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## Sediment accumulation in a shallow-water meadow carpeted by a small erect bryozoan

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### Abstract

A marine meadow covered 80–90% by a turf of the erect bryozoan *Cellaria* occurs over an area >10<sup>4</sup> m<sup>2</sup> west of Banjole Island (Croatia) in the northeastern Adriatic Sea. Surrounding areas are bare to patchily covered by isolated clumps of bryozoans, sponges, and ascidians attached to scattered shell and rock debris. Silt and clay comprise >90% of the mass of sediment within the meadow, and *Cellaria* branch fragments are the next-most-abundant component. From 13-cm to at least 25-cm depth in the meadow sediment coralline algal branch fragments are abundant, and silt and clay comprise over 50% of the sediment's mass. In contrast, sediment accumulated in the bare area adjacent to the meadow is predominantly coarse carbonate sand composed of diverse skeletal grains. Mud comprises <50% of the mass of this sediment. Concentration of mud in the sediment below the meadow apparently is due primarily to baffling by the erect bryozoans and earlier by the coralline algae, because composition and texture of the muds and fine sand are identical within and outside the meadow. The proportion of bryozoan skeletal fragments to mud in the upper sediment is similar to that of erect delicate bryozoans to sediment in shallow ramp buildups of Late Ordovician age in the southern Appalachians and of fenestrate bryozoans to mud plus cement in bryozoan-rich cores of Carboniferous mounds. The Paleozoic mounds also are surrounded by coarser sediment. By analogy with the *Cellaria* meadow, trapping and deposition of muds by erect bryozoans can be inferred for many of these Paleozoic mounds, even though bryozoans are a relatively small proportion of the total sediment. © 2001 Elsevier Science B.V. All rights reserved.

**Keywords:** Bryozoa; Mudmounds; Baffling; Adriatic; *Cellaria*; Cool-water carbonate

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### 1. Introduction

In an attempt to understand the effect on sediment accumulation of a local marine ‘meadow’ of erect bryozoans in the northeastern Adriatic Sea, we have

studied the biota of the meadow and the composition and texture of sediment within the meadow and in an adjacent area. This previously unstudied depositional environment potentially gives insight into processes involved in the formation of some ancient mud-dominated buildups in which erect bryozoans are the dominant skeletal element.

The Adriatic is an oligotrophic, nearly landlocked sea that communicates with the Mediterranean through the 72-km-wide, 740-m-deep Strait of

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Otranto. In contrast with the 1233-m-deep basin of the southern Adriatic, the northern third of the sea constitutes an epeiric sea averaging 30 m and nowhere exceeding 70-m depth (Buljan and Zore-Armanda, 1976). The northern Adriatic was flooded by seawater only during the past few thousand years, with maximum ingression reached 5000 years BP (Trincardi et al., 1994; Correggiari et al., 1996).

The mouth of the Po River, located on the far northwest coast, is the primary source of terrigenous sediment entering the northern Adriatic and is the largest single source of sediment entering the entire Adriatic. Sediment from the Po is distributed south along the Italian coast by the counterclockwise current system of the northern Adriatic (Buljan and Zore-Armanda, 1976; Trincardi et al., 1994). A weakly developed easterly flowing current may reach the Istrian coast from the Po River during late summer (Brana and Krajcar, 1995), and a narrow zone of fine terrigenous sediment extends eastward from the Po to about the middle of the northern

Adriatic (e.g., Puškarić et al., 1990). Only a trivial amount of terrigenous debris is derived from the karstic northeastern coast of the Adriatic, where Cretaceous through Neogene carbonates constitute the coast line and only a few small surface streams flow into the sea. In contrast with the western coast of the northern Adriatic, the middle and eastern portions are regions in which little or no sediment accumulates and where most sediment in the water column is re-suspended material (Paul, 1970; Meischner, 1973; Stefanon, 1984; Trincardi et al., 1994; Correggiari et al., 1996).

Yet, some local areas in the northeastern Adriatic do accumulate sediment, either ephemerally or for longer periods. We first describe a local, shallow-water meadow formed by dense, at least decades-long growth of small, erect bryozoans in the genus *Cellaria*. We then describe the texture and composition of the sediment accumulating within the meadow and in nearby areas outside the meadow. Finally, we explore some implications of the meadow and sediment

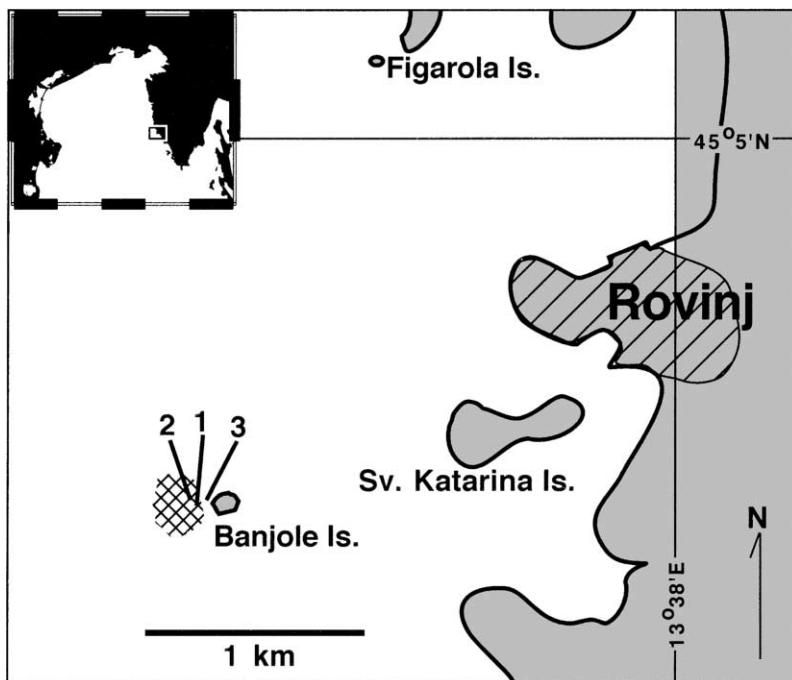


Fig. 1. Map of the Adriatic coast in the vicinity of Rovinj, Croatia, with the geographic position of the map indicated by the boxed area in the inset map of the northern Adriatic. The *Cellaria* meadow (cross-hatched pattern) is located immediately west of Banjole Island. Sample locations within the *Cellaria* meadow are indicated by numbers 1 and 2, and the location of the barren area sample is marked by the number 3.

within it for growth of some bryozoan-rich carbonate mounds found in the rock record worldwide.

The *Cellaria* meadow of this study covers an area greater than 100 × 100 m, where the water is 35 m deep, west of Banjole Island (45°04.4'N, 13°36.6'E), approximately 1.5 km offshore from Rovinj, Croatia (Fig. 1). The meadow is located on a sediment-floored plain and is separated from the rocky base of Banjole by a 7-m-wide belt of sediment that lacks sedentary epifauna and that has a sharply defined border with the meadow. Here the border is slightly sinuous but occupies a zone less than 0.5 m wide over which there is a transition on the sea floor from 'clean' shell debris in the barren area, completely lacking attached epifauna, to mud and an essential cover of *Cellaria* with diverse other attached epifauna. Although there has been extensive diving by the scientific staff of the Center for Marine Research-Rovinj, this apparently is the only known case of such sudden change in the sedimentary and biotic constituents on the sedimentary surface of the Adriatic Sea floor along the Istrian Peninsula. The meadow is surrounded along the remainder of its less clearly demarcated perimeter by sediment on which are isolated clumps of sedentary epifauna attached to shell debris, as well as mobile epifauna, especially ophiuroids and holothurians (Seneš, 1988, 1989). Temperatures at 29-m depth near Banjole range annually between approximately 7 and 18 °C (Marija, 1959).

*Cellaria* is a genus of the cheilostomate Bryozoa characterized by rigid CaCO<sub>3</sub>-skeletalized branch segments that proliferate at flexible cuticular joints where dichotomous branching occurs. Branch segments are approximately 1 cm in length and 1 mm in diameter. *Cellaria* colonies in the meadow grow to about 10 cm height and in normal conditions cover 80–90% of the meadow surface (McKinney and Jaklin, 2000). Two species of *Cellaria* occur in the meadow: *C. fistulosa* (Linnaeus) and *C. salicornioides* Audouin.

Other erect, rigid bryozoans (*Pentapora fascialis*, *Adeonella pallasii*, *Reteporella septentrionalis*) intergrow with *Cellaria*, and at least 58 metazoan species live as epifauna attached to the *Cellaria* (McKinney and Jaklin, 2000). The stalkless crinoid *Antedon mediterranea* and abundant ophiuroids (*Ophiothrix fragilis*) climb up on the bryozoans, using them as surrogate stalks from which to filter-feed higher in the water column (Fig. 2). The benthic fauna of the northeastern



Fig. 2. (A) Typical view of *Cellaria* meadow. Field of view dominated by colonies of *C. fistulosa*, with a conspicuous colony of the bifoliate branched bryozoan *Schizotheca serratimargo* (Hincks) in the left foreground (arrow). Branches of *S. serratimargo* are approximately 4 mm wide. (B) An approximately 12-cm diameter stalkless crinoid, *A. mediterranea* (Lamarck), perched on *Cellaria*.

Adriatic in general is dominated by epifaunal filter-feeders (Gamulin-Brida et al., 1968; Zavodnik, 1971; Gamulin-Brida, 1974; Fedra et al., 1976; Fedra, 1977; Ölscher and Fedra, 1977). However, even relative to this general filter feeder-dominated trophic structure of the regional benthos, mobile epifaunal detritus feeders are remarkably few within the *Cellaria* meadow, and infaunal detritus feeders are virtually absent (McKinney, submitted for publication).

*Cellaria* has a broad depth and geographic distribution, occurring from less than 20 to over 1000 m deep; it commonly occurs as individual arborescent tufts attached by stolons to various hard (skeletal and

rock) and firm organic (hydroid, octacoral, thecate ascidian) substrata (summarised in McKinney and Jaklin, 2000). Dense, patch-like thickets of intergrown *C. sinuosa* (Hassall) and *C. fistulosa* are known at 80-m depth in the English Channel off Roscoff, France (Henrich et al., 1995). These thickets occur on gravel to boulder substrata and are the principal source of nearby storm-generated bryomol sediment dominated by *Cellaria* skeletons. Thus, the habitat is different for the English Channel thickets off Roscoff and the meadow off Banjole Island, the latter of which developed on a fine sediment substratum and in which the skeletal debris accumulated in situ, rather than being swept into banks and dunes.

## 2. Materials and methods

Two push cores 11 cm in diameter and  $\geq 24$  cm in length were taken in the eastern half of the *Cellaria* meadow, one in November 1997 and the other in July 1998. A single push core was taken within the barren area between the meadow and the base of Banjole in July 1998. From each core, a continuous channel strip, approximately 1 cm<sup>2</sup>, was sectioned in  $\sim 1$ -cm-deep increments to produce a continuous series of  $\sim 1$ -cm<sup>3</sup> samples.

The sediment samples were dried, weighed, then placed into a dilute CALGON solution and dispersed by ultrasound or by a combination of ultrasound and boiling. The samples were then wet-sieved through a 65-μm screen, dried, and dry-sieved through a nested set of 355-, 180-, 125-, 90-, and 65-μm screens, and the fraction on each screen weighed. Fines that passed through the 65-μm screen were stirred into 10% HCl solution that was renewed until effervescence ceased. The residue was dried and weighed, and the carbonate fraction of the fines was calculated as equal to the difference in mass between the original sample and the sum of the weighed fractions. Each of the sieved fractions  $\geq 65$  μm at 3–4 cm depth in the November 1997 *Cellaria* meadow core and the July 1998 core from the barren area was examined with a scanning electron microscope (SEM), as were representative chips of dried but unprocessed sediment from the 2–3, 8–9, and 20–21 cm samples of the same two cores.

Three types of sedimentary units were recognized: (1) near-surface *Cellaria*-rich mud from within the

meadow, (2) coralline alga-rich mud lying below the *Cellaria*-rich mud within the meadow, and (3) mollusk-dominated sediment from the barren area. From each of these three units, we identified over 100 grains of each sediment fraction larger than silt from five samples from different depths. The grains were identified as specifically as possible. The mean  $\pm$  1 standard deviation was determined for each kind of grain in each set of five samples. Data on grain types given in the Results are derived from these counts. In addition, the dominant grain type was separated from the >335-μm fractions of five samples within the *Cellaria*-rich mud and also from five samples within the coralline alga-rich mud, and the proportion of the mass of these dominant grains was determined so that this measure could be compared with the numerical dominance of the grains.

## 3. Results

### 3.1. *Cellaria* meadow sediment

Both cores from the meadow had similar grain-size distribution patterns, with medium-dark gray silt-dominated mud constituting well over half the mass from sediment surface to bottom of the cores (Fig. 3). Both cores from the meadow had a change at about 13-cm depth, from dominance of *Cellaria* branches in the coarsest size fraction within the upper part of the cores to dominance of coralline algae in the coarsest size fraction within the lower part of the cores. This section of the paper addresses the upper, *Cellaria*-rich portions of the two cores from the meadow, and the following section addresses the lower portions.

The upper few millimeters of the sediment at the surface had a higher proportion of skeletal debris ( $\sim 25\%$ ) than did the deeper *Cellaria*-rich sediment, which was about 95% mud and 5% coarse sand to granule size skeletal debris. The high proportion of coarse sediment down to 3 cm depth in meadow core #1 was due to the presence of a robust colony of the branched bryozoan *Smittina cervicornis* (Pallas), portions of which were included in each of the top three samples. In both meadow cores, *Cellaria* dominated the coarse skeletal component (Figs. 4B and 5A) down to about 13 cm. The number of *Cellaria* grains

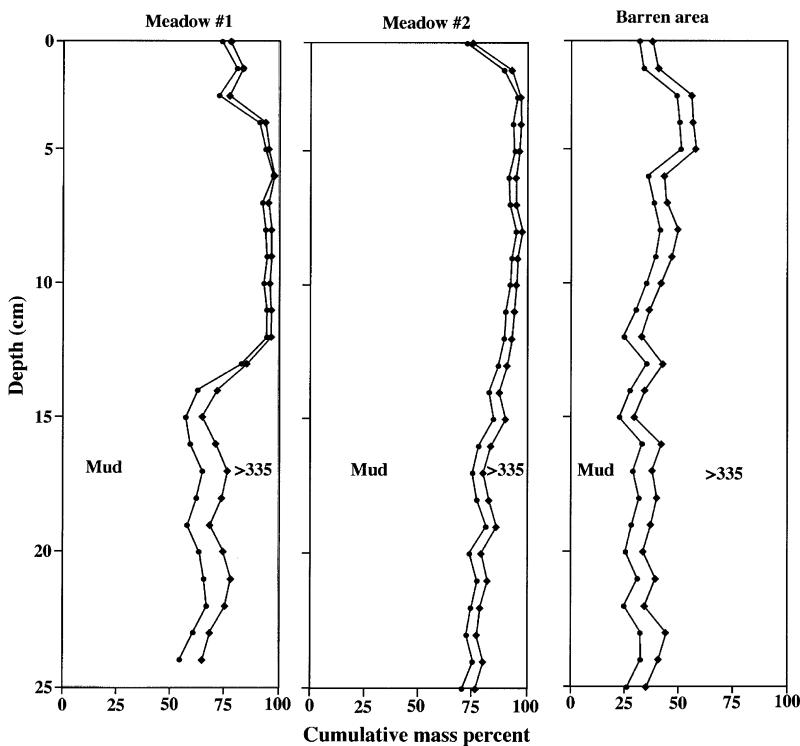


Fig. 3. Plots of particle-size distributions in the three cores. Each plot is divided into three fields; the left portion of the plot is mud ( $<65\text{ }\mu\text{m}$ ), the narrow central strip represents  $65\text{--}335\text{-}\mu\text{m}$  sand, and the right portion represents  $>335\text{-}\mu\text{m}$  sand and granules.

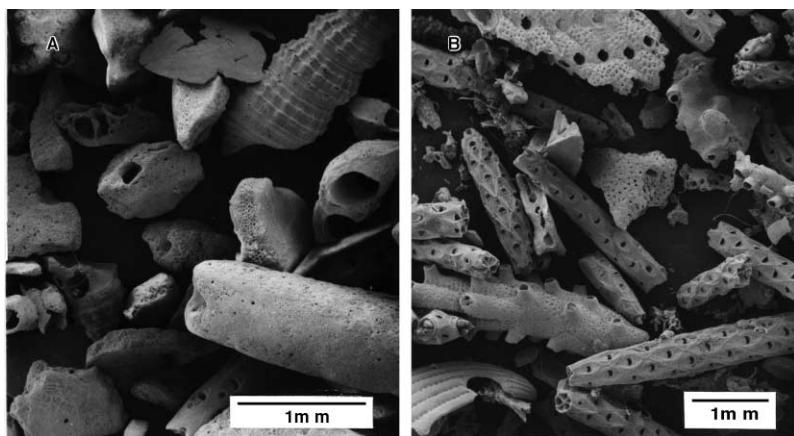


Fig. 4. SEM photographs of coarse sediment ( $>335\text{ }\mu\text{m}$ ) from 3–4 cm depth in the barren area (A), dominated by mollusk shells and shell fragments, and *Cellaria* meadow (B), dominated by branch segments of *C. fistulosa*. This figure and Figs. 6 and 7 consist of paired photographs of progressively finer sediment from the barren area (left) and *Cellaria* meadow (right). Note the dissimilarity of coarse sediment from the two areas and the progressively greater similarity in finer grain sizes.

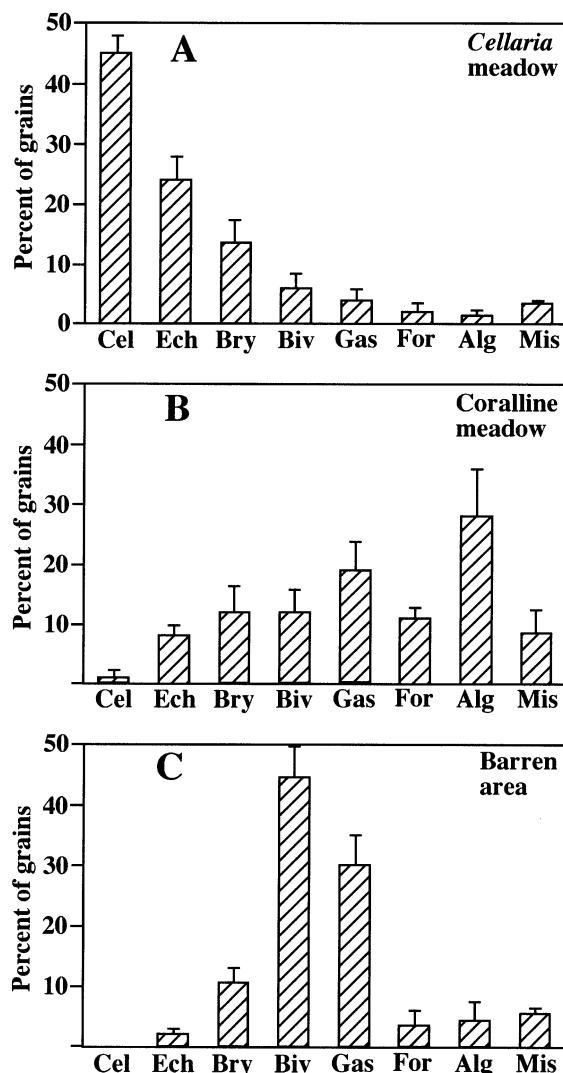


Fig. 5. Bar graphs plotting proportions of grain types in coarse sediment samples for (A) shallow (0–12 cm) and (B) deep ( $\geq 14$  cm) samples from core #1 in the *Cellaria* meadow and (C) samples from the core in the barren area. Each graph represents the average of five samples from haphazardly chosen depths. Alg = coralline algae; Biv = bivalves; Bry = bryozoans (including *Cellaria* for the barren area); Cel = *Cellaria*; Ech = echinoderm plates and spines; For = foraminiferans; Gas = gastropods; Mis = miscellaneous and unidentified grains.

averaged  $45 \pm 3\%$  of the counts of  $>335 \mu\text{m}$  grains, but *Cellaria* constituted a somewhat smaller proportion of the total mass of the  $>335 \mu\text{m}$  grains ( $29 \pm 5\%$ ). *Cellaria* fragments were on average larger than the other  $>335 \mu\text{m}$  grains, and their smaller proportional

mass compared with the number of grains apparently is due to the small proportion of skeleton surrounding the relatively large voids where the tissues and fluids of the living animals were located.

Echinoderm plates and skeletal fragments were the second-most common constituent of the coarse sediment fraction ( $24 \pm 4\%$ ); most were ophiuroid arm plates, with a few echinoid plates and spines. Almost as common were fragments of diverse bryozoans ( $13 \pm 4\%$ ) that were associated with or grew as epibionts on *Cellaria* in the living meadow (e.g., *P. fascialis*, *A. pallasii*, *R. septentrionalis*, *Margareta cereoides*, *Caberea boryi*, *Entalophoroecia gracilis*, *Plagioecia patina*). Generally small bivalve (6%) and gastropod (4%) skeletons were the next most abundant, and foraminiferan, coralline, arthropod, and other miscellaneous grains constituted the remaining 8%.

The 180–335- and 125–180- $\mu\text{m}$  sediment fractions were dominated by echinoderms ( $56 \pm 6\%$  for 180–335  $\mu\text{m}$  size;  $43 \pm 6\%$  for 125–180  $\mu\text{m}$  size) (Fig. 6). Echinoderm skeletal elements constitute  $19 \pm 4\%$  of the 90–125  $\mu\text{m}$  and  $13 \pm 4\%$  of the 65–90  $\mu\text{m}$  fraction; they are the most common identifiable grains in these size fractions (Fig. 7). Essentially all echinoderm grains in the 65–335- $\mu\text{m}$  size fraction were ophiuroid arm plates and short spines; a few in the 65–125- $\mu\text{m}$  size fraction were holothurian spicules.

The proportion of unidentifiable grains abruptly increased below 125  $\mu\text{m}$ , with only 3% of the 125–180- $\mu\text{m}$  grains being unidentifiable or miscellaneous (predominantly ostracodes and malacostracan skeletal fragments), and  $73 \pm 3\%$  unidentifiable in the 90–125- $\mu\text{m}$  fraction. Presumably, most of the unidentifiable grains were finely broken bryozoan and mollusk fragments.

Siliceous sponge spicules became an important part of the smaller size fractions. From the 180–335-, 125–180-, 90–125- and 65–90- $\mu\text{m}$  fractions, they constituted 3%, 6%, 4%, and 8%, respectively. Approximately half the spicules in all but the 65–90- $\mu\text{m}$  fraction were sterrasters of the demosponge *Geodia cydonium* (Jameson) (Fig. 8). *G. cydonium* sterrasters constituted 85% of the spicules in the 65–90- $\mu\text{m}$  fraction.

The mud accumulated below the *Cellaria* meadow is predominantly silt, which was estimated to be at least 80% of the mass of the mud. This was a visual estimate, based on volume of the mud that settled

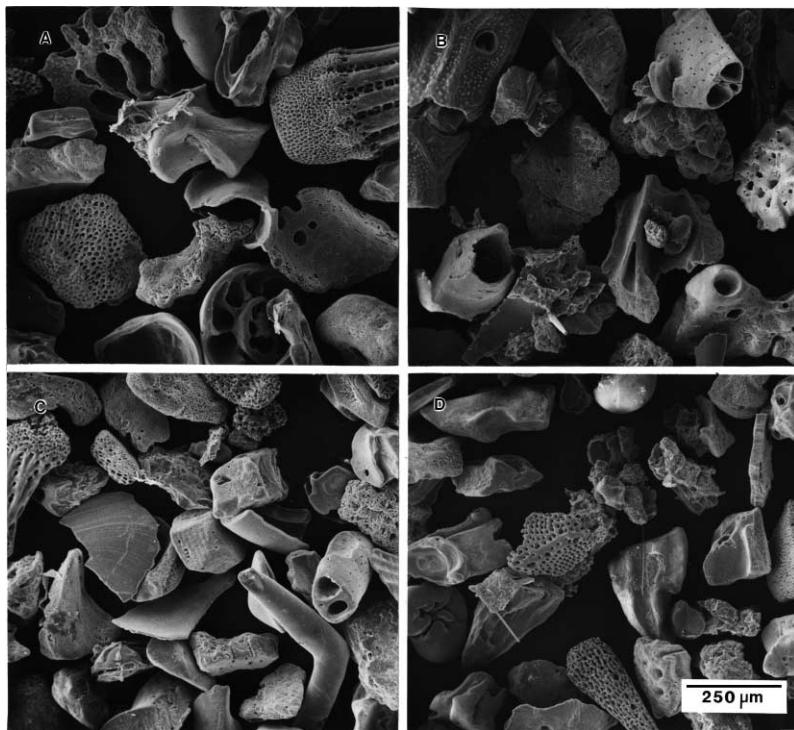


Fig. 6. SEM photographs of 180–335- $\mu\text{m}$  (top row) and 125–180- $\mu\text{m}$  (bottom row) fractions from 3–4-cm depth in the barren area (A, C) and the *Cellaria* meadow (B,D). All photographs are at same scale as D.

within 2 min following vigorous agitation and that remained after suspended clays had been decanted several times. Slightly over 50% of the mud was insoluble in HCl (Fig. 9). SEM examination of the silt portion of the mud indicated that it is almost entirely finely broken skeletal material, similar to the coarser fractions. The insoluble portion is predominantly broken ray segments of sponge megascleres, with a smaller proportion of entire microscleres.

### 3.2. Algal precursor of the *Cellaria* meadow

At about 13-cm depth in the meadow cores, *Cellaria* is abruptly replaced as the dominant coarse skeletal element by the branched coralline alga *Lithophyllum racemus* (Lamarck) (Fig. 5B), which constituted roughly 30% of the sediment in the bottom half of the core (proportion of grains:  $28 \pm 8\%$ ; proportion of mass:  $31 \pm 16\%$ ). Like the *Cellaria* higher in the core, *L. racemus* is within a matrix dominated by silt and clay. In one meadow core, the transition from *Cellaria* to *L. racemus* occurred abruptly

between 12- and 13 cm-depth, and few *Cellaria* were seen deeper than the transition (Fig. 3). In the other meadow core, the transition from *Cellaria* to *L. racemus* occurred more gradually between 13 and 15 cm, and *Cellaria* was found along with the abundant *L. racemus* throughout the lower half of the core.

Gastropods ( $19 \pm 5\%$ ) and bivalves ( $12 \pm 4\%$ ) were much more common in the coralline alga-dominated parts of the meadow cores than in the overlying *Cellaria*-dominated sediment (Fig. 5). The prevalent mollusks in these parts of the cores were microgastropods, many of which presumably grazed on the algae.

Finer sediment fractions in the coralline-dominated portions resembled the finer fractions in the overlying *Cellaria*-dominated sediment. However, mud in the *L. racemus*-rich portions of the cores is slightly lighter-coloured than in the top 13 cm.

### 3.3. Sediment of the barren area

The core from the barren area contained less than 50% mud throughout, and well over 50% of the

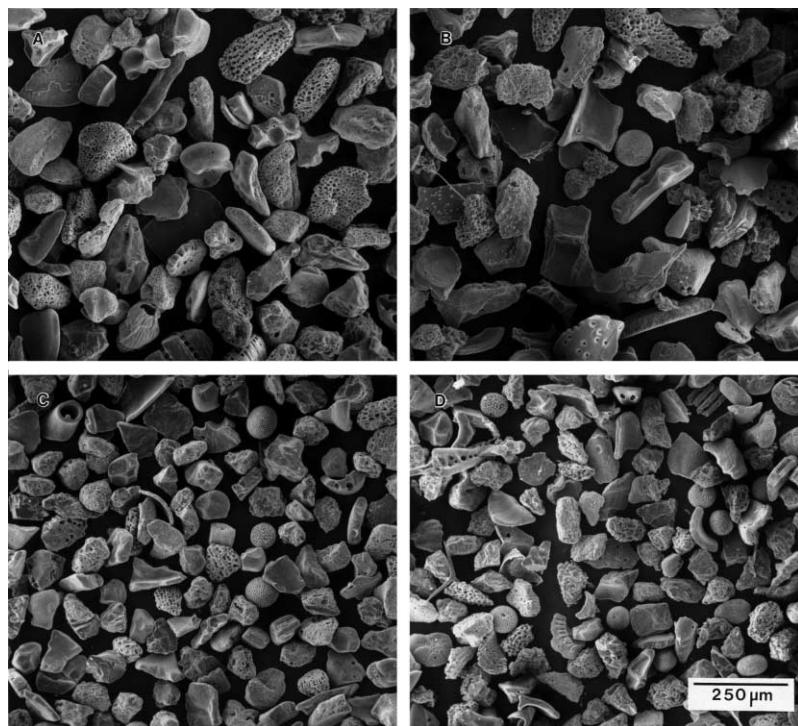


Fig. 7. SEM photographs of 90–125- $\mu\text{m}$  (top row) and 65–90- $\mu\text{m}$  (bottom row) fractions from 3–4-cm depth in the barren area (A, C) and the *Cellaria* meadow (B, D). All photographs are at same scale as D.

sediment consisted of >355  $\mu\text{m}$  carbonate skeletal grains in all but three of the 1- $\text{cm}^3$  samples (Fig. 3). The coarse skeletal grains were overwhelmingly dominated by mollusk fragments (Fig. 4), most of which were broken or complete bivalves ( $44 \pm 6\%$ ) followed closely by gastropod shells and shell fragments ( $30 \pm 5\%$ ) (Fig. 5C).

Various bryozoan fragments among the >335- $\mu\text{m}$  grains were relatively common, though few were *Cellaria*. Echinoderm grains consisted largely of echinoid spines and constituted a very small percentage, along with coralline algae, foraminiferans, and crustaceans.

The majority of 180–335- $\mu\text{m}$  grains were mollusk shell fragments ( $63 \pm 6\%$ ), most of which could not be recognized by us as specifically bivalve or gastropod pieces so were lumped together. Echinoderm skeletal parts were also abundant ( $27 \pm 5\%$ ), and the remaining few percent included foraminiferans, bits of coralline algae, ostracodes, and unidentifiable grains. The 125–180- and 90–125- $\mu\text{m}$  fractions also were dominated by apparent mollusk fragments ( $68 \pm 5\%$  and  $79 \pm 4\%$ , respectively) and echinoderm skeletal parts ( $20 \pm 3\%$ ,

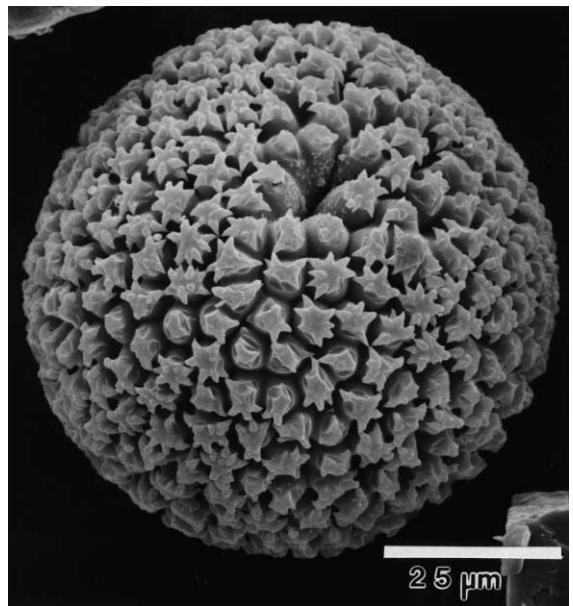


Fig. 8. SEM photograph of a sterraster spicule of *G. cydonium* (Jameson).

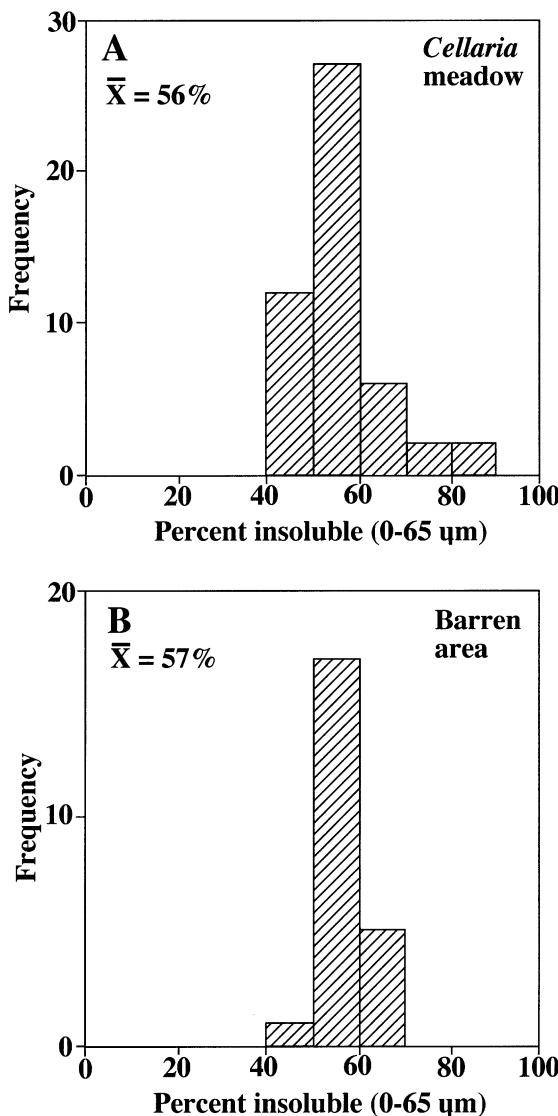


Fig. 9. Insoluble proportion of mud (A) in the two meadow cores ( $N=49$ ) and (B) in the barren area ( $N=25$ ).

$16 \pm 3\%$ ). Most grains in the 65–90- $\mu\text{m}$  fraction may also have been derived largely from mollusks but could not be identified with confidence ( $79 \pm 2\%$ ), and echinoderms were the most abundant of the identifiable grains ( $15 \pm 3\%$ ).

As for the sediment in the *Cellaria* meadow, siliceous sponge spicules became an important part of the smaller size fractions. From the 125–180-, 90–125- and 65–90- $\mu\text{m}$  fractions they constituted 3%, 1%, and

4%, respectively. Also as in the *Cellaria* meadow, approximately half the spicules in each of these size fractions were sterrasters of the demosponge *G. cydonium*, except for the 65–90- $\mu\text{m}$  fraction in which *G. cydonium* sterrasters constituted over 90% of the spicules.

The mud fraction from the barren area is similar in composition to that of the *Cellaria* meadow, although it composes a smaller percentage of the sediment than in the meadow.

#### 4. Discussion

##### 4.1. Comparison of sediment within *Cellaria* meadow and barren area

Coarse skeletal components of the sediment accumulating in the *Cellaria* meadow are very different from those accumulating in the adjacent barren area. The preponderance of *Cellaria* branch segments in the meadow sediment, followed by abundant ophiuroid arm plates and common fragments of diverse bryozoans, is consistent with the community composition of the meadow. Diverse bryozoans are the most abundant megascopic epibionts that encrust the *Cellaria* in the meadow (McKinney and Jaklin, 2000), and the ophiuroids *O. fragilis* (Abild.) are common inhabitants of the *Cellaria* meadow. The skeletons of ophiuroids consist of several thousand to over 10,000 individual calcitic plates (Dobson, personal communication), most of which are small spines, covering plates and vertebrae of the arms (all of which were common in one or more of the coarser sediment fractions of the meadow).

The fauna around Banjole has been monitored for decades, and no *G. cydonium* have been recorded there. Consequently, the occurrence of abundant sterrasters of *G. cydonium* attests to an external source of much of the fine sediment in both the *Cellaria* meadow and the adjacent barren area. The sponge is common southwest of Sv Ivan island, which is about 3 km south of Banjole, and also northwest of Figarola, which is about 2 km north of Banjole (Center for Marine Research-Rovinj, unpublished data). The spicules must have migrated to Banjole from either the north or the south during intermittent periods of suspension during tidal flow, and perhaps during storms.

The *G. cydonium* sterrasters constitute approximately equal proportions of the 65–90- $\mu\text{m}$  fraction in the meadow and in the barren area (Mann–Whitney *U*-test,  $p=0.120$ ,  $N=6+5$ ). This similarity in proportion of *G. cydonium* sterrasters further supports a largely exogenous source for the fine sediment fraction.

Mud in the meadow cores and in the core from the barren area cannot be distinguished on the basis of percent insolubles (Fig. 9) (Mann–Whitney *U*-test,  $p=0.059$ ,  $N=49+23$ ). Mean insoluble percent is virtually identical (56% in the meadow, 57% in the barren area). The similarity in insoluble portion of the muds suggests a similar sediment source or range of sources, plus a mechanism for homogenizing the fines from whatever source(s) they are derived.

In summary, the sediment that has accumulated in the *Cellaria* meadow differs most profoundly from that of the barren area in the coarser fractions. The coarse fractions in the meadow are conspicuously endogenous, reflecting the skeletalized inhabitants of the meadow with great fidelity. Coarse grains in the barren area are made of durable skeletal parts (dominantly molluscan), most or all of which were transported an unknown distance from nearby, non-*Cellaria* meadow communities. Progressively finer size fractions show greater and greater similarity between meadow and barren areas, with the 65–90- $\mu\text{m}$  and mud fractions lacking any conspicuous discriminating attributes between the two environments.

#### 4.2. Enhanced accumulation of fine sediment by *Cellaria*

During maximum tidal flow, and during major storms, fine sediment is resuspended into the lower 1–2 m of the water column across the 30–35-m-deep sedimentary floor in the vicinity of Banjole. During the low flow velocities at and near the slack intervals between maximum flood and ebb flow, the water column clears as sediment settles back to the sea floor (Jaklin, personal observation).

The dense mat of *Cellaria*, which is characterized by dendroid growth, projects almost 10 cm above the sediment–water interface. As is the case with any objects projecting into moving fluid, the finely textured obstruction formed by *Cellaria* generates a zone of decreased ambient flow, which likely diminishes to zero within the upper half of the mat. This is indicated

by local regions of reducing conditions where organic matter has turned black in the lower half of the mat, despite the gentle flow that is maintained by the cilia-driven feeding currents of the bryozoans.

Where moving fluid carries sediment, either as bed load or—as in this case—in suspension, the sediment settles where it is transported into a zone of reduced flow. In the marine environment, this enhanced sedimentation of fine particles and their stabilization in situ has been most extensively studied in marine grass beds (e.g., Ward et al., 1984; Fonseca and Fisher, 1986; Fonseca, 1989; Terrados and Duarte, 2000).

Although no in situ measurements or experiments were conducted on rates of sedimentation, we infer that there is enhanced rate of settling, accumulation and relatively long-term stabilization of suspended sediment within the *Cellaria* meadow compared with surrounding areas. Several lines of evidence support this inference. First is the well-documented enhancement of fine particle sedimentation in seagrass beds (cited above), which are analogous with the *Cellaria* meadow in consisting of erect, flexible elements projecting upwardly into the water column. The second is the fact that the density of skeletalized organisms covering the sea floor is at least an order of magnitude higher within the *Cellaria* meadow than in the surrounding regions, yet mud constitutes approximately 95% of the sediment accumulating in the meadow. In contrast, in the more barren adjacent area, skeletal elements dominate in the sediment. This indicates that mud-sized particles are preferentially accumulating within the meadow, although the primary sediment production within the meadow is that of coarser skeletal grains. Third, the skeletal elements accumulating in the *Cellaria* meadow are largely unbroken, whereas the skeletal elements accumulating in the adjacent barren area are almost all broken. Therefore, grain movement, including bedload, is common in the barren area and uncommon in the meadow sediment. Finally, exogenous *G. cydonium* sterrasters constitute similar proportions of the finest sand fraction in both the meadow and in the barren area, suggesting active transport of fine-grained suspended sediment into the general area.

A similar though less extreme difference apparently prevailed during growth of the algal thicket that was a precursor to the *Cellaria* meadow. Mud primarily accumulated here too, in contrast with the

adjacent barren area, although the dendroid *L. racemus*, with local patches of *Cellaria*, was the primary in situ sediment producer.

Severe ultrasound disaggregation in CALGON was necessary to break up cohesive mud aggregates, especially in the sediment from the *Cellaria* meadow. Unfortunately, this treatment destroyed faecal pellets, which were conspicuous in the dried, untreated sediment when examined with the SEM (Fig. 10). Based on qualitative examination of the untreated sediment, a substantial but unknown portion of silt and clay was deposited as faecal pellets rather than as individual grains. The pellets were about 30 µm in diameter and roughly 55 µm in length. These pellets are slightly shorter and are equal in diameter to the smallest cheilostome bryozoan pellets previously documented (Winston, 1977; Best and Thorpe, 1987; McKinney et al., 1987) and slightly larger than the only documented cyclostome bryozoan pellets (Winston, 1977). We presume that most of the

pellets were produced by *Cellaria*, which had by far the greatest feeding surface area among the suspension feeders in the meadow. Such pellets, composed of particles as small as 1 µm bound in a matrix of mucous, have higher settling velocities and are more difficult to resuspend than would be their individual components (e.g., Haven and Morales-Alama, 1972; Tagnorn et al., 1984).

The somewhat higher proportion of the mass of coarse skeletal elements in the sediment of the coralline precursor relative to that in the sediment presently accumulating in the *Cellaria* meadow (Fig. 3) is in part due to the greater density of *L. racemus* relative to *Cellaria* branches. The latter have a low specific gravity because of the high volumetric proportion of living chambers to skeleton, whereas *L. racemus* does not have such large void spaces except for the occasional conceptacles. However, even if the coralline meadow had the same density of cover and depth of growth as presently exists in the *Cellaria* meadow, the

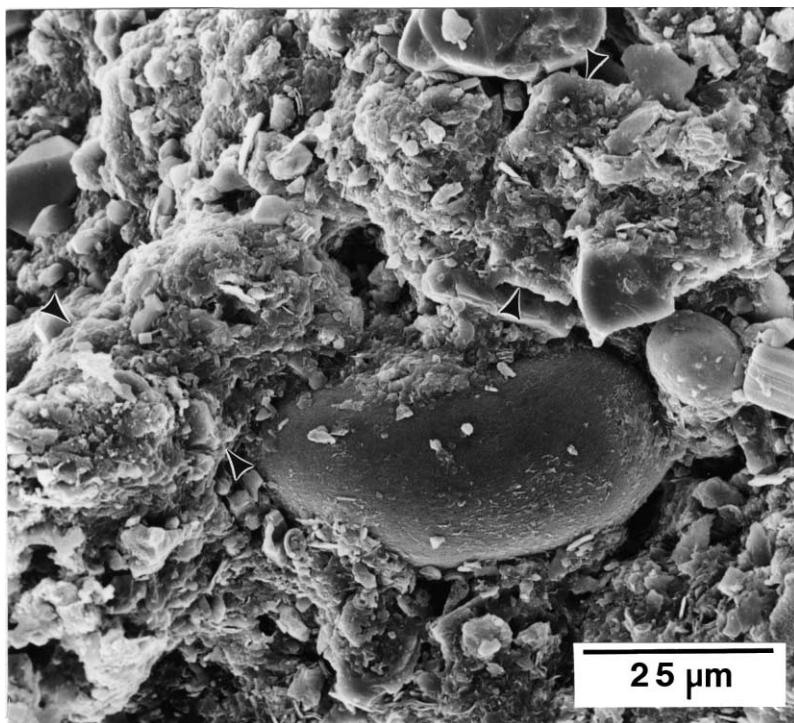


Fig. 10. SEM photograph of unprocessed *Cellaria* meadow sediment from 8–9-cm depth, showing faecal pellets (between paired arrows) likely produced by *Cellaria*.

*Cellaria* meadow likely—in similar flow and suspended sediment density—has accumulated sediment at a slightly more rapid rate. The self-generated feeding currents of erect bryozoans have the potential to draw into the baffled zone water that otherwise would pass over without being diverted. This delivers more sediment onto the sea floor than would be delivered by the baffling effect alone, as has been experimentally demonstrated for the erect flexible bryozoan *Bugula* (McKinney et al., 1987).

#### 4.3. Paleozoic bryozoan-containing mud mounds

Mudstone to wackestone buildups, in which bryozoans are the dominant or co-dominant skeletal elements, developed during the Middle Ordovician and from the Lower Carboniferous into the Permian (reviews in Monty et al., 1995; Wood, 1999). Modern analogues for these mounds are generally unknown. Sediment-drowned Quaternary bryozoan-dominated mud mounds have recently been discovered on the upper continental slope of the Great Australian Bight (James et al., 2000), but apparently growth of the mounds corresponds with lowstands and was shut off about 26,000 years ago. The sediment of the Australian Quaternary mounds shares several features with sediments in the northern Adriatic meadow, most especially dominance by mud matrix that is rich in delicate erect bryozoans, including branch segments of bushy articulated colonies. As in the Adriatic meadow, faecal pellets, sponge spicules, and foraminiferans are abundant in the mud of the Australian mounds.

Lithification of the sediment accumulating in the *Cellaria* meadow would generate a calcareous mudstone, whereas lithification of the sediment of the adjoining barren area would generate a skeletal packstone, following the classification of Dunham (1962). In some facies of Late Paleozoic deep water-originating Waulsortian mud mounds, delicate erect (fenestrate) bryozoans are either the dominant or co-dominant skeletal elements, contained within a much greater volume of clotted and peloidal carbonate mud and void-filling sparry cement (e.g., Lees, 1988; Lees and Miller, 1995; Gutteridge, 1995, and references in these). The mud in these mounds is interpreted as autochthonous, microbially mediated deposits. Deposits in the *Cellaria* meadow contain approxi-

mately the same proportion of bryozoan skeleton to mud as in these Waulsortian facies. However, they are apparently not a good model for the deep bryozoan-bearing facies of Waulsortian mounds because they are shallow water deposits and the mud accumulating in the modern *Cellaria* meadow is primarily allochthonous and bi detrital.

Some shallower-originating Paleozoic mudmounds dominated by bi detrital muds and in which erect bryozoans are the dominant or co-dominant—though still minor—skeletal component may have been initiated and maintained by baffling by dense bryozoan or bryozoan/pelmatozoan thickets. For example, Lower Carboniferous shallow-water mounds in the Mississippi Valley (Ausich and Meyer, 1990; Meyer et al., 1995) and southern Appalachians (Gibson, 1986; Kopaska-Merkel and Haywick, in press) of North America appear to have accumulated because of baffling by fenestrate bryozoans and pelmatozoan echinoderms. Middle Ordovician examples of shallow ramp buildups are well developed in the southeastern United States (Walker and Ferrigno, 1973; Read, 1980). The shallow buildups in southwestern Virginia are predominantly biostromal and have mudstone/wackestone bi detrital cores that are “unbedded, light-gray, and contain variable amounts of ramose and encrusting bryozoan and echinoderm debris and locally abundant spicules” (Read, 1980, p. 1594). Dominant skeletal elements in some of the mudstone/wackestone facies of the shallow ramp buildups are arthrostylid bryozoans, which had articulated, branched colonies that were analogous in structure and branch size to *Cellaria*.

Large skeletal elements constitute a very small proportion of the sediment in many of the core facies of the mud mounds cited above. A similarly small proportion (~5%) of large skeletal elements in the *Cellaria* meadow muds (which if lithified would generate a lime mudstone) suggests that the skeletal elements present in these ancient, overwhelmingly mud-dominated deposits may well have been sufficient to act as baffles to trap and protect the buildup of mud. Many authors have invoked causes (e.g., presence of abundant, additional non-preserved bafflers) for mud buildups other than such volumetrically minor potential baffling organisms preserved in the sediment. Deposits in the *Cellaria* meadow demonstrate that such other causes of baf-

fling are not needed (though not necessarily ruled out).

## 5. Summary and implications

(1) The sediment of the *Cellaria* meadow confirms that organisms other than seagrasses can baffle allochthonous fine sediment, generating a local mud-dominated accumulation surrounded by coarser sediment.

(2) Deriving from item 1, Paleozoic carbonate mud mounds surrounded by coarser-grained or siliciclastic sediment were not ipso facto built up by authochthonous production of carbonate mud.

(3) A relatively small proportion of skeletal elements of potential baffling organisms can accurately represent the organisms that actually caused a buildup to occur (the proportion of the remains of bafflers to mud trapped by them is approximately 1:20 in the *Cellaria* meadow sediment).

(4) In the vicinity of Banjole Island, the area that has the densest growth of sedentary benthic organisms has the smallest proportion of large skeletal elements in the underlying sediment.

(5) Coarse sediment of the *Cellaria* meadow is autochthonous and accurately reflects the skeletalized portion of the resident community, but the fine to very fine sand and mud is largely allochthonous and contains elements (e.g., *Geodium* sterrasters) derived from over 1 km away. Ancient mud accumulations due to baffling organisms may also represent local and regional components in the coarse and fine components, respectively.

(6) Faecal pellets about 35 µm in diameter, apparently generated by *Cellaria*, constitute an undetermined but large proportion of the mud accumulating in the meadow.

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