CONSTRUCTIONAL AND DESTRUCTIONAL PATTERNS—VOID CLASSIFICATION OF RHODOLITHS FROM GIGLIO ISLAND, ITALY

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ABSTRACT: Micro-CT analysis has been established as a useful, non-destructive method for assessing the inner arrangement of rhodoliths. In this study, micro-CT analyses and sectioning techniques are used for void space assessment, the reconstruction of growth histories, and their related environmental conditions in present-day rhodoliths from Giglio Island (Tyrrhenian Sea, Italy). The rhodoliths are investigated with respect to shape, taxonomy and growth forms of coralline red algae, constructing fauna and flora, degree of porosity, and types of void formation. Porosity within the nodules is calculated using image processing software based on slab surfaces and micro-CT, enabling recognition of different void types at various scales as well as their distribution throughout the rhodoliths.

The studied rhodoliths range in sizes from 4 to 16 cm and are spheroidal to sub-spheroidal in shape. The nodules are dominated by coralline red algae and associated with subordinate serpulid worm tubes and bryozoans. Calculated porosity values range from 3 to 41% in volume. Two different types of porosity were distinguished within the rhodoliths: (1) constructional voids are present as primary voids present within single cells and conceptacles and as voids produced by conjoined protuberances of coralline algal thalli, and (2) destructional voids are caused by dissolution and decay of nuclei as well as soft-body organisms and a wide range of bioerosion, including Gastrochaenolites and Trypanites ichnotaxa. The degree of bioerosion (bioerosion index, BI) ranges from low (BI = 2) to moderate (BI = 3).

INTRODUCTION

Coated grains and organisms showing "circumrotatory" growth (Kissling 1973) include "free-living forms" of several organisms such as rhodoliths dominated by calcareous red algae, coralliths (corals), bryoliths (bryozoans) and balanoids (balanid barnacles), and macroids, which are composed of a mixed assemblage of various encrusters (Hottinger 1983; Bassi et al. 2012). The formation of these coated grains can be considered as a complex equilibrium of sedimentation rate and periodicity of water energy (Bosence 1983a; Hottinger 1983). They develop on a wide range of substrates under low sedimentation rates. The periodic turning needed to attain a rounded form can be initiated and maintained by current or wave motion as well as by bioturbation (Bosence 1983a; Hottinger 1983; Marrack 1999; Gischler and Pisera 1999). Fluctuations of water energy must be sufficiently high to clean the environment of fine sediment falling out of suspension but low enough to prevent transport of these coated grains out of the environment (Hottinger 1983).

Coralline algal sediments represent important depositional environ-ments in the Mediterranean Sea where various types are present. They are widely distributed and represent highly diverse bioconstructions (see Laborel 1961; Laubier 1966; Bosence 1985; Pfannschmidt 2002; Ballesteros 2006; Martin et al. 2014). Rhodoliths are produced by coralline red algae (Rhodophyta) and are defined as free-living, unattached nodules formed by more than 50% of non-geniculate crustose coralline algae (e.g., Bosellini and Ginsburg 1971; Adey and Macintyre 1973; Bosence 1983b, 1991). These accretions can be constructed when crustose or branching coralline algae settle on non-cohesive particles such as sediment particles including biogenic debris (e.g., Bosence 1983a).
Rhodolith morphology, including both general shape as well as specific algal growth-forms, is dependent on a number of environmental factors including water movement, biological activity, and light levels. Although morphology has been used as an indicator of water energy (Bosence 1983a, 1991; Basso 1998), this is not always the case as shown in both recent and fossil studies on rhodoliths (Braga and Martı´n 1988; Steller and Foster 1995; Lund et al. 2000; Brandano et al. 2005; Basso et al. 2009). Biological activity, such as fish behavior, has also been shown to play a significant role in overturning and displacing rhodoliths (Marrack 1999; Gischler and Pisera 1999; Amado-Filho et al. 2012). The coralline algal taxonomic assemblage characterizing the nodules and their growth-form morphologies can be used as indicators of environmental conditions such as light levels and turbulence as well as of changes of these parameters over time (e.g., Steller and Foster 1995; Basso 1998; Bassi et al. 2012; Aguirre et al. in press).

Micro-computed tomography (Micro-CT) has been established as a non-destructive method to analyze bioerosional features, allowing a detailed understanding of complex endolithic structures and formation patterns in three-dimensions in various substrates (e.g., Scho¨nberg and Shields 2008; Tapanila 2008b; Bromley et al. 2008; Higgs et al. 2011). As a first approach, Leal et al. (2012) suggested for recent rhodoliths of the Abrolhos Bank, Brazil, that the technique could be an appropriate tool in determining porosity and calcium carbonate production, resulting in a better resolution in quantification of these parameters (see also Teichert 2014). The aim of this paper is to implement image processing software and micro-CT-analysis for present-day rhodoliths of Giglio Island (Tyrrhenian Sea) in order to determine morphological features as well as porosity patterns

MATERIAL AND METHODS

Depositional Environments of Giglio Island

Giglio Island (42u20'N, 10u52'E) is the second largest island of the Tuscan Archipelago, 20 km off the Tuscan coastline in the northern Tyrrhenian Sea. The present study focuses on rhodolith samples collected north of the Bay of Campese on the western coast (Fig. 1), which is characterized by a gently sloping, sandy coastal area framed by granitic cliffs to the NW and calcareous dominated lithostratigraphic units to the SW. Detailed geologic overviews of Giglio Island are given in Poli (1992), Faggioni et al. (1998), and Reinhardt and Rossetti (2004).

A general description of ecosystems around Giglio Island is found in Valentin (1986) and a detailed sedimentological study is present for the Bay of Campese south of the collection site (Niemeyer 1993). Shallow

FIG. 2.—Coralline species composition of the rhodolith samples of the west coast of Giglio Island. A) Sporolithon ptychoides Heydrich, longitudinal section of sporangial compartments and the row of elongated cells at their base (arrows), scale bar 5 200mm. B) Multiporate conceptacles of Lithothamnion minervae Basso, scale bar 5 200mm. C) Multiporate conceptacles of Lithothamnion cf. philippi Foslie, scale bar 5 400 mm. D) Lithophyllum incrustans Philippi/L. racemus (Lamarck) Foslie species complex, uniporate (carposporangial) conceptacle, scale bar 5 200mm. E) Lithophyllum pustulatum (Lamouroux) Foslie. Longitudinal section of laminar thallus with oblique section of uniporate conceptacles, scale bar 5 200mm. F) Spongites fruticulosus Ku¨tzing, longitudinal section of a uniporate conceptacle and the ventral non-coaxial cell filaments, scale bar 5 200mm.

water areas of the western coast of Giglio Island are characterized by a variety of substrates including large boulders close to the breaker zones, scattered rocks of varying sizes to coarse and finer sands. Areas of seagrass (Posidonia oceanica, Zostera marina) and algal meadows (Caulerpa racemosa), ranging from 10 to 20 m water depth, are abundant. Deeper waters (below 20 m water depth) are characterized by fine sediments on the one hand, but also by a coarse grained bioclastic substrate dominated by coralline algal fragments as well as other bioclastic remains (bivalves, gastropods, echinoids) and rounded granitic pebbles. Investigations of rhodoliths in the Tyrrhenian Sea have been carried out in detail for Capraia Island by Basso and Tomaselli (1994), the Bays of Naples and Pozzuoli by Toscano et al. FIG. 3.—Shape distribution of rhodolith samples of the west coast of Giglio Island (n 5 36). Spheroidal and sub-spheroidal rhodoliths dominate the assemblage.

(2006), and the Pontian Islands by Basso (1998) and Bracchi and Basso (2012).

Taxonomy, Growth-Forms, Size and Shape Parameters

In total, 31 rhodolith samples as well as two samples of the surrounding sediment (GC 01-02) were collected by scuba diving in two batches in 2011 (GC 03-18) and 2012 (GP 01-15) from 35 m water depth north of the Bay of Campese in the same sampling location (Fig 1), focusing on living samples. Rhodoliths here are loosely distributed on coarse bioclastic sediments. Size and shape parameters of each rhodolith were determined by measuring the three following dimensions: longest (L), intermediate (I) and shortest (S), following Sneed and Folk (1958). These were used to calculate the sphericity index, using a modified triangular diagram after Sneed and Folk (1958) and the TRI-PLOT Excel spreadsheet of Graham and Midgley (2000). The sphericity formula

$$Y \sim \sqrt[3]{\frac{S_2}{(L\,I)}}$$

after Friedmann and Sanders (1978) was also applied. Terminology of the subdivisions (e.g., sub-spheroidal, sub-ellipsoidal, sub-discoidal) follows Bassi et al. (in press).

From the first sampling, eleven rhodoliths were chosen randomly for thin sections (ranging from 5 3 5 cm to 10 3 10 cm) and analyzed to evaluate taxonomic diversity of coralline algae, microtaphonomic aspects included encrustation patterns and bioerosion traces leading to the production of constructional and destructional voids (Nebelsick et al. 2011). Coralline algal growth-forms were determined in thin section, on rhodolith slabs and CT scans following Woelkerling et al. (1993). The Bioerosion Index (BI; Bassi et al. 2012) was assessed for all the studied rhodoliths. The family, subfamily and genus classification scheme proposed by Harvey et al. (2003) in conjunction with the recognition of the Sporolithales, Hapalidiales and Corallinales as distinct orders (Le Gall et al. 2010; Nelson et al. 2015) has been used. Molecular evidence (e.g., Broom et al. 2008) suggests that Lithophyllum and Titanoderma FIG. 4.—Histogram on the size distribution of the studied rhodoliths (n 5 36); classification following Bassi et al. (2015).

represent distinct genera, but generic boundaries remain blurred on morphological/anatomical grounds (see Braga 2003; Harvey et al. 2009; Villas-Boas et al. 2009; Iryu et al. 2012), and as a result, these genera have been treated as a complex (Woelkerling et al. 2002) using the oldest generic name, Lithophyllum.

Porosity Determination

Specimens were cut along the longest dimension to analyze inner thallus arrangement as well as to determine porosities by quantifying the voids within the rhodoliths. Slab rhodolith specimens were scanned using an Epson Perfection V700 Photo Scanner with 4800 dpi, and processed by using Adobe Photoshop CS6 and Image J, coloring skeletal material black and voids white. Porosity was determined by comparing the void area to complete bulk area (skeletons + voids) of the specimen using the "Analyze Particles" function of Image J. Statistical analysis of the void distribution has been processed using Microsoft Excel 2010. Three randomly chosen samples (GP 07, GP 11, and GP 14) were scanned by Micro-CT at "Hema-CT Q-Technologie und Messtechnik GmbH" Denkendorf, Germany using a model Werth Tomoscope HV 225 KV. The set parameters were: 185 kV, with 800 steps and a voxel size of 75 mm. Each rhodolith was scanned along the three main axes. The results were analyzed using SPIERSEdit-Version 2.15 (Serial Palaeontological Image Editing and Rendering System; see Sutton 2008), whereby threshold images were generated in order to clearly delineate skeletal material from empty space as well as exclude sedimentary infilling. The results were visualized in three-dimensions using SPIERSView.

RESULTS

Taxonomy, Growth-Forms and Morphology

The studied rhodoliths are multispecific and consist of eight species of coralline algae and one peyssonneliacean species. Coralline algae belong to the orders Sporolithales: Sporolithon ptychoides Heydrich, S. sp. (Fig. 2A); Hapalidiales, subfamily Melobesioideae: Lithothamnion miner-vae Basso (Fig. 2B), L. cf. philippi Foslie (Fig. 2C), and Phymatolithon calcareum (Pallas) Adey and McKibbin; Corallinales, subfamilies Lithophylloideae: Lithophyllum incrustans Philippi/L. racemus (Lamarck) Foslie species complex (Fig. 2D), L. cf. orbiculatum (Foslie) Foslie, and L. pustulatum (Lamouroux) Foslie (Fig. 2E), and Mastophoroideae

TABLE 1.—Results table of the grain-form analysis, calculation of the sphericity, surface morphology, and porosity determination techniques. Abbreviations: L 5 longest dimension; I 5 intermediate dimension; S 5 shortest dimension; d 5 discoidal; e 5 ellipsoidal; s 5 spheroidal; enc. 5 encrusting; war. 5 warty; lum. 5 lumpy; frut. 5 fruticose; - 5 absent; + 5 common; ++ 5 abundant; +++ 5 highly abundant; 5 porosity. Calculation of porosity [%]:

$$W \sim \frac{\text{void cm}^2}{\text{cut}\delta_{cm2}\flat} \; 100.$$ In GC- samples both cut surfaces were used for porosity determination (cut A and B), while in GP-samples only one side was used. Missing values refer to samples not used for porosity calculation with slab surfaces either because of their stage of development within rhodolith formation or because of usage for Micro-CT analysis.

Spongites fruticulosus Kützing (Fig. 2F). One peyssonneliacean species (Peyssonnelia spp.) is also present. Although the general lack of diagnostic features such as conceptacles makes determination of relative abundance of species difficult within the rhodoliths, members of the Lithophylloideae can be determined as the most abundant taxa.

The smallest studied rhodolith specimen is 3.7 cm, the largest 15.9 cm in maximum length. Rhodoliths are dominated by spheroidal- to sub-spheroidal shapes (s), with only four samples with discoidal shapes (d) trending towards ellipsoidal (d-e) and spheroidal (d-s) (Fig. 3; Tab. 1). Most rhodoliths have sphericity values of at least 0.75, while the four discoidal samples (GC 02, GC 15, GP 02 and GP 03) have a more angular shape with values ranging from 0.46 to 0.64 (Tab. 1). Size distribution shows that most specimens have lengths (mean of the three dimensions) between 5 and 9 cm (Fig. 4).

The rhodoliths are totally dominated by coralline red algae associated with subordinate serpulids along with encrusting bryozoans (Figs. 5, 6). Isolated vermetid gastropods and bivalves (Chlamys) occur in some of the rhodoliths. Encrusting hydrozoans, fleshy algae and byssate ark clams (arcidae) are present on the rhodolith surface though they either lack preservable skeletons or are not permanently attached (as is the case with

Fig. 5.—Rhodolith specimens GC 05 (A), GC 08 (C), GP 03 (E), and GP 08 (G) and their corresponding slabs (B, D, F, H); scale bar 5 2 cm. A) Spheroidal shape with a sphericity of 0.76. a 5 serpulid tube (Protula sp.); b 5 coralline protuberances with lumpy to fruticose growth-form. B) Cuts are characterized by boring traces with causing organisms, in some cases, preserved in living position. BI 5 3. a 5 Gastrochaenolites; b 5 dense coralline crusts; c 5 serpulid tube encrusted by coralline; porosity 29.6 %. C) Spheroidal shape with a sphericity of 0.75. a 5 serpulid tubes encrusted by coralline; b 5 dense bryozoan crusts; lumpy coralline growth-form. D) Dense rhodolith inner arrangement with low bioerosional signatures; a 5 encrustation of a serpulid tube by Sporolithon sp. with clear growth bands. BI 5 2. b 5 relicts of serpulid tubes highly encrusted by coralline; porosity 5 10.1 %. E) Discoidal to spheroidal shape with a sphericity of 0.55. a 5 bryozoan crusts with multilaminar growth-form; b 5 lumpy coralline growth-form encrusting serpulid tubes; c 5 bivalve shell of the genus Chama sp. F) Slab is defined by a strong influence of bioerosion in a dense rhodolith framework with a high amount of constructional void porosity. BI 5 3. a 5 Gastrochaenolites; b 5 typical constructional void; porosity 5 22.6 %. G) Spheroidal shape with a sphericity of 0.90. a 5 chimney-like serpulid tubes; b 5 coralline protuberances with lumpy to fruticose growth-form; c 5 bryozoan crust with multilaminar growth-form morphology. H) Dense inner arrangement highly influenced by constructional and bioerosional void features. BI 5 3. a 5 bioerosional void; b, c 5 constructional voids; porosity 5

the byssate bivalves). Numerous vagile organisms are present living on and within the rhodoliths including gastropods, crabs and the echiuran worm Bonellia viridis Rolando.

Various coralline algal growth-forms are present with an equal percentage of encrusting (35.5%), lumpy (32.3%) and fruticose (29%) growth-forms; warty morphologies (3.2%) are subordinated. The possibility of mapping the volumetric portion of specific taxa with respect to rhodolith contribution or to specific growth-forms is precluded by the vuggy nature of the rhodoliths and general lack of conceptacles needed to identify taxa to the species level.

Void Formation by Other Encrusters and Bioerosion

Isolated and intertwined serpulid tubes are common and present on all rhodoliths; they can also occur within larger pore spaces. Species identification of empty worm tubes is difficult and, in thin section analysis, not possible. Observations of serpulids on rhodoliths shortly after collection as well as shape and size of individual tubes suggest that various taxa are present including Protula sp. and Spirobranchus triqueter Linnaeus. The degree of bryozoan encrustation varies highly with dense bryozoan encrustation in few samples only (Table 1), while the others show either isolated crusts or none at all. Bryozoan growth forms are represented by unilaminar crusts and multilaminar, hemispherical types.

Destructive voids are formed by bioerosion and can be attributed to the ichnotaxon Trypanites represented by small tubes up to 1 mm in diameter. Gastrochaenolites is present as comparatively large, smooth walled, oblong cavities up to 1.5 cm in length and 1.0 cm in diameter, which increases in size inward from the rhodolith surface. In some cases, double holes representing the openings of the boring bivalve siphons can be seen on the rhodolith surface. The BI ranges from 2 (low bioerosion: inner arrangement distinct, low trace density, boring structures often common) to 3 (moderate bioerosion: inner arrangement sharp, traces discrete, can reach the nucleus).

Finally some voids cannot be assigned with certainly to either constructional voids or bioerosion. These cavities include large irregular hollow areas in the center of some rhodoliths as is the case for two rhodoliths scanned by micro-CT. In some cases, surface parallel voids are present suggesting encrustation by non-skeletal organisms, which are subsequently bioimmurated by successive superimposed layers of coralline algae and then degraded.

The sectioned rhodolith specimens show a strong variation in porosity, ranging between 3 and 41%, independent of the sample size (Table 1). This variation in porosity is also reflected in the micro-CT scans that show porosity values between 13 and 28 % (Table 1) in axial sections. Variations of porosity within a single rhodolith can be seen by comparing the CT scan along a single axis of a single rhodolith (Fig. 7).

DISCUSSION

General Morphology and Form of the Rhodoliths

In a soft-sediment environment, skeletal remains of organisms as well as other hard substrates can serve as benthic micro-islands, and can provide a habitat for hard substrate communities in mobile environments (Seilacher 1982; Kidwell and Jablonski 1983; Hattin 1986; Zuschin and Perveiser 1996; Zuschin et al. 1999; Taylor and Wilson 2003; Belau´stegui et al. 2013). Encrustation and settlement of such hard substrates is governed by size, shape, stable orientation, and surface residence time as key factors. Furthermore, factors controlling the success of

settlement of different encrusters are complex and involve both constructional and destructional processes (e.g., Stachowitsch 1980; Nebelsick et al. 1997; Tapanila 2008a; Checconi et al. 2010).

The formation and shape of these accretions are a function of overturning-frequency and the presence, shape and form of the nucleus 45.5 %. that they initially encrust (e.g., Cabioch 1972; Lund et al. 2000). Growth occurs on the exposed side of the aggregate until water energy (or biological disturbance) increases at a level sufficient to enable over-turning-events (Basso 1998), while more symmetric rhodoliths are more easily turned by current activity. Overturning-frequency depends on the hydrodynamics and biological activity of the environment in which they occur (Bosence 1983a, 1983b; Basso 1998; Marrack 1999; Foster 2001; Bassi et al. 2009). Studies of the cellular structures of coralline red algae suggest that rhodoliths can also continue to grow even if infrequent turned due to the ability of the plants to survive on the photo-negative lower surface by utilizing starch accumulations and cellular connections (Woelkerling 1988; Basso 1998; Basso et al. 2009).

Most of the studied rhodoliths do not show a clear, distinguishable nucleus, although a single case is present of a rounded granitic pebble at the core. In some cases, there is a clear large cavity at the center of the rhodolith as in two of the micro-CT sectioned samples. It is not clear whether these cavities represent a non-preservable core (such as a sponge) or result from bioerosion.

The fact that most of the rhodoliths are spheroidal to sub-spheroidal in shape suggests that in some cases they are still being actively turned either by rare seasonal storm events or by biological activity. The depositional environment in which the rhodoliths are found are influenced by periodic storm-induced high-current events between the fair weather wave base and the storm wave base, which reaches down to 30 to 40 m water depth in the Mediterranean Sea (Betzler et al. 1997). Spheroidal rhodoliths, comprising sphericity values larger than 0.75 and size ranges between 3.7 and 15.9 cm (Table 1) are considered frequently turned rhodoliths. Irregular discoidal forms (GC 03, GC 15, GP 02 and GP 03), with sphericity values between 0.46 and 0.64 and range in sizes from 3.9 to 11 cm (Table 1) are interpreted as longer turned and highly affected by destructional processes. Since the rhodoliths from Giglio Island are complex multispecific coralline algae dominated by spheroidal to sub-spheroidal shapes and exhibit strong variations in micro- and macro-cavities, they are integrated as "boxwork" structures into the morpho-logical distinction of Basso (1998) and Basso and Tomaselli (1994).

Constructional and Destructional Voids

In a sedimentological context, void classification is necessary to understand the porosity and permeability properties of carbonate rocks in order to characterize a possible reservoir, whereby the pore structure and thus permeability reflects various depositional and diagenetic processes. Based on Lucia (1995), the bulk pore space is divided into interparticle and vuggy pores, which are separated in subclasses. The interparticle pore class distinguishes between interparticle and intergrain porosity, while vuggy porosity is defined as pore space within grains or significantly larger than grains (Lucia 1983). The definition of vugs comprises leached grains, fossil chambers, fractures, and large, irregular cavities, whereby vugs are distinguished with regard to their interconnection in separated and touching vugs, an important distinction with respect to the determination of permeability. Porosity distribution in rhodolith nodules can be distinguished in constructional and destructional voids. While construc-tional voids comprise vugs, as defined by Lucia (1995), and cavities formed by the irregular growth of coralline algae (Minnery 1990), destructional voids are formed due to biogenic and physical erosion patterns (e.g., Bromley 1970; Checconi and Monaco 2008; Tapanila 2008a).

Crustose coralline red algae can be considered as "bio-engineers" and "framework builders" by binding sediment particles and shell debris, and sealing off the formed structure from direct connection to the ambient seawater by production of multicellular organic blankets of living algal filaments. While most of the framework building skeletons can be considered as dead, the organic blankets contribute to the isolation of the internal environment (Alexandersson 1977; Foster 2001; Amado-Filho et

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FIG. 6.—Micro-CT scans of rhodoliths (XY-section): surfaces and sections of GP 14 (a, b; scale bar 51 cm) and GP 07 (c, d; scale bar 5 2 cm), edited using SPIERS-software package. Studied rhodoliths reflect complex encrustation successions of different biota resulting in varying surface morphologies and encrustation patterns

al. 2007; Leal et al. 2012). These constructional patterns are increased by accessory organisms, such as serpulids, encrusting foraminifera, and bryozoans.

Destructive patterns, in contrast, result as a consequence of bioerosion and embedment in small cavities with sharp contacts to the substrate, forming connections between the isolated pore space and the ambient seawater affecting cementation and mineralization patterns (Bromley 1970; Alexandersson 1977; Tapanila 2008a). Mineralization processes of the cell walls and infillings were described by Alexandersson (1974, 1977), Borowitzka (1977) and Basso (2012). The cell walls of the coralline algal thalli are completely calcified. These cells consist of a "primary layer" of elongate Mg-calcite parallel to the cell wall, following the cell matrix, and a "secondary layer" of elongate Mg-calcite perpendicular to the cell wall, resulting in a double-walled construction of two adjacent cells (Bosence 1991). In the pseudoparenchymatous coralline thallus, vegetative cell filaments and conceptacles, which are covered concurrently by layers of growing tissue, can, but not necessarily, be filled by Mg-calcite during growth of the algae; aragonite cements can also be produced, but is considered minor in occurrence (Alexandersson 1974, 1977; Basso 2012). Coralline algal mineralization has been shown to be strongly affected by ambient water chemistry especially with respect to ocean acidification and Mg/Ca ratios of seawater (Ries 2006, 2011; Kuffner et al. 2007; Basso 2012; Ragazzola et al. 2012; Kamenos et al. 2013).

A schematic void classification of the rhodoliths of Giglio Island is summarized in Figure 8. It should be noted that void classification is strongly scale-dependent. Thus, constructional voids can be reduced to

FIG. 7.—Example for Micro-CT analysis: rhodolith specimen GP 07 together with corresponding CT-scans in XY-section, steps 70–770 (A–K). Mean porosity 5 19.2 % A) Step 70, porosity 5 10.5 %. B) Step 140, porosity 5 10.3 %. C) Step 210, porosity 5 8.6 %. D) Step 280, porosity 5 59.6 %. E) Step 350, porosity 5 13.7 %. F) Step 420, porosity 5 18.0 %. G) Step 490, porosity 5 14.3 %. H) Step 560, porosity 5 27.8 %. I) Step 630, porosity 5 20.8 %. J) Step 700, porosity 5 23.9 %. K) Step 770, porosity 5 4.2 %.

cellular and reproductive features, such as cementation of conceptacles and spore compartments, irregular growth of coralline thalli, and hollow skeletal remains. In contrast, destructional patterns result as a conse-quence of different scales of bioerosion as well as decomposition of soft material. They can be compared to the few further studies on void presence especially bioerosion in other rhodoliths (see below).

The lowest hierarchy of voids are those found within coralline algal cells, which typically range from 10 to 70 mm in height and length as measured in both Recent and fossil (as measured from figures in Woelkerling 1988 and Bassi and Nebelsick 2000) coralline algae. Exceptional cell lengths of 160 mm can be reached for example of sinuous primigenous cells of Tenarea tortuosa (Woelkerling 1988). These measurements obviously depend on the section (transverse or oblique) as well as in the position of the thallus. Conceptacles are larger than cells of the vegetative thalli with uniporate and multiporate compartments typically ranging between 100 and 800 mm in diameter; single sporangial compartments of Sporolithon range in height from 80 to 200 mm again as measured in both Recent (Woelkerling 1988) and fossil (Bassi and Nebelsick 2000) coralline algae. Some conceptacles and sporangial cavities (e.g., Aguirre et al. 2007) can also be smaller in size. It is important to note that buried cells and conceptacles within the algal thallus undergo during outward surface growth of the rhodoliths an early calcification and thus are infilled by micron-sized Mg-calcite (Alexan-dersson 1974; Bosence 1991).

The formation of constructional voids within the rhodoliths is highly dependent on the type of coralline algal growth-forms (Woelkerling et al. 1993; Nebelsick and Bassi 2000). Thus rhodoliths with tightly encrusting growth-forms will not lead to voids, while the presence of protuberances especially that of the "lumpy" types will be highly conducive to void formation. Rhodoliths can also change growth-form modes during growth (e.g., Bassi and Nebelsick 2010; Checconi et al. 2010) thus lumpy protuberances can be capped by highly encrusting forms. The investigated rhodoliths show encrusting, lumpy, and fruticose growth-forms. Larger voids can be filled by further encrusting organisms especially by serpulids in the studied material (Figs. 6, 7).

Fig. 8.—Schematic diagram of different porosity types including both constructional (CV) and destructional voids (DV) found within rhodoliths at different scales. Scale bars are approximate. A) High resolution section through a coralline algal thallus with vegetative cell filaments (CV1A) and a uniporate conceptacle (CV1B). B) Longitudinal section through a Sporolithon thallus with compartments grouped in sori (CV1B) and destructional voids (DV1A) consisting of bioerosion expressed as small tubes (Trypanites). The vegetative cell filaments of the coralline algal pseudoparenchymatous thallus are indicated within the rectangle at upper left. C) Random section through an outer rhodolith surface showing constructional voids consisting of coralline algal conceptacles (CV1B), hollow serpulid tubes (CV1C) as well as constructional voids created by intra-growth-forms (CV2). Destructional voids are present as small holes (DV1A) as well as larger smooth boreholes derived from bivalve bioerosion (Gastrochaenolites, DV1B). D) Complete rhodolith showing constructional voids built by serpulid tubes (CV1C) and intra-growth-forms (CV2) as well as destructional voids created by bivalve bioerosion (DV1B) and by the dissolution or decomposition of the rhodolith core (DV2).

flask-shaped borings with narrow apertures leading to a wider chamber in the substrate, are referred to the bivalve taxa Lithophaga sp. and Gastrochaena sp. (e.g., Kelly and Bromley 1984; Checconi and Monaco 2008; Bassi et al. 2013). Trypanites is a long cylindrical trace produced by polychaetes (Bromley 1994). Middle Miocene rhodoliths from Southern Apennines showed a dominance of Entobia and Gastrochaenolites (Checconi and Monaco 2008; Checconi et al. 2010). Entobia, defined as partly interconnected, sub-rounded to rounded chambers, formed by clionid sponges (Bromley and D'Alessandro 1989; Silvestri et al. 2011), was not recognized in the Giglio Island rhodoliths. Bioerosion traces of surface grazers such as that of sea urchins (compare Sartoretto and Francour 1997) were also not found.

In present-day macroids from Kikai-Jima, Central Ryukyu Islands, Bassi et al. (2012) found that the Entobia–Gastrochaenolites–Trypanites–Maeandropolydora (EGTM) ichnocoenosis occurs in low sedimentation rates and occasional movement due to current action. In Fraser Island (eastern Australia), the 'shallow' water ichnocoenosis (at 60 m and shallower) is dominated by Entobia, Gastrochaenolites, Trypanites and Trypanites/Maeandropolydora network. The 'deep' water ichnocoenosis (from 68 to 117 m water depths) is characterized by Trypanites and the Trypanites/Maeandropolydora network (TM). Rare Entobia and Gastro-chaenolites (EG) are locally present (Bassi et al. 2013). In general, the decrease in ichnodiversity from the EGTM ichnocoenosis to the TM ichnocoenosis corresponds to a decrease in nodule size and coralline thallus thickness with water depth. The occurrence of a low diversified ichnocoenosis (GT) along with the Giglio Island rhodolith growth characteristics confirms the ecological relationship between ichnocoenosis diversity and the coralline algal thallus thickness.

CONCLUSIONS

1. The taxonomic red algal assemblage of the rhodoliths from Giglio Island is characterized by eight species belonging to Lithophylloi-deae, Mastophoroideae, Melobesioideae, and Sporolithoideae as well as one peyssonneliacean species. Rhodoliths shapes show spheroidal to sub-spheroidal forms and are consistent in size and shape with infrequently (seasonally) turned rhodoliths on mobile substrates in 35 m water depth.
2. The rhodoliths consist of a complex succession of encrusting organisms predominantly coralline algae with subordinated serpulids and bryozoans. Coralline algae are dominated by encrusting, lumpy, and fruticose growth-forms while warty growth-forms are subordinated. Bioerosion rates range from low to moderate.
3. Porosity investigation of slab surface of the rhodoliths are highly affected by cut-effects; micro-CT analysis can be used to avoid these affects as well as follow changes along different axis of the rhodo-liths. Porosity values range from 3 to 41 % in volume.
4. Voids can be subdivided into constructional and destructional voids and can be observed at different scales. Constructional voids are present within the coralline vegetative cell filaments and the reproductive features. Growth-form network can also form constructional voids. Destructional voids in the studied rhodoliths are caused by bioerosion represented by the ichnotaxa Gastro-chaenolites and Trypanites.

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