The Roles of Bryozoans in Modern Coral Reefs

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With 1 figure

Zusammenfassung

Sammlungen an lebenden Korallenriffen in der Nähe Bermudas, Eniwetoks und Eleutheras weisen darauf hin, daß Bryozoen hier häufig und differenziert in den Korallenriffen vorkommen, was bisher in der Literatur wenig beachtet wurde.

In all den hier untersuchten Riffen sind die inkrustierenden Cheilostomen die häufigsten und vielfältigsten Bryozoen. Büschel-ähnliche Cheilostome sowie lichenoporide und idmoneide Cyclostome besitzen häufig einige Bedeutung. Außerdem werden dort ab und zu auch reteporide und aeteide Cheilostome und crisiide Cyclostome gefunden.

Obwohl sie niemals das primäre Riffgerüst bilden, unterstützen die Bryozoen den Aufbau des Riffes erheblich dadurch, daß sie die Unterseite der Korallenstöcke sowie Felsenkanten und -fragmente inkrustieren. Teilweise füllen die Bryozoen auch Hohlräume, die tief im Riff eingelagert sind. Diese Tiere bilden keine bedeutenden Mengen von Karbonatablagerungen; sie können auch kein loses Sediment einfangen und binden. Manche Bryozoen treiben epiplanktonisch in den oberen Wasserschichten in der Umgebung von Riffen. Einige cyclostome Bryozoen sind in geschützten Bereichen zusammen mit Sclerospongien und Brachiopoden vergesellschaftet. Wahrscheinlich lassen sich einmal Beziehungen zwischen der Morphologie der Bryozoen und der Veränderungen im Biotop herstellen.

Die Klärung der Rolle, welche Bryozoen in rezenten Riffen spielen, wird nicht nur das Interesse der Forscher wecken, die die lebenden Riffe und Bryozoen untersuchen, sondern es wird auch den Paläontologen anziehen, der sich mit fossilen Riffen oder der Bryozoen-Evolution befaßt.

Abstract

Contrary to impressions gained from the literature, collecting in the living reefs of Bermuda, Eniwetok, and Eleuthera implies that bryozoans are common and diversified in at least some modern coral reefs.

In all the reefs examined, encrusting cheilostomes are the most abundant and diversified bryozoans. Tuft-like cheilostomes, and lichenoporid and idmoneid cyclostomes, frequently are moderately important. Reteporid and aeteid cheilostomes, and crisiid cyclostomes, are also occasionally encountered.

Never the principal frame-builders, the bryozoans do reinforce the reef mass by encrusting the undersides of coral heads, rock ledges, and rock fragments, and by locally partially filling cavities deep within the reef. These animals do not form significant amounts of loose carbonate sediment, nor do they trap or bind such sediment. A few bryozoans drift epiplanktonically through the surface waters around some reefs. Some cyclostome bryozoans may participate in the cryptic sclerosponge-brachiopod community of modern reefs. Correlation of bryozoan morphologic variations with environmental-factor fluctuations may eventually be possible.

Of interest to students of living reefs and bryozoans, clarification of the roles played by bryozoans in modern reefs will also be valuable for paleontologists studying both fossil reefs and bryozoan evolutionary history.

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Résumé

Contrairement aux impressions données par la littérature, il apparait d'après des collections faites dans les récifs vivants de Bermuda, Eniwetok, et Eleuthera que les bryozoaires s'y présentent souvent et de façons diverses.

Dans tous les récifs examinés, les cheilostomes incrustés sont des bryozoaires se présentant le plus souvent et sous des aspects les plus différents. Les cheilostomes comme des touffes, les cyclostomes lichenoporides et idmoneides sont fréquemment de quelque importance. Par ailleurs les cheilostomes rétéporides et aétéides, et les cyclostomes crisides n'y sont rencontrées qu'occasionnellement.

Bien qu'ils n'aient jamais bâti le cadre du récif, les bryozoaires en renforcent la masse en s'incrustant au-dessous des têtes coralliennes, des bords et fragments de rochers; ils remplissent aussi en partie des cavités profondes du récif. Ces animaux ne forment pas de quantités significatives de carbonate et ils ne peuvent ni capter ni lier des sédiments détachés. Quelques bryozoaires flottent epiplanktoniquement dans les eaux de surface de quelques récifs. Quelques bryozoaires cyclostomes participent à la communauté cryptique des sclérosponges et brachiopodes dans les récifs modernes. Des corrélations entre les variations morphologiques des bryozoaires et les fluctuations environnantes seront éventuellement possibles.

Intéressante pour les chercheurs étudiant les récifs vivants et les bryozoaires, la clarification des rôles joués par les bryozoaires dans les récifs modernes aura aussi de la valeur pour le paléontologue s'occupant de récifs fossiles et d'évolution des bryozoaires.

Краткое содержание

Изучение современных коралловых рифов вблизи **Bermuda**, **Eniwetok** и **Eleuthera** установило, что здесь в коралловых рифах мшанки встречаются чаще и более многообразны, о чем до сих пор в литературе не отмечалось. В симбиозе с кораллами живут самые разнообразные мшанки (кустоподобные **Cheilostoma, Lichenoporida** и **Idmoneida** — **Cyclostomata** —, иногда **Reteporida** и **Aeteida** — **Cheilostomata** —, а также и **Cyclostomata.** Хотя мшанки никогда не образуют рифовых построек, однако, живя в симбиозе с кораллами, они способствующие образования первых. Они заполняют также и полости, образовавшиеся в глубине рифа. Эти организмы не способствуют образованию значительных количеств известковых отложений, т. к. они не удерживают и не связывают осаждающийся материал. Многие мшанки образуют в верхних слоях воды вблизи коралловых рифов эпипланктон. Другие, именно **Cyclostomata,** живут в отдельных защищенных областях в сообществе с **Sclerospongia** и **Brachiopoda.** Вероятно, со временем удасться найти взаимосвязь между морфологией мшанок и изменениями среды. — Выяснение роли мшанок при образовании современных рифов интересно не только для исследователей, изучающих современные рифы и мшанки, но и для палеонтологов, изучающих ископаемые рифы и эти виды организмов.

Introduction

Examination of either the literature concerning reefs or that concerning bryozoans would suggest that bryozoans are not significant components of modern coral reefs. In surprising contrast, however, field work employing SCUBA-diving techniques in several modern reef complexes (CUFFEY, 1971 a, 1971 b) indicates that bryozoans are common, widespread, and diversified in at least some such environments. As a result, some delineation of the roles played by bryozoans in modern reefs is now possible for the first time, although detailed understandings of the exact roles played by particular species must await considerable basic systematic work just being begun. Scientists whose primary interests are either in bryozoans or in reefs will find relevant the information presented herein.

Moreover, although the paleontological literature reports bryozoans as significant contributors to a number of fossil reefs or bioherms, accurate understanding of their role there has been seriously hindered by our ignorance of their role in modern reefs. Consequently, much of benefit to paleoecology can be derived from studying the participation of bryozoans in present-day reefs. Although a potentially valuable complement to this paper, a survey of bryozoans' involvement in fossil reefs is beyond the scope of this summary, but will appear later (CUFFEY, in preparation). Also, because of lack of first-hand experience with them, this paper excludes oyster-reef occurrences, and restricts its attention to bryozoans found in modern coral reefs.

History of Studies of Bryozoans in Modern Reefs

That reef-dwelling bryozoans are seldom mentioned in both the reef- and bryozoan-oriented literature seemingly implies that bryozoans are either absent from living reefs, or at most are only insignificant elements in modern reef communities.

Much of the reef literature, like the excellent summary of atolls by WIENS (1962), fails to even mention bryozoans in present-day reefs. Some, on the other hand, mentions bryozoans briefly and incidentally as occurring in reefs in Bermuda (VERRILL, 1900, 1901; GARRETT, 1969), east Africa (ORTMANN, 1892), Florida (GINSBURG, 1956, p. 2398), Madagascar (VASSEUR, 1964), and Yucatan (KORNICKER, 1962, p. 652).

The bryozoan literature has been largely taxonomically oriented, and only sometimes in very brief occurrence records even hints that bryozoans dwell on modern reefs. Examples of such references concern reefal environments in Florida (SMITT, 1872, 1873; OSBURN, 1914; CANU & BASSLER, 1920, 1923), the Gulf of Mexico (CANU & BASSLER, 1928; LAGAAIJ, 1963), Hawaii (CANU & BASSLER, 1927), and the Philippines (CANU & BASSLER, 1929).

In view of this implicit paucity of bryozoans in living coral reefs, the finding that bryozoans are important in the modern reef complexes of both the Bermuda Platform in the western Atlantic and Eniwetok Atoll in the western Pacific (CUFFEY, 1971 b) came as a personal surprise. In addition to being significant elements at Bermuda and Eniwetok, preliminary examination of reefs along the northern coast of Eleuthera Island in the Bahamas (SCHROEDER, in preparation) indicates that bryozoans are important there also (CUFFEY, 1971 a). Brief personal inspection of several other modern coral reefs — at Looe Key in Florida, Oahu in Hawaii, and Isla Mujeres in Yucatan — suggests similar conclusions for those reefs, as do discussions with scientists working on reefs in Barbados (R. K. MATTHEWS & R. L. STEINEN, 1971, personal communication) and Hawaii (J. D. SOULE & D. F. SOULE, 1970, personal communication). In summary, then, bryozoans seemingly are significant components in at least some modern reef complexes, but so far they have apparently been largely overlooked.

At the present moment, three principal problems hamper progress toward better understanding of modern reef-dwelling bryozoans.

First, little bryozoan material has been collected from reefal environments and made available for study. Reef students have so far tended to concentrate their attention on the more conspicuous corals, algae, mollusks, crustaceans, and fishes, while bryozoan students have not yet become involved with modern reefs. Moreover, Scuba diving is essential for adequate bryozoan collecting in the modern reefs where I have investigated, and this technique has only recently become widely available to marine scientists. Hopefully, increased awareness on the part of both reef and bryozoan workers (in part as a result of this paper) will eventually provide enough collections — and bryozoan students! — to solve this first problem.

Second, identifying bryozoan species collected from modern reefs has proved to be unexpectedly difficult. The potentially pertinent literature is frequently contained in obscure and widely scattered sources. Additionally, the species' descriptions contained therein tend to be very incomplete, particularly with respect to morphologic variability (whether genetically or environmentally induced), and thus are often inadequate for positive identifications. The ecologic distribution of the species described, moreover, usually is only barely mentioned. Available literature concerning the cheilostome bryozoans seems somewhat better than that concerning cyclostomes, but both are seriously deficient at the species level by modern systematic standards.

A third, closely related problem is that many bryozoan higher taxa, especially among cyclostomes, are so poorly conceived at present (Brood, 1968; Hillmer, 1968; Cuffey, in press) that they are essentially unusable. Basic systematic research necessary to correct this situation is now being undertaken, particularly for cyclostome bryozoans (Cuffey & Nye, in preparation), as part of the revision of the bryozoan volume of the *Treatise on Invertebrate Paleontology* (Boardman et al., in preparation). Eventually, a soundly based classification of bryozoans — one which Can serve the usual helpful functions in studying the various reef-dwelling bryozoans — will emerge from these efforts, but our understanding of these interesting animals will be somewhat handicapped until then.

Bryozoan Groups Involved in Modern Reefs

Among the bryozoans which I have collected from the more thoroughly investigated reef complexes (i. e., Bermuda, Eniwetok, and Eleuthera), noticeably different colony growth forms permit distinguishing several major kinds, illustrations of examples of which can be readily seen in Bassler (1953) and Hyman (1959). These kinds among the cyclostomes and some of the cheilostomes also coincide with currently recognized families, while two of the cheilostome kinds (encrusting and tuft-like) each include several families. Eventually, more refined identifications — down to species — will greatly expand our understanding of bryozoan involvement in modern reefs, but such identifications await much future morphologic and taxonomic work.

Bryozoans as a whole are relatively common and diversified in all three reef complexes, especially in the deeper (below 15 to 30 feet) waters examined (Cuffey, 1971 a, 1971 b). All the various kinds of bryozoans are found in the same types of microhabitats, mostly attached to the undersides of coral heads, rock ledges, and rock fragments.

Encrusting cheilostomes, growing as thin sheet-like crusts on the undersides of corals and rocks, are the most abundant kind of bryozoan in all three reef complexes. This colony growth form includes a number of species, some of which fall among the anascan cheilostomes, others among the cribrimorph cheilostomes, and still others among the ascophoran cheilostomes. In Bermuda, but not in Eniwetok and not (so far as yet known) in Eleuthera, one encrusting cheilostome species — *Crassimarginatella crassimarginata* — locally tends to fill intrareefal cavities.

Tuft-like cheilostomes — erect, delicate, and flexible or jointed — are moderately common in the Eleutheran, and rare in the Bermudian and Eniwetokese, reefs examined. Many of these forms are anascan cheilostomes.

Lichenoporid cyclostomes, small disk-shaped colonies, occur moderately commonly and ubiquitously on Bermuda, and also apparently commonly on Eleuthera, but only very rarely (on lagoon pinnacles) on Eniwetok. At least two lichenoporid species occupy the Atlantic reefs, of which one is tentatively thought to be *Lichenopora radiata* (Cuffey, in preparation).

Idmoneid (or diaperoeciid or tubuliporid; Brood, 1968; Hillmer, 1968) cyclostomes are encountered moderately commonly at Eniwetok, particularly in deeper (below 30-feet depths) waters on the leeward ring-reef and the lagoon pinnacles there. Growing as small branching tubes closely adhering to the substrate, these forms are seen only rarely at Bermuda — where they are represented by the species *Idmonea atlantica* (Cuffey & Mertz, in preparation) — and have not yet been seen at Eleuthera.

The very delicate, erect, tuft-like colonies of crisiid cyclostomes (entirely *Crisia eburnea* on Bermuda; Cuffey & Foerster, in preparation), and the very fine, thread-like encrusting networks of aeteid cheilostomes, occur sparsely scattered through all three reef complexes.

Found rarely only at Eniwetok, but not Bermuda nor Eleuthera, are erect perforated sheets belonging to the reteporid ascophoran cheilostomes. These dwell in the same habitats at Eniwetok as do the idmoneids there.

Finally, no entoprocts, ctenostomes, or phylactolaemates were encountered in appropriate environments during my field work in all three reefal areas.

Possible Roles Played by Bryozoans in Modern Reefs

The present preliminary state of our knowledge does contribute significantly to clarifying the role of bryozoans as a whole within modern coral reefs. Of course, final detailed insight into the various roles played by bryozoans there will follow the thorough taxonomic studies necessary to achieve reliable identifications of all the bryozoan species involved in several important modern reef complexes.

As indicated elsewhere (Cuffey, 1970, p. 44—45), we can distinguish several different types of bryozoan involvement in reefs, carbonate banks, and bioherms through geologic time. These include bryozoan gardens, bryozoan-stabilized mud banks, bryozoan-veneered dead reefs, small quiet-water bryozoan-framework bioherms, bryozoans growing deep on fore-reef slopes of major reefs, and bryozoans filling cavities within major reefs. The Bermudian, Eniwetokese, and Eleutheran reefs examined fall into the last two categories. With this in mind,

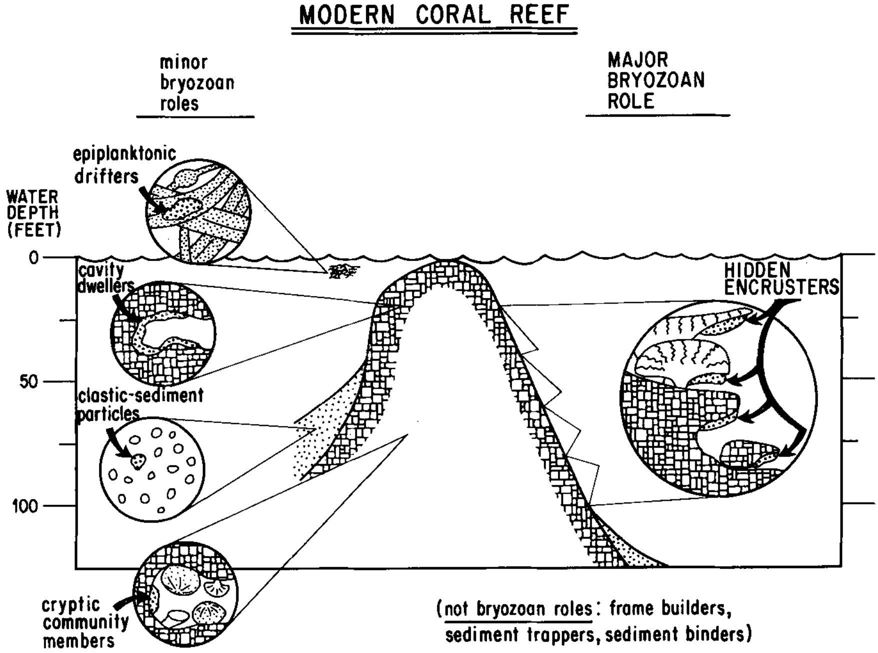

Fig. 1. Roles played by bryozoans in the modern reefs of Bermuda, Eniwetok, and Eleuthera.

we can now consider in more detail the roles played by the bryozoans in these modern reefs (see Fig. 1).

In none of the reef complexes examined do bryozoans function as the principal frame-building organisms. They thus are not direct competitors of the hermatypic corals and calcareous algae in these environments.

Most of the bryozoans found in the reefs investigated encrust the undersides of coral heads, rock ledges, and rock fragments. There, they must compete for attachment space especially with serpulids, sponges, encrusting foraminifers, and some calcareous algae. In this role as "hidden encrusters", both cheilostomes and cyclostomes contribute a small quantity of calcareous skeletal material which may help somewhat reinforce the reef framework.

Closely related to this "hidden-encruster" role of modern reefal bryozoans is their occasional cavity-dwelling role. Sheet-like cheilostome colonies encrust and cover the walls of some of the small cavities located deep within the dark recesses of the reef. Prolonged growth, layer upon layer, of such bryozoans results in at least partial filling of these cavities and thus further reinforcement of the reef mass. Although not encountered at Eniwetok or Eleuthera, some reefs on the Bermuda Platform contain cavity-dwelling bryozoans (GINSBURG, 1968, personal communication; GARRETT, 1969, p. 82—84, 86)· There, although several encrusting cheilostome species participate in this role, preliminary examination indicates that the anascan cheilostome *Crassimarginatella crassimarginata* (BASS-

LER, 1953, p. 163—164; CANU & BASSLER, 1920, p. 131, pl. 24, fig. 13—14) contributes a major share.

Because of the moderate quantity of bryozoan skeletal material found in the modern reefs examined, significant amounts of bryozoan debris might be expected among the clastic carbonates produced by mechanical erosion of the reefs. However, preliminary examination of the loose sediments accumulating around the Bermudian, Eniwetokese, and Eleutheran reefs thus far reveals very little recognizable bryozoan detritus. Consequently, these animals seemingly play only a very minor sediment-forming role in these reefs, thus confirming KORNICKER & BOYD's (1962, p. 652) conclusion for Alacran Reef.

Similarly, the reef-dwelling bryozoans observed do not function in a sediment-trapping role. The colonies seen are relatively low and do not project significantly above their solid substrates, which moreover are usually located in sheltered niches within the reef mass. Consequently, loose sediment washing down from the reef crests is not trapped to a significant degree by the activity of bryozoans. All bryozoan specimens personally examined encrust only solid substrates; none grow out over loose-sediment substrates. The bryozoans thus apparently also play no role in consolidating or binding loose sediment into the lithified reef mass.

Around both the Atlantic reefs examined, surface waters frequently contain drifting brown algae, some of which are encrusted by the epiplanktonic anascan cheilostome *Membranipora tuberculata* (CANU & BASSLER, 1923, p. 22—23, pl. 33, fig. 3—5). A few fragments of this species are consequently encountered among the occasional bryozoan debris in the loose sediments around these reefs.

Some of the cyclostome bryozoans may also play an interesting role in modern reefs as members of the recently recognized cryptic community involving sclerosponges and brachiopods (JACKSON, 1970; GRANT, 1971, p. 1444). The suggestion that the sclerosponges may be closely related to the Paleozoic tabulate "corals" (HARTMAN & GOREAU, 1970) raises the possibility that this association might be a relict community surviving from long-past geologic times. The lichenoporid cyclostomes are particularly intriguing in this respect, since their many morphologic resemblances to the extinct mid-Paleozoic botrylloporid fistuliporoids suggest that lichenoporids might be regarded as "living fossils" (UTGAARD, 1968, p. 1033—1035; CUFFEY, in preparation).

Finally, the range in environmental characteristics found in the three modern reef complexes examined is sufficiently great that some of the morphologic variations — such as in colony growth form — displayed by the bryozoans there may be correlatable with fluctuations in particular environmental factors (like water turbulence). However, our present knowledge of these species is so scant that detailed studies of the morphology, variability, and ecology of several important species — like that done of Bermuda *Crisia eburnea* (CUFFEY & FOERSTER, in preparation) — must be completed before sound conclusions concerning these matters can be made.

Conclusions

In contrast to implications which might be drawn from examination of the reef and bryozoan literature, my personally collecting bryozoans from the living reefs of Bermuda, Eniwetok, and Eleuthera suggests that bryozoans are comparatively common and diversified in at least some modern coral reefs. Problems such as the present paucity of collections, difficulty of identifying bryozoan species, and inadequacy of bryozoan higher taxa hinder our progress toward complete understanding of modern reef-dwelling bryozoans.

Encrusting cheilostomes comprise the most abundant and diversified bryozoan type encountered in all three reef complexes examined. Tuft-like cheilostomes, lichenoporid cyclostomes, and idmoneid cyclostomes are each moderately important in at least one of these reef complexes. Reteporid and aeteid cheilostomes, and crisiid cyclostomes, are occasionally found in at least some of these reefs.

While nowhere functioning as the major frame-builders of modern coral reefs, the bryozoans seen do contribute some calcareous skeletal material reinforcing the reef mass, by encrusting the undersides of coral heads, rock ledges, and rock fragments, and locally also by partially filling some of the cavities deep within the reef. However, the bryozoans do not form significant amounts of loose carbonate sediment, nor do they trap or bind such sediment to any degree. A few bryozoans drift epiplanktonically through the surface waters around some of the reefs studied. Some cyclostomes may participate in the peculiar, cryptic, sclerosponge-brachiopod communities found in modern reefs as possible relict survivals. The morphologic variations exhibited by different bryozoans may eventually be correlated with environmental fluctuations.

Finally, clarifying the possible roles played by bryozoans in modern reefs will be of interest not only to students of living reefs and bryozoans, but also to paleontologists studying both fossil reefs and bryozoan evolutionary history.

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