S. horridum* related to the season, encrusting nongeniculate coralline algae and *Helminthocladia australis* and an increase in “mixed red algal turf”. Temporal variation in these invertebrates was characterized by reduction in taxa between March and October, with similar diversity as observed for macroalgae and fishes. In contrast to both macroalgae and benthic invertebrates, the average abundance/site in fish was highest in October, largely due to an increase in juveniles. The most abundant species (>4 individuals/200 m²) in March were the Mexican barracuda (*Sphyræna lucasana*), spottail grunt (*Haemulon maculicauda*), Panamic sargent major (*Abudefduf troschelii*), and Pacific porgy (*Calamus brachysomus*). Cryptofaunal invertebrates living within large rhodoliths (more than 5 cm), greatly exceeded the number that was found in the smaller (less than 5 cm) size classes of rhodoliths: 114 total invertebrate taxa with an average of 40 taxa/individual large rhodolith, with polychaetes (52 taxa) and crustaceans (29 taxa) as the primary contributors, followed by molluscs (14 taxa) and echinoderms (10 taxa).

Riera et al. (2012) have studied the structure of the macrofaunal assemblages on different habitat types (*Cymodocea*, *Caulerpa*, sabellid field, garden eel and maërl beds) with samples taken from 14 to 46 m in depth. Significant differences were found in macrofaunal assemblages among seabed types, with highest abundances and lowest biodiversity in sabellid fields, where the sabellid *Bispira viola* dominated. The polychaetes *Aponuphis bilineata* and *Chone filicauda* and the mollusc *Turritella brochii* were the most abundant taxa on maërl beds in the Canary Islands. The mosaic of granulometric conditions would explain the associated macroinfaunal community structure and contribute to the creation of diversity on these relatively well preserved seabeds at a local scale.

In rhodolith beds from north New Zealand, Neill et al. (2014) found a highly diversified biota with 238 taxa: 197 invertebrates, 37 algae and 4 fish taxa. The highest abundance and taxon richness occurred in a bed in a high sedimentation rate. This finding points to the importance of sampling individual rhodolith beds and suggests that it would be risky to extrapolate findings to other beds, even those in close proximity. The findings of Neill et al. (2014) are well supported by Tamega et al. (2014), who described deep rhodolith beds dominated by bryozoans, cnidarians, brachiopods and sponges, a community composition structurally very different

from shallow-water rhodolith beds. Sheehan et al. (2015) documented a similar situation comparing live and dead beds and highlighted the relevance of living material for the great abundance of epifauna that are not commonly found in dead areas.

1.4 Conservation and Protection Initiatives

During the 1990s and at the beginning of the 2000s, concerns about marine ecosystems around European waters resulted in the development of Special Areas for Conservation and Community Directives to protect ecosystems. The Decree 1626/94 of the European Union on conservation of Mediterranean living resources has a bearing on the conservation of maërl beds since it prohibits demersal trawling in the waters shallower than 50 m (Barbera et al. 2003). The Mediterranean Action Plan of the United Nations Environment Programme (UNEP/IUCN/GIS Posidonie 1990) considered 'les fonds de maërl' should be included in the Red Data Book of threatened marine vegetation. This document had no legislative standing but it served to highlight species and habitats that need protection (Barbera et al. 2003).

Birkett et al. (1998) developed the first evaluation of the maërl as a special habitat for conservation. BIOMAËRL (1999) was a project dedicated to understand the value of maërl/rhodolith beds in European waters (Atlantic and Mediterranean). Maërl is included as a key habitat for Ireland and the UK within the Annex I habitats, 'large shallow inlet and bays' and 'sand banks which are slightly covered by seawater at all times' such Special Areas of Conservation (SACs) designated under the Directive 92/43/EEC on the Conservation of Natural Habitats and Wild Fauna and Flora (Hall-Spencer et al. 2010). Costello (2000) developed the biodiversity plan in Ireland in which maërl was one of the main ecosystems considered for protection. Two maërl-forming species, *Lithothamnion corallioides* and *Phymatolithon calcareum*, are listed in Annex V of the Habitats Directive and in some locations maërl is also listed as a key (Hall-Spencer et al. 2010).

De Grave et al. (2000) evaluated the potential extraction of maërl beds in Ireland, concluding that a proposal to extract a live maërl bed or a maërl debris facies requires approval from the regulatory authorities and the application should be carefully scrutinized. They concluded that the inclusion of both the main maërl bed forming species in the EU Habitats Directive is desirable for an integral protection. In addition, any application to extract live or dead maërl should be required to submit an Environmental Impact Statement (EIS). However, there are no basic requirements in their EIS for maërl beds and De Grave et al. (2000) stated the need for generic guidelines dealing with the extraction of marine gravel deposits. No other country has regulated sand extraction for commercial purposes. Nicolletti et al. (2006) have documented how to monitor the impact of beach restoration on seagrasses and maërl in coastal areas where storms removed sand in nearshore areas. Lauwaert et al. (2009) have evaluated the impact of seabed extraction for beach replacement and construction, where maërl is one of the major components in the benthic environment, producing habitat fragmentation and degradation by the seabed extraction.

As a consequence of the concern about the state of the ecosystems in Europe, the EU developed a network of protected areas known as Natura 2000 sites. A series of publications on the conservation status of the maërl/rhodoliths in Atlantic and Mediterranean waters (Barbera et al. 2003), Brittany (Grall and Hall-Spencer 2003), Gulf of California (Steller et al. 2003) and their relationship with fisheries (Hall-Spencer et al. 2003) stated clearly that the health of rhodolith habitat in some areas of the world is decreasing, and there is an urgent need for management strategies. Bordehore et al. (2003) found that trawling activities that disturbed the sediments of fishing areas change the associated flora and fauna and thus the productivity of the area. The combination of the interest in developing rhodolith/maërl conservation in other countries, the decline of the Atlantic French maërl deposits, and the correlation of rhodolith/maërl presence in or near oil deposits has motivated the exploration of rhodoliths in other areas such as Brazil, México, Australia and New Zealand. Fredericq et al. (2014) have shown that rhodolith beds serve as seed banks for the fast recovery of the subtidal flora after the BP oil spill in the northern Gulf of México. It is necessary to develop monitoring methods for this habitat to understand potential impacts from other human activities.

Understanding is increasing about the ecological role of rhodoliths in nearshore environments worldwide, the biodiversity associated with rhodoliths, and how human activities are having an increasing impact. The importance of rhodolith beds as biodiversity centers has increased with the number of published papers and the growth in knowledge about the taxonomic status of the associated species.

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