Beitr. Paläont., **20**:7–19, Wien 1995

Sedimentological and biological aspects in the formation of branched rhodoliths in northern Norway

Sedimentologische und biologische Aspekte bei der Bildung von ästigen Rhodolithen im nördlichen Norwegen

by

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FREIWALD, A., 1995. Sedimentological and biological aspects in the formation of branched rhodoliths in northern Norway. — Beitr. Paläont., **20**:7–19, 4 Figures, 2 Plates, Wien.

Contents

Abstract

Rhodoliths are very commonly distributed in Cenozoic deposits. However, processes leading to the development of rhodolith accumulations are poorly documented. This study reveals insight into the relationship between reefal coralline algal frameworks, framework-derived rhodoliths and maerl-type sediments from coastal platforms in northern Norway. The rhodolith factories are reefal build-ups which generate branched, non-nucleated rhodoliths by fragmentation of hemispheroidal branched algal heads. The major driving forces which enhance widely spread dislocation of algal heads are storm events. The different rhodolith facies can be related to storm depositional processes. Characteristic tempestitic rhodolith facies are large on-shore and lobate off-shore pavements, megabars and algal gravels (maerl-type deposits). Aside from the sedimentological treatment of rhodoliths, there also exist a phycological point of view with respect to rhodolith formation. According to this, branched and non-nucleated rhodoliths represent only an advanced stage in the coralline algal life history. The early stages are the initial algal crusts which remain on the autochthonous frameworks. After the dislocation of the branched heads, the remaining crusts have the potential to develop new branches thus leading to more rhodolith production by the same plant. Considerations on phycological and geological aspects in rhodolith formation offer some interesting perspectives in coralline algal life histories.

Zusammenfassung

Rhodolithe sind in känozoischen Ablagerungen weit verbreitet. Dennoch sind Prozesse, die zur Bildung von Rhodolithen bzw. -ablagerungen führen, kaum bekannt. In dieser Studie werden die Beziehungen von nordnorwegischen Algengerüsten zu Rhodolithen und Algenkiesen (Maerl-Typ) dokumentiert. Die riffartigen Algengerüste sind wichtige "Rhodolithfabriken". Bedingt durch die vorwiegend mechanische Fragmentierung hemispheroidaler Algenaggregate entstehen ästige und kernlose Rhodolithe. Pulsgeber der räumlich weit verbreiteten Rhodolithfazies sind Sturmereignisse. Sämtliche Rhodolithfazies lassen sich auf eine tempestitische Genese zurückführen. Küstenwärts entstehen proximal von den autochthonen Kalkalgengerüsten ausgedehnte Rhodolithdecken, die distal in Rhodolithbarren und Algenkiese übergehen. Seeseitig sind schmale, in der Aufsicht lobate Rhodolithdecken vorhanden. Neben der rein sedimentologischen Betrachtungsweise der Rhodolithgenese, tragen auch phykologische Aspekte wesentlich zum Verständnis dieses Phänomens bei. Nach der Festheftung der Algenspore bilden coralline Algen ein Krustenstadium aus, bevor, artlich verschieden, ästige Thalli ausgebildet werden. Den ästigen Rhodolithen fehlt jedoch dieses Krustenstadium. Das initiale Krustenstadium ist auf der autochthonen Bildungsstätte, den riffartigen Algengerüsten verblieben. Diese Krusten wiederum besitzen das Potential durch erneut einsetzende Astbildung weitere Rhodolithe zu produzieren. Demnach repräsentieren ästige und kernlose Rhodolithe nur den späten Abschnitt im Lebenszyklus coralliner Algen. Die Berücksichtigung

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phykologischer und sedimentologischer Prozesse läßt die Rhodolithgenese in einem neuen Licht erscheinen.

1. Introduction

Rhodoliths are unattached coralline algal nodules that are formed by coralline algae. These algal nodules are commonly distributed in subtropical-tropical, temperate and in polar environments (BOSENCE, 1983a). Principally, three different growth forms occur in rhodoliths, laminar crusts, columnar, and branched nodules (BOSELLINI & GINSBURG, 1970, BOSENCE, 1983a, b). Due to fragmentation of branched rhodoliths, their occurrences are generally linked with maerl-type (algal gravel) carbonate deposits (SCHLANGER & JOHNSON, 1969; BOSENCE, 1976; HOTTINGER, 1983; FREIWALD et al., 1991). The term 'maerl' is used here to describe a bed of living or dead algal branches that are accumulated mostly by a hydrodynamically-driven process on the sea-bottom. Maerl as a sedimentary facies is very common on the boreo-subarctic shelves in NW-Europe.

Branched rhodoliths and maerl-type carbonate deposits are rare or absent in the shallow subtidal zone of the tropics (STENECK, 1986). One prominent exception is the tropical Brazilian shelf from 0° to 15°S, where large occurrences of branching corallines together with the codiacean *Halimeda*, and the benthic foraminifer *Amphistegina* but no coral reefs were recorded (KEMPF, 1970; MILLIMAN, 1977; CARANNANTE et al., 1988). In non-tropical climates, branched corallines and algal gravels are often the dominating growth form in the subtidal zone. This is true for the Mediterranean (JACQUOTTE, 1962; HOTTINGER, 1983) and for the eastern North-Atlantic shelves, from Spain (ADEY & MCKIBBIN, 1970), the Brittany coast (LEMOINE, 1910; CABIOCH, 1969), southern England (FARNHAM & JEPHSON, 1977), western Ireland (BOSENCE, 1976, 1980), western Scotland and the Orkney Islands (FARROW et al., 1984; SCOFFIN, 1988), and along the northern Norwegian shelf (FOSLIE, 1895; FREIWALD et al., 1991; FREIWALD & HENRICH, 1994). Many Cenozoic coralline algal deposits containing large amounts of branched rhodoliths and/or maerl-type carbonates existed under non-tropical climatic conditions, mostly on warm-temperate shelves (NELSON, 1978; BOSENCE & PEDLEY, 1982; BURGESS & ANDERSON, 1983; MACGREGOR, 1983; SCUDELER BACCELLE & REATO, 1988; NEBELSICK, 1989). The paleoecologic significance of branched coralline algal frameworks has been widely discussed (see ADEY & MACINTYRE, 1973; BOSENCE, 1983a-c, 1991; and STENECK, 1986 for review). However, processes leading to the development of rhodolith banks and maerl-type carbonate deposits are still poorly understood.

This study focuses on high-boreal to subarctic reefal coralline algal build-ups in northern Norway. These build-ups are a major source for the formation of branched, non-nucleated rhodoliths. A basic report of the morphology and structure of these framework constructions is given by FREIWALD & HENRICH (1994).

The inner shelf off northern Norway is structured by coastal platforms, the so-called "strandflats" (KLEMSDAL, 1982), which lie mostly within the photic zone. Numerous shoals and islet archipelagoes pierce through the sea-level. In this environmental setting a wide spectrum of distinct hydrodynamic regimes is present on the coastal platforms. This is reflected on a dichotomous facies distribution of specific carbonate secreting communities which exist on the windward and leeward side of the coastal platforms (FREIWALD, 1993a, b). Along the wave-exposed seaward flanks, cirriped-bryozoan-mollusc carbonate deposits are produced within kelp forests. In the subtidal zone, these sediments form veneers of skeletal sands on the rocky seabed. This strongly contrasts to the maerl-type carbonate deposits which prevail in the inner parts of islet archipelagoes (FREIWALD, 1993b). The sounds and channel systems offer wave-sheltered but strong tidally effected regimes for coralline algae to produce rhodolith pavements and bank-like structures. A first geological study of these high latitude rhodolith occurrences was provided by FREIWALD et al. (1991) approximately 100 years after the fundamental botanical reports by KJELLMAN (1883) and FOSLIE (1895, 1905) on extended rhodolith beds which exist at several places of the high-boreal and arctic coasts of northern Norway and Svalbard.

A water depth interval ranging from 9 to 25 m was recorded for the rhodolith occurrences, but they are most abundant in 10 to 15 m water depth. The rhodoliths exist in various depositional environments including muddy, sandy and gravel substrates (see FREIWALD et al., 1991, for a detailed description). In addition, reefal coralline algal structures are developed which form banks elevated up to 50 cm above the surrounding sea floor. Common characteristics of the rhodoliths studied are their almost monospecific composition and their branching growth form. These branched rhodoliths show no central nucleus. Therefore, they are non-nucleated. In most types of rhodoliths, a nucleus acts as the initial substrate for settling algal spores and subsequently developed crustose algal thalli. This raises the question as to the mode of formation of this type of branched non-nucleated rhodolith banks. Do these banks result from vertical in situ growth advance or are they simply hydrodynamically transported accumulations of algal nodules? According to CABIOCH (1988), after spore settling each coralline algae starts with a crust stage: *"One of the most striking and important features of morphogenesis, common to most coralline algae ..., is the existence, during their life-cycle, of a crustose form, whatever its development and duration might be"(p. 498).* However, the lack of a prostrate creeping stage in the northern Norwegian branched rhodoliths indicates a differentiated developmental history.

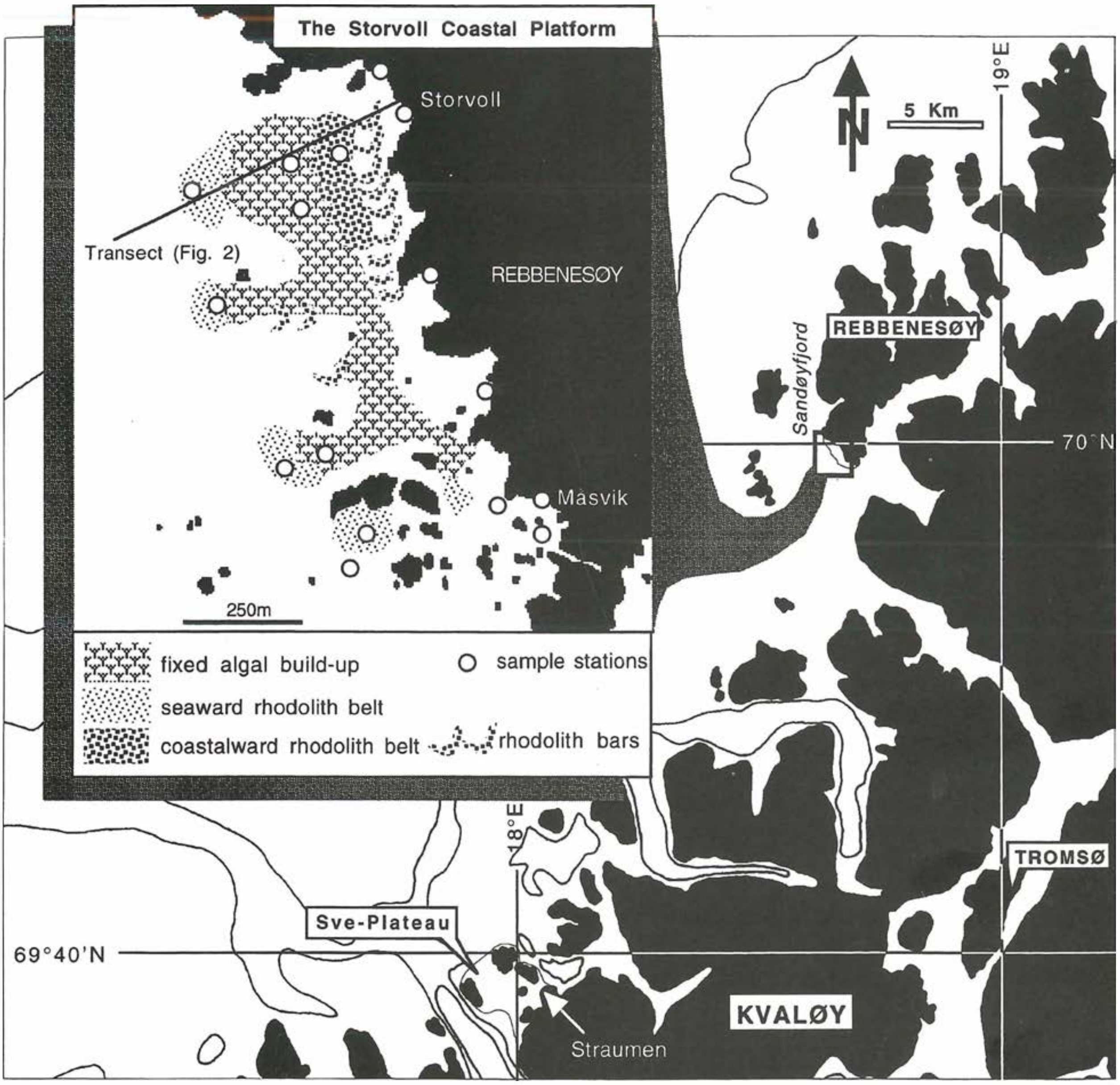

Figure 1: Geographic map of the study area in the Troms District, northern Norway. The location of the reefal coralline algal build-up is situated at the southern tip of Rebbenesøy on the Storvoll coastal platform. The inlet map shows the coralline algal build-up and the distribution of adjacent rhodolith facies.

2. Study area and methods of study

On a coastal platform in the Troms district at 70°N, northern Norway (Fig. 1), a large reefal build-up formed by coralline algae is fringed by extended rhodolith pavements and maerl-type carbonate deposits (FREIWALD & HENRICH, 1994). The reefal coralline algal framework grows on a small coastal platform near Storvoll at the southern tip of Rebbenesøy (Fig. 1). This platform is formed by metamorphic series of the Caledonian Basement. Most of the Storvoll Platform is shallower than 10m water depth. At 30 to 35 m water depth, the western margin of this coastal platform steeply slopes down to the Sandøyfjord-Trough at 120 m water depth. About 2.5 nautical miles to the west, the platform is protected by a belt of shoals and islets against the Norwegian Sea swell. These islet archipelagoes act as breakwater. Due to strong tidal currents and numerous rocky shoals in the area, ship operation with *R/V OTTAR* was restricted to the northern Storvoll Bay and west of the small skerry archipelago near Måsvik. We used a towed underwater television system (OSPREY-OE-1360-CCD-Color Camera system) fixed on a frame with a pan/tilt operation unit. In addition, a still camera (CAMEL-CI-2005-Mk II) was mounted on the frame about 60 cm above seabottom for taking colour slides. After the video survey, a grab-sampling transect with a VAN VEEN Grab was carried out in order to obtain large framework slabs from the build-up and rhodoliths from the adjacent pavements (see inlet map in Fig. 1 for sampling locations).

3. Results

3.1. A transect through the coralline algal build-up and rhodolith accumulations

Two types of carbonate frameworks which are constructed by coralline algal thalli are present on the Storvoll-Plateau: the fixed in situ reefal build-up described by FREIWALD & HENRICH (1994) and rhodolith pavements. All together, these frameworks cover approximately 125,000 m^2 on this coastal platform in the 6 to 15 m water depth interval.

The reefal build-up is fringed by rhodolith belts (Fig. 2). Towards the sea, the rhodoliths form a thin pavement of branched algal thalli from the margin of the build-up in 12 m water depth down to 15 m water depth. This pavement has a maximum width of 50 m and lobes out distally. The boundary of this seaward rhodolith belt to the sandy echinoderm-bivalve facies (FREIWALD, 1993a) is sharply developed. The shoreward rhodolith accumulations are structurally more complex. Proximal to the fixed build-up, thick rhodolith pavements of several tens of meters in width are developed. Distally, these pavements fade out into complex rhodolith bars and megaripple systems in 3 to 4 m water depth. The crestlines of these ridges and bars are orientated longshore, with crest lengths of 10 to 20 m. The sediment between the ridges and bars consists of algal gravels or maerl-type deposits. The maerl facies continues to the surf zone and is piled up supratidally into beach-ridges (Fig. 2).

3.2. The living coralline algal build-up surface: a rhodolith factory

The vertical growth of the build-up is maintained primarily by branching *Lithothamnion* spp. (Pl. 1, Fig. 1). Crustose *Phymatolithon* sp. stabilize the branched framework vertically and laterally (Pl. 1, Fig. 1, 4). Of special interest for this study is the composition of the living build-up surface. The determination of the coralline algae was carried out by Woelkerling and Daume (Bundoora, Australia).

3.2.1. Branched carpets versus hemispheroidal heads

Branch development arises from the initial crusts of *Lithothamnion* cf. *glaciale*. This change of growth mode from a prostrate creeping system to an erect system is a common phenomenon among benthic macroalgae. In cases where the encrusting *Phymatolithon* sp. is not present, a dense monospecific carpet of *Lithothamnion* cf. *glaciale* branches exists (Pl. 1, Fig. 2). However, competition with *Phymatolithon* sp. seems to suppress the carpet development of *Lithothamnion* cf. *glaciale* by overgrowth of their branches (Pl. 1, Fig. 3). In this case, only a few branches continue to grow upright. These branches form the base for the hemispheroidal *Lithothamnion* heads (Pl. 1, Fig.4; Pl. 2, Fig. 1). The average diameter of these heads is 3 cm. On the build-up surface, hemispheroidal heads are much more abundant than the carpet growth pattern. When detached, these hemispheroidal heads form the major source for rhodolith production (see Pl. 2).

3.2.2. Branch morphology

The branches of the *Lithothamnion* heads have distally broadened apices, each with a slight central depression (Pl. 1, Fig. 3). Regardless of the manner in which the branches are orientated within a hemispheroidal head, their terrace-like apices are directed towards the illuminated sea surface, thus pointing to a phototactic growth reaction (Pl. 1, Figs. 1–4). This specific growth pattern of algal branch tips was reported by STENECK & ADEY (1976) from *Lithophyllum congestum* in the Caribbean. No secondary fusion of branches within the heads is observed.

3.3. The rhodoliths: morphology and aspects of mobility and degradation

The overwhelming mass of *Lithothamnion* rhodoliths shows a spheroidal (92%) shape (Pl. 2, Fig. 3). This sphericity (with 0.71 according to the method given by BOSENCE, 1976) is maintained by intense radial growth of the branches. The diameter of the spheroidal rhodoliths is 3 to 4 cm on average. The modes of development of these rhodoliths are found at two sites adjacent to the reefal framework where pavements consist of non-spheroidal rhodoliths predominantly. These rhodoliths are formed by a group of branches which grow into the same direction. These branches emerge from a basal branch

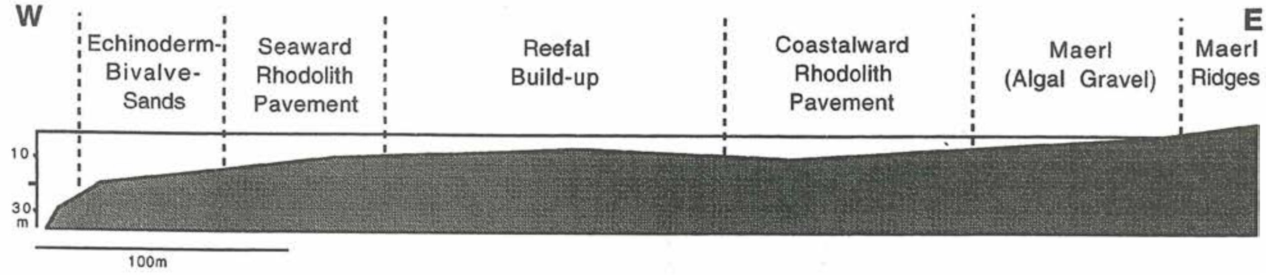

Figure 2: The spatial distribution of sedimentary facies patterns in relation to the coralline algal build-up is shown on a W-E-transect through the Storvoll coastal platform at the southern tip of Rebbenesøy.

that is slightly thicker (Pl. 2, Fig. 2). Originally, the basal stem arises from the ontogenetic initial crust-stage of *Lithothamnion* cf. *glaciale*. The breakage between the crust and the basal stem always follows the suture that separates the growth tierings of the medullary core of the branches. After getting detached, the coralline algae starts with wound-healing around the breakage by closure of dead or damaged cells (GIRAUD & CABIOCH, 1979, 1981).

All in all, these rhodoliths show the same morphological habit as the hemispheroidal heads from the fixed build-up (Pl. 2, Fig. 1). This is strong evidence for rhodolith redistribution from the build-up onto the rhodolith pavements. In addition, these non-spheroidal rhodoliths represent an early rhodolithic stage. The large amount of rhodoliths, the size of the sampled area bearing non-spheroidal rhodoliths and the unhealed breakages at the basal stems all show characteristics of an event-like mass dislocation of hemispheroidal heads from the build-up caused by a severe storm. If this is true, the spheroidal rhodoliths must be interpreted as a "mature" rhodolithic stage, at which intense intercalary branching around the basal stem results in increased sphericity (Pl. 2, Fig. 2).

3.3.1. Intensity and processes of rhodolith movements and transportation

An underwater video survey was carried out to demonstrate the mobility of rhodoliths during high tidal current velocities (>1 to 1.5 knots). The result of this survey is that no large-scale rhodolith movements occur under normal tidal current activity. This implies that the rhodolith bank-like structures and megabar systems are formed under extreme, highly energetic hydrodynamic regimes such as storm waves. Consequently, non-nucleated branched rhodolith accumulations are allochthonous in origin. Although a certain degree of self-maintenance caused by fragmentation of branches in the rhodolith accumulations, which can form the core for new rhodolith development is present, the main driving forces for the generation of rhodolith pavements, megabars, ripples and maerl-type deposits are storms. Judged from the sedimentological point of view, these algal structures can be regarded as tempestites.

During high tidal current velocities, slight movements of rhodoliths were observed by outwashing of the sandy substrates beneath the rhodoliths. However, these movements do not include rolling or turnover of rhodoliths. Another important source for rhodolith redeposition under normal tidal current conditions is induced by filamentous algae and single laminarian fronds, which can colonize the coralline algal thalli. When the buoyancy of the filamentous algae exceeds the gravity and friction forces of the rhodolith lying on the substrate, kelp-rafting occurs (KUDRASS, 1974). Kelp-rafted rhodoliths as well as other organisms or boulders of the subtidal zone are transported by longshore currents with a coastward component. Finally, the kelp-rafted rhodoliths strand on the high tide level together with well-sorted fine sands on the beach. After subsequent decay of the laminarian fronds, a sediment of striking bimodal texture is left behind. Especially in leeward positions of spits or rocky outcrops in the intertidal zone, large accumulations of kelp-rafted rhodoliths alternating with well-sorted sands are deposited (FREIWALD, 1993a).

3.3.2. Degradation of rhodoliths: bioturbation, bioerosion and mechanical fragmentation

The role of bioturbation triggered by carnivorous fishes as a process of rhodolith rolling and fragmentation is presumed to be important. The branched rhodoliths serve as an ecological niche for the brittle star *Ophiopholis aculeata*. The brittle stars hold their arms for suspension feeding into the turbid water, whereas their central bodies are protected by the rhodolith branching meshwork. Carnivorous fishes, such the wolffish *Anarhichas lupus* and cods, prey on brittle stars. During the biting action of the fish, the brittle star bearing rhodoliths may be turned and/or fragmented. At the moment, the data base is too weak for quantifying this kind of rhodolith rolling and degradation. However, it should be pointed out that, as in tropical reefs, bioerosion and sediment supply caused by biting fishes finds an analogon in non-tropical carbonate production zones (see also HOSKIN, 1980).

Bioerosional processes in rhodolith associations can be related to grazing marks of echinoderm teeth or the radulae of chitonids and limpets (see FREIWALD, 1993b). Due to the dense branching mode with respect to the large size of the herbivores, grazing is resticted to the distally broadened apices of the branches. Internal weakening of rhodolith frameworks by boring activities of endolithic algae, fungi and sponges is sparsely present in living, but very abundant in dead, algal thalli. Therefore, it can be concluded that endolithic bioerosion strongly weakens dead rhodolith frameworks rather than living ones. However, if a rhodolith becomes fragmented into single branches and are thus converted into a maerl-type deposit, then mechanical abrasion due to rapid redeposition hampers endolithic infestation. Most of the maerl algal gravels show a polished appearence (Pl. 2, Fig. 4). The most important process in rhodolith degradation is mechanical fragmentation during severe storms.

4. Discussion

4.1. Sedimentological aspects

Investigations of cold-water coralline algal build-ups (FREIWALD & HENRICH, 1994) from northern Norway offer insights into the formation of branched non-nucleated rhodolith occurrences.

The coastal platforms off Troms are mostly structured by shoals and islet archipelagoes, thus providing a complex coastal topography with distinct hydrodynamical environments which is reflected in differentiated types of carbonate-secreting communities. At wave-exposed shallow coastal platforms dense kelp forests exist. These kelp forests provide a distinct zone of carbonate production. The large fronds of the kelp harbor numerous carbonate-secreting invertebrates (e.g. cirripeds, molluscs, echinoderms and bryozoans) but also layers of encrusting coralline algae. In the photic zone of swell-protected areas, reefal coralline algal build-ups and rhodolith occurrences form the most important type of a framework constructing ecosystem in northern Norway. These habitats are impinged upon by very strong but predictable tidal current regimes (FREIWALD, 1993a). The branched coralline algae are very susceptible to physical disturbances such as storm waves. Due to slow growth rates (FREIWALD & HENRICH, 1994), this kind of disturbance cannot be compensated by the corallines. However, when storm waves enter the inner reaches of the coastal platforms, severe destruction occurs in the coralline algal systems, thus leading to the formation of tempestitic rhodolith bars, pavements and maerl-type carbonate deposits.

The bank-like rhodolith accumulations strongly resemble autochthonous frameworks. In the geological record, these bank-like rhodoliths will be preserved as carbonate lenses, that very well might get confused with autochthonous algal biostromes. However, these elevated structures are allochthonous in origin. Moreover, the bank-like structures studied result from event-like storm accumulation. According to AIGNER (1985) and SEILACHER & AIGNER (1991), the whole set of sedimentary rhodolith structures adjacent to the reefal build-up is suggested to be interpreted as a spatially differentiated series of storm deposits (Fig. 3).

4.1.1. On-shore rhodolithic storm deposits

The production zone of branched non-nucleated rhodoliths are reefal build-ups which are situated in the subtidal zone of the coastal platform. The main direction of storm redeposition is directed on-shore or longshore with a pronounced on-shore gradient. Leeward of the build-up, a hierachy of proximality trends is developed on a facies scale: a) thick rhodolith pavements, b) rhodolith megabars, c) maerl-type (algal gravel) deposits as a result of mechanical fragmentation of the branched rhodoliths, and d) supratidally deposited maerl ridges.

4.1.2. Off-shore rhodolithic storm deposits

Seaward to the coralline algal build-up, a thin and lobate rhodolith pavement is developed. This indicates minor off-shore transport of branched heads from the build-up. It is assumed that the off-shore rhodolith pavements originated from near bottom counter or gradient currents. These gradient currents act as compensative back-flow of water masses against the on-shore and longshore directed high energenetic wind-driven currents (see AIGNER, 1985).

A very similar relationship between autochthonous branched coralline algal frameworks and framework-derived rhodoliths with subsequent gravel formation is described by BOSENCE (1985) from the Tavernier Keys, Florida. The rhodoliths are generated from collapsed parts of the framework and migrated on-shore during storms. In contrast to BOSENCE (1976), the shape of the rhodoliths studied is not related to a specific hydrodynamic environment. The different degrees in sphericity observed in the branched rhodoliths display different stages of maturity after dislocation from the initial production site.

4.2. Phycological aspects

In contrast to redeposited sessile invertebrates, coralline algae have the potential to be eroded and survive in parautochthonous or allochthonous sites and thus form a very efficient type of a spreading carbonate factory. This is only possible by the large potential of cytological repair reactions, internally and externally, which have been developed in coralline algae (see GIRAUD & CABIOCH, 1979, 1981). These physiological adaptations are a major prerequisite for the formation of rhodolith pavements which fringe the autochthonous build-ups.

Initial growth of the framework starts with large-scaled encrustations of a hardsubstrate by *Lithothamnion* sp. (Fig. 4 and compare with CABIOCH (1988), FREIWALD & HENRICH (1994)). Continued growth induces the formation of protuberances which, in turn, forms branches. The branching mode is mainly dichotomous. *Lithothamnion* cf. *glaciale* develops densely branched heads consisting of numerous branches with broadened apices which arise from a basal stem. These heads were dislocated from the autochthonous build-up during storm events.

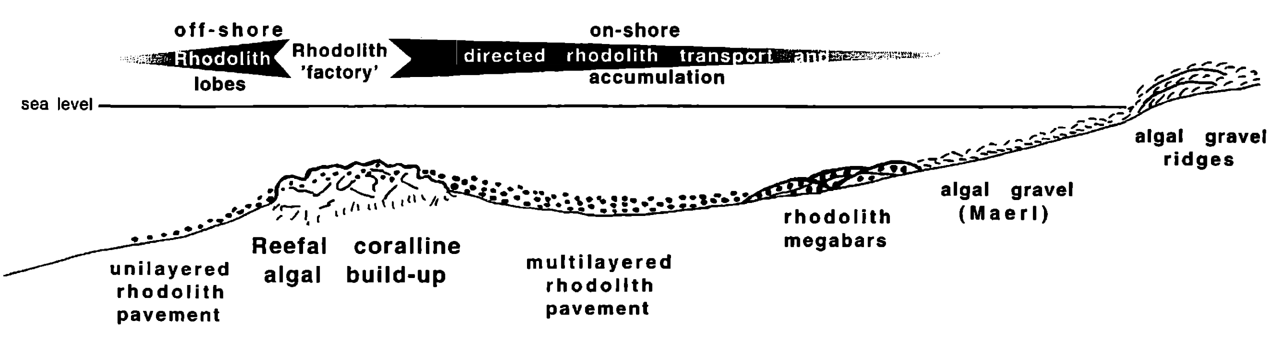

Figure 3: Rhodolith formation as a sedimentological process. The reefal coralline algal build-up acts as a rhodolith factory. The adjacent rhodolithic facies are generated by storm redeposition.

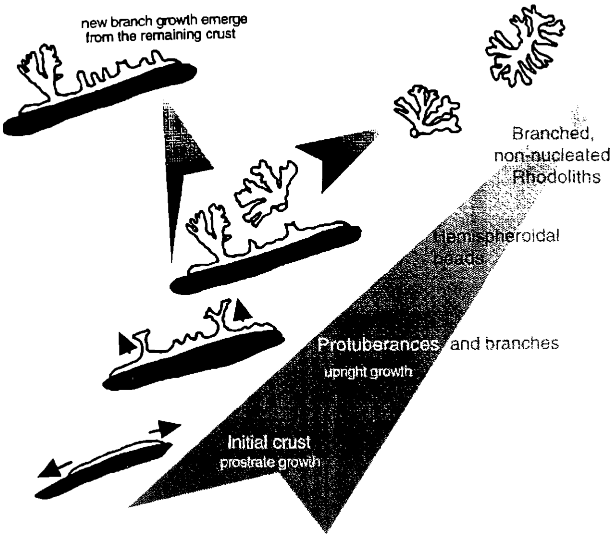

Figure 4: Rhodolith formation as a sedimentological process. The morphogenesis of *Lithothamnion* cf. *glaciale* is characterized by dissimilar morphologies. After spore germination the initial crust stage is formed by prostrate growth. Later on, the development of protuberances initiate the upright growth stage that leads to branch formation. Single branches form the base for hemispheroidal algal heads which can be dislocated by physical and biological disturbances. This is the begin of the rhodolith stage. The dispersion of rhodoliths represents a distinct mode of asexual species distribution. The remaining crust stage on the autochthonous sites can develop more branches and more rhodoliths

After the dislocation of the branched heads, the remaining initial crusts bear the potential to repair and then develop new branches which, in turn, may form the base for a new hemispheroidal head. This would imply that the branched and non-nucleated rhodoliths represent only one stage in the life history of *Lithothamnion* cf. *glaciale*, and the crusts of the same species another stage. Most obviously, the transition from the fixed stage to the unattached and free-lying stage is made possible by a change in growth form. According to LITTLER & KAUKER (1984), the development of dissimilar morphological stages provides coralline algae with some considerable ecological advance over purely crustose growth forms in the same environment. The initial crust radiates outwardly and thus new space is occupied. If environmental conditions are favorable, upright growth of protuberances and branches commences. The upright portions are supposed to have competitive advance in harvesting light and nutrients. Additionally, LUBCHENCO & CUBIT (1980) suggest from studies on heteromorphic life histories of ephemeral filamentous marine algae that the crustose stage is well-adapted for surviving through times of high grazing pressure, whereas the upright stage is adapted for high rates of growth and reproduction. It is not suitable to convert the assumptions given by LUBCHENCO & CUBIT (1980) for ephemeral algae to perennial algae such as coralline algae. But it should be kept in mind that the branching growth of *Lithothamnion* cf. *glaciale* in the autochthonous build-up provides effective protection against deep-excavating sea-urchin grazing (see STENECK, 1985, 1990; FREIWALD, 1993b).

Whatever the adaptations for dissimilar morphological stages in *Lithothamnion* cf. *glaciale* are based on, they are the most important prerequisite for the formation of branched non-nucleated rhodoliths in the area studied. Moreover, this kind of rhodolith formation enhances the ability of a large spatial distribution of this algal species by fragmentation. Viewed on a reproductive aspect, the autochthonous reefal framework emerges from sexual tetraspores which form the initial algal crusts after germination. The dislocation of the branched heads, then may be regarded as an effective mode of vegetative multiplication.

5. Conclusions

This study stresses the close relationship between reefal coralline algal frameworks and branched non-nucleated rhodoliths in northern Norway. This rhodolith type is accumulated in distinct sedimentary features, such as pavements, megabars, and maerl-type carbonate deposits which derive from event-like storm redeposition processes. The rhodoliths originate from the autochthonous reefal framework. Therefore, the rhodolith accumulations are primarily parautochthonous and allochthonous in origin. Phycologically, rhodolith formation is made possible by a change in algal growth form. The dissimilar morphologies within this coralline algae represent different stages in life history. An ontogenetically initial crust stage is succeeded by formation of branches in *Lithothamnion* cf. *glaciale*. After detachment of these branches, the free-lying rhodolith stage provides the potential for large-scaled spatial distribution of this algal species by their branched non-nucleated rhodoliths.

Acknowledgments

This contribution is part of the German Science Foundation (DFG) project He 1671/1 "Controls in formation of cold-water carbonates" which is part of the priority research program "Global and regional controls in biogenic sedimentation". The manuscript benefitted from the constructive review carried out by Mme. Cabioch, Biological Station, Roscoff. We thank T.O. Vorren, M. Hald and J. Hansen from the University of Tromsø for their enormous support and their invitation to work on *R/V Ottar* and *R/V Hyas*. The photographic work was provided by S. Perbandt. Special thanks to P. Schäfer, A. Munnecke and A. Wehrmann for their valuable discussions and comments on this topic. Mrs. Jayne Welling-Wolf kindly improved the language. The preparative part of this study was carried out at the GEOMAR Research Center, Kiel.

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PLATE 1

Figs. 1–4. Details from slabs sampled from a coralline algal build-up on the Storvoll coastal platform, northern Norway. The living surface of the algal bioherm is dominated by the branching *Lithothamnion* cf. *glaciale* (L) and by the encrusting *Phymatolithon* sp. (P). Hemispheroidal heads are indicated with arrows (Fig. 1). *Lithothamnion* carpet growth pattern is developed in absence of *Phymatolithon* crusts (Fig. 2). The competition for space between the two corallines is shown in Fig. 3. The *Phymatolithon* crusts (arrows) overgrow branches of *Lithothamnion* cf. *glaciale*. The hemispheroidal algal heads emerge from a single basal stem (Fig. 4). All offspring branches have whitish, distally broadened apices which all show phototactic growth reactions. Scale bars = 1 cm.

PLATE 1

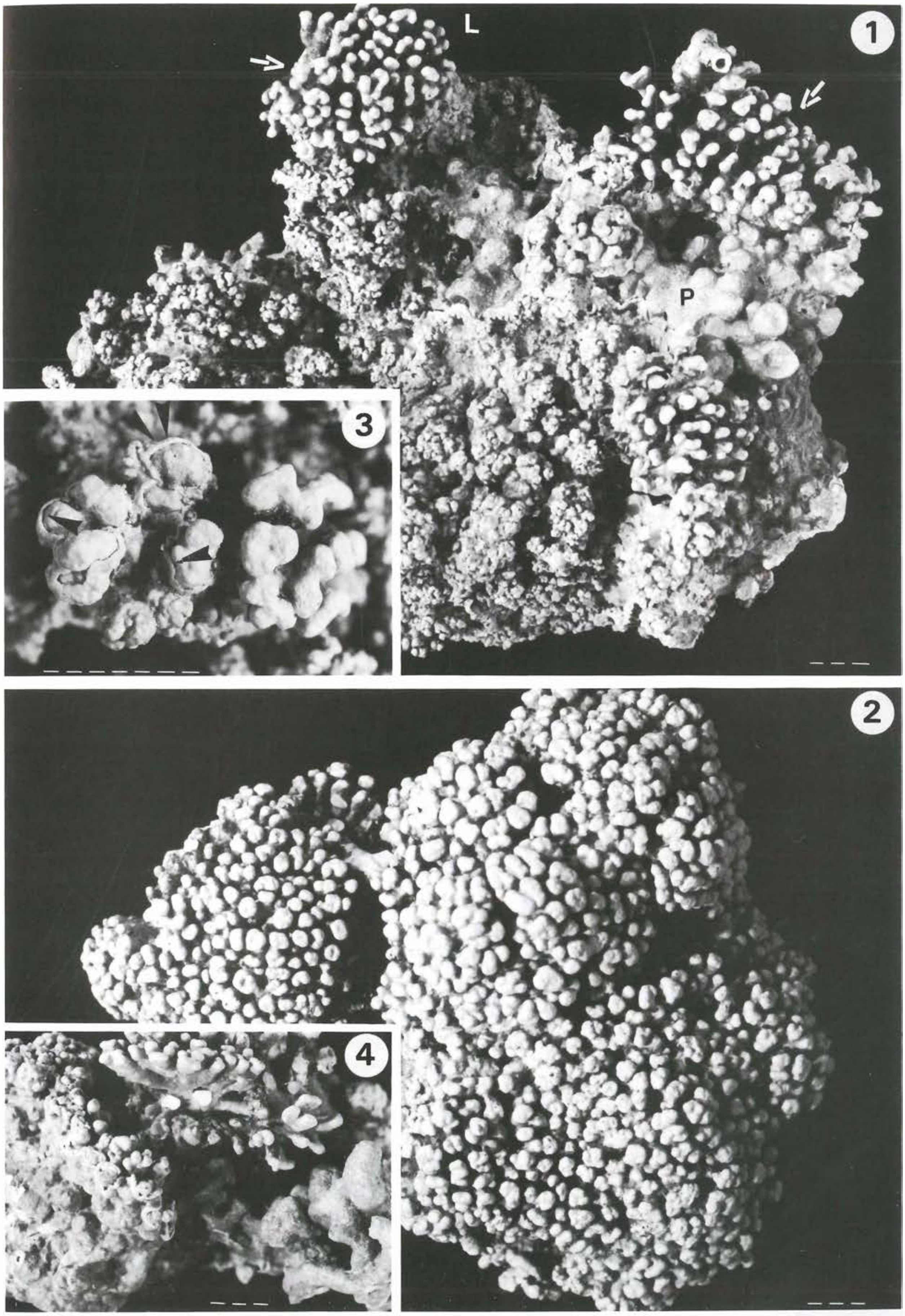

PLATE 2

Figs. 1–4. From hemispheroidal algal heads to non-nucleated rhodoliths. The fixed hemispheroidal algal heads (Fig. 1) form the base for rhodolith formation. The dislocated algal heads show non-spheroidal shapes. Increased sphericity is maintained by enhanced intercalated growth of branches around the breakage of the former algal heads (Fig. 2). Spheroidal non-nucleated rhodoliths represent a mature rhodolith stage (Fig. 3). Grey arrows stress the possibility of algal gravel formation by fragmentation of algal heads and from rhodoliths (Fig. 4). Scale bars = 1 cm.

PLATE 2

From hemispheroidal branched algal heads to non-nucleated rhodoliths