

MOLTING BY *CUPULADRIA DOMA*, A FREE-LIVING BRYOZOAN

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ABSTRACT

In contrast to most shallow water bryozoans, which grow attached to vertical or under-surfaces of substrata, the free-living colonies of cupuladriid bryozoans occur on sand bottoms. In this open and well-illuminated habitat the colonies, raised like tiny domed islands above the sand grains, are subjected to intense overgrowth, particularly by algae. Cupuladriids cope with biological fouling by periodically molting their chitinous outer body layer.

Colonial animals must maintain the surface integrity of their colonies to prevent settlement by fouling organisms, burial by sediment, and overgrowth by neighbors. Both physical and chemical means may be employed in solving these problems. Sponges manufacture toxic chemicals that discourage foulers, predators and spatial competitors (Green, 1977). Corals produce mucus sheets that shed sediment (Hubbard, 1973). They also digest neighbors by using extra-oral mesenterial filaments (Lang, 1973), and sweeper tentacles (Chornesky, 1983). Some bryozoans use bristle-like vibracula to clear their colonies of sediment or debris (Cook, 1963), while toxic allelochemicals with antimicrobial and anti-fouling activity are produced by other bryozoans (Dyrynda, 1985; Winston and Bernheimer, 1986).

Despite such defenses colonies of most bryozoan species are not found on exposed, well-illuminated upward-facing substrata. Instead, they are generally restricted to vertical or downward facing surfaces, or to caves and crevices (Ryland, 1976). In part, this may be because they cannot compete for space with more rapidly growing competitors (e.g., sponges, corals, ascidians, macroalgae) which overgrow them. It may also be that under illuminated conditions their colonies are susceptible to fouling, particularly by diatoms and filamentous algae.

An exception to this restriction to vertical or cryptic habitats occurs among free-living cupuladriid bryozoans, whose small disk- or dome-shaped colonies are found on the surface of sandy and muddy sea floors in warm-water areas (Cook and Chimonides, 1983). Colonies of several species of this family are abundant on sand-bottoms of the continental shelf off the southeastern coast of the United States (Maturo, 1968). Over a period of 12 months we sampled populations of the most common of these, *Cupuladria doma* (d'Orbigny), in order to determine life history parameters for the species. Fortuitously, we discovered, that, under conditions of heavy fouling colonies, of *C. doma* molt frontal and basal membranes. This molting may be important in explaining their success on open surfaces.

ORGANISMS AND AREA STUDIED

Cupuladria doma is illustrated in Figure 1. Each adult colony forms a solid cone. The upper surface is covered by a few hundred zooids, each zooid with an associated bristle-like vibraculum (Fig. 1A). The basal surface consists of a common (colonially produced) skeleton, coelom, epidermis, and cuticle (Fig. 1B). Buried colonies actively seek the sediment surface, using their vibracular setae in a coordinated way to row upward through overlying sand. They also use them to move laterally across the sediment, to right themselves when overturned, and to raise and anchor themselves on the sand surface.

The study site was Capron Shoal, located off the northern end of South Hutchinson Island, on the



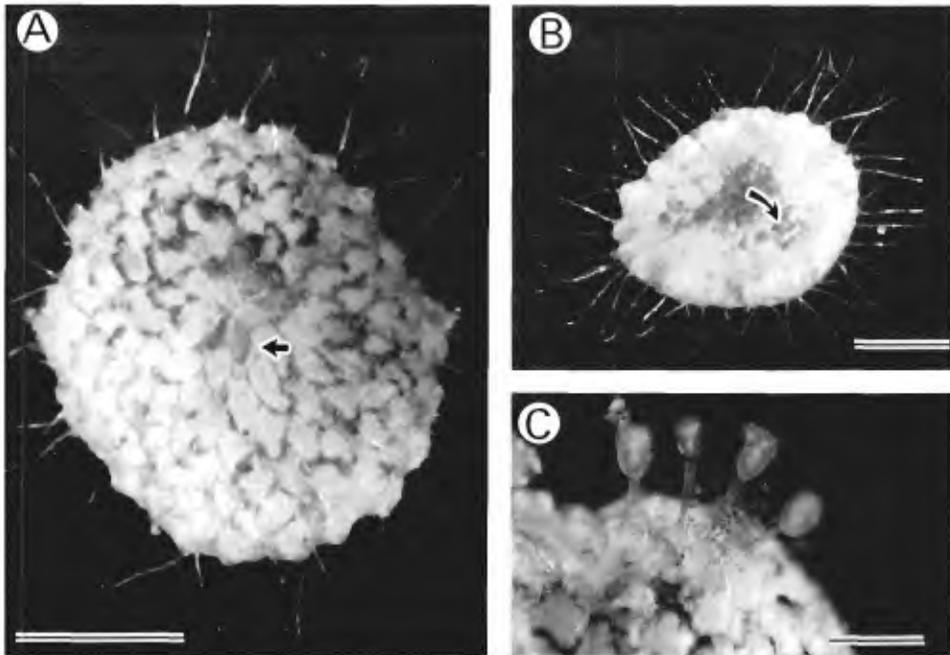


Figure 1. Molting and fouled colonies of *Cupuladria doma*. (A) Upper surface of colony. Dark zooids (arrow) still have old, fouled frontal membrane; light zooids have recently molted. Scale = 1 mm. (B) Basal surface undergoing molting (arrow points to peeling cuticle). Scale = 1 mm. (C) Close-up of upper surface fouled by entoprocts and diatoms (scale = 400 μ m).

Atlantic coast of Florida. The environment was a well-swept very unstable sandy bottom, in 8–10 m depth. The most abundant macrofauna were the sand dollars *Encope michelini* Agassiz and *Mellita quinquesperforata* (Leske), and the lancelet, *Branchiostoma virginiae* Hubbs. The well-oxygenated medium coarse biogenic sand supported a diverse interstitial meiofauna, both motile and encrusting, including over 30 species of sand grain encrusting bryozoans (Winston and Håkansson, 1986). Two cupuladriid species, *Discoporella umbellata* subspecies *depressa* (Conrad) and *Cupuladria doma* were found on the shoal. *Cupuladria* colonies occurred in much higher densities at every census, showing a finite growth pattern and a high level of sexual reproduction. They were mostly annual, with many colonies killed over the winter, probably due to the physical effects of winter storms. *Discoporella* colonies were much rarer, reproduced more commonly by fragmentation than by sexual reproduction, and appeared to be longer-lived (Winston, 1988).

METHODS

Bryozoans were sampled in January, April, July–August, and November 1984, using a small sled-type dredge. During the July–August census they were also observed in situ by SCUBA diving and transects were made to establish surface densities.

In the laboratory the collected sediment was spread out in layers a few cm deep in shallow trays of seawater. Adult cupuladriids emerged from the sediment over the next few days. All colonies present were measured and examined for condition, presence of embryos, type and amount of fouling, and injury or regeneration of zooids.

RESULTS AND DISCUSSION

During late July and early August, when light intensity and water temperatures at Capron Shoal peaked, sand grains on or near the sediment surface became coated with diatoms. Filamentous algae proliferated to the extent that the bottom

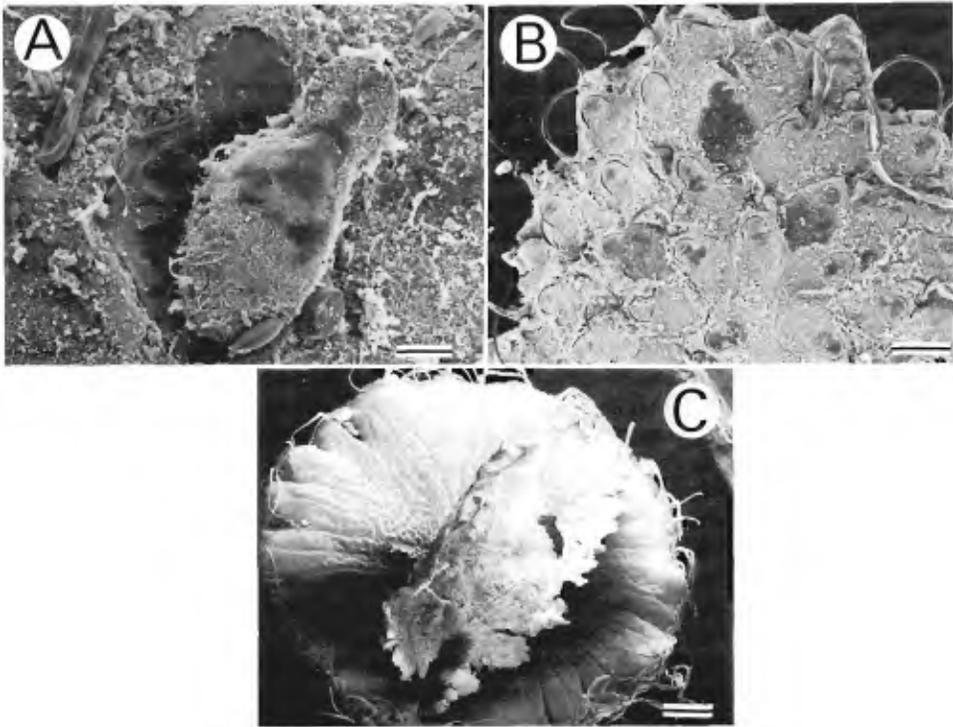


Figure 2. Molting in *Cupuladria doma*. SEM illustration after critical point drying of specimens. (A) Partially detached operculum and frontal membrane. Scale = 40 μm . (B) Upper surface of colony showing 3 recently molted zooids. Scale = 200 μm . (C) Basal surface, showing molting cuticle. Scale = 400 μm .

layer of water encountered by a diver was glutinous with floating, grayish brown, slimy strands. Colonies of *C. doma* collected at this census were particularly heavily fouled. The normal pinkish brown coloration of zooid tissues was masked by brownish, reddish, or greenish encrustation, and often the entire colony was almost hidden by tufts of algal filaments one cm or more in length.

Under the microscope, however, patches of clean, pink and shiny zooids were visible on the upper surfaces of colonies (Fig. 1A). Some colony bases were partially or completely free of fouling and covered by shining white cuticle. On closer examination of zooids we discovered that a new frontal membrane, complete with chitinous operculum, had formed under the old fouled one (Fig. 2A, B). Continued examination of living colonies and study of critical point dried specimens by SEM showed that once new frontal membrane forms the old surface cracks all around the zooid margin and eventually sloughs off or is brushed away by the vibracula, exposing the new membrane and operculum. On the colony base, the entire cuticle cracks, bubbles up, and peels off in irregular patches (Fig. 1B, 2C). Underneath is clean new cuticle (Fig. 2C).

The phenomenon we observed seems to be a type of regeneration. Degeneration-regeneration cycles of polypides occur periodically over the life cycle of bryozoan colonies and occur seasonally in temperate species. These cycles serve excretory functions. They often indicate the onset of sexual reproduction in a zooid, and they may occur in response to temporary unfavorable conditions (Hyman, 1959).

In addition, regeneration can occur in response to injury; zooids destroyed by grazers or predators may be repaired in a few days to several weeks' time (Palumbi and Jackson, 1982).

Molting in these colonies is not linked to growth, as in crustaceans, for example, since *C. doma* grows only by budding new zooids around the margin, and by deposition of skeletal material beneath the basal colony coelom (Håkansson, 1973). However, molting in cupuladriids may serve another function that it serves in arthropods. Many crustaceans continue to molt, even when adult size has been reached, in order to rid themselves of fouling. As the exoskeleton of crustaceans is a non-living surface, composed of chitin impregnated by calcium salts, it is very susceptible to fouling. The situation in bryozoans is thus like that in crustaceans and unlike that in other groups of slow-moving or sessile invertebrates in which the outer layer consists of live epidermis. Fungiid corals and sand dollars also live exposed on well-illuminated sandy substrata. Corals use ciliated epidermis, tissue distension, and sloughing of mucus to shed debris and sediment and prevent fouling (Hubbard, 1973). In sand dollars, epidermal glands also produce mucus, while the test and even the spines are covered with a ciliated epidermis (Hyman, 1955).

The fouling problem experienced by *C. doma* colonies is severe. Data collected for population studies (Winston, submitted ms.) showed the importance of molting in enabling *Cupuladria* colonies to cope with fouling. Over 35 taxa of plants and invertebrates occurred on colonies from our samples. Three-quarters of all colonies at any census were fouled by more than one kind of organism. Entoprocts (see Fig. 1C) and ctenostome bryozoans fouled a small percentage of colonies year-round. Other groups of foulers, particularly sabellariid worms and tube-building amphipods showed more seasonal distributions. Diatoms were the most abundant category of foulers; 75–100% of colonies were fouled by diatoms, depending on the season. The percentage of colonies fouled by benthic diatoms and green algal films increased between January and November, but fouling by filamentous algae was highest in August and decreased by November. The intensity of algal fouling declined by November also.

The number of colonies molting was highest in August, but in November 7% of colonies were still actively molting either top or basal surfaces. Twenty-five percent showed evidence of having recently molted the cuticle of one or both surfaces; such colonies had clean frontal membranes with algal fouling confined to interzooidal depressions. Filamentous algae were still present, primarily on very heavily fouled colonies which showed no signs of any molting.

Because the frontal cuticle is attached to the calcareous skeleton in the depressed areas between the zooids, molting cannot occur in those areas, and algae and other organisms eventually grow back over the new zooid surfaces from their refuges in these crevices. However, Figure 3 presents evidence that molting did reduce fouling. If colonies were acting as passive islands, then according to island biogeography theory (MacArthur and Wilson, 1967), one would expect that the number of species fouling cupuladriid colonies would increase with colony size. In fact, this did not happen. The number of species fouling colonies was constant over colony size, and for any colony was much lower than the total pool of species available for colonization.

Molting enables *C. doma* to survive an environment conducive to producing heavy infestations by epibionts. Colonies can grow, reproduce and maintain themselves even during the season of heaviest fouling, and although many colonies do perish over the winter for other reasons (see above), those that survive can conceivably make a clean start in the spring.

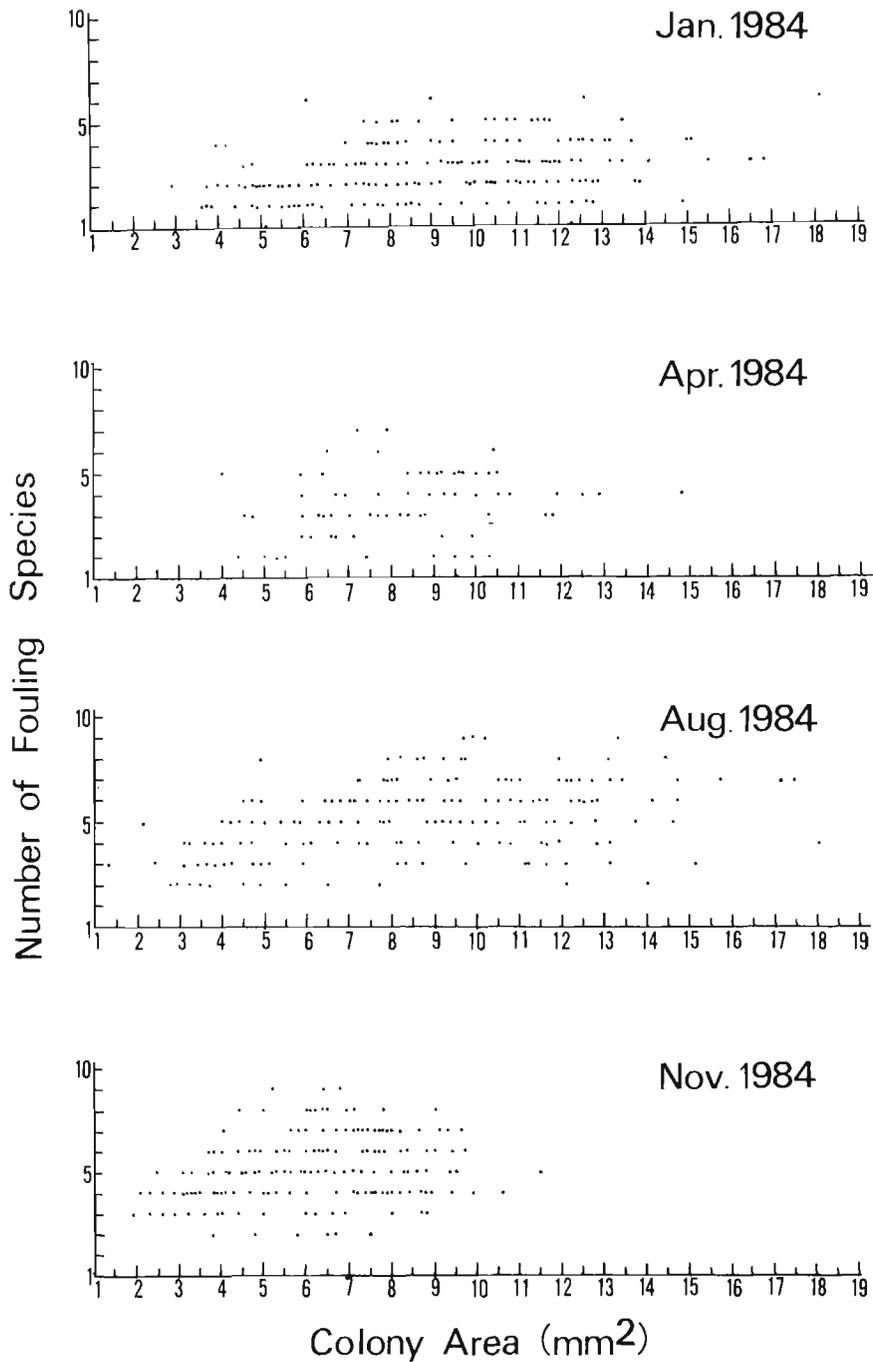


Figure 3. Number of species fouling *C. doma* colonies in relation to colony area.

Colonies of *Discoporella umbellata depressa* molted in the same way as those of *Cupuladria*. Patterns of molting appeared to be similar in terms of timing, types and incidence of fouling, although their numbers were too low to allow quantitative comparison of fouling data for the two species.

Molting is an almost unrecognized phenomenon in bryozoans. The only mention we could find in the literature was in a species description of a West African ctenostome, *Alcyonidium sanguineum* (Cook, 1985). That species was described as sloughing large areas of outer cuticle, under which new cuticle, complete with orifices, had formed. One of us (J.E.W.) also observed a colony of another cheilostome, *Crassimarginatella tuberosa*, from a reef habitat in Belize, that had some distended zooids and others with peeling frontal cuticles under which clean and transparent new cuticle could be seen. Further investigation may reveal that molting is of widespread occurrence in the phylum.

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LITERATURE CITED

- Chornesky, E. A. 1983. Induced development of sweeper tentacles on the reef coral *Agaricia agaricites*: a response to direct competition. *Biol. Bull.* 165: 569-581.
- Cook, P. L. 1963. Observations on live lunulitiform zoaria of Polyzoa. *Cah. Biol. Mar.* 4: 407-413.
- . 1985. Bryozoa from Ghana, a preliminary survey. *Koninklijk Mus. voor Midden-Afrika. Zool. Wetenschappen.* 238: 1-315.
- and P. J. Chimonides. 1983. A short history of the lunulite Bryozoa. *Bull. Mar. Sci.* 33: 566-579.
- Dyrynda, P. E. J. 1985. Functional allelochemistry in temperate waters: chemical defences of bryozoans. Pages 95-100 in C. Nielsen and G. P. Larwood, eds. *Bryozoa: Ordovician to Recent*. Olsen and Olsen, Fredensborg, Denmark.
- Green, G. 1977. Ecology of toxicity in marine sponges. *Mar. Biol.* 40: 207-215.
- Håkansson, E. 1973. Mode of growth of the Cupuladriidae (Bryozoa, Cheilostomata). Pages 287-298 in G. P. Larwood, ed. *Living and fossil Bryozoa*. Academic Press, New York.
- Hubbard, J. A. E. B. 1973. Sediment-shifting experiments: a guide to functional behavior in colonial corals. Pages 31-42 in R. S. Boardman, A. H. Cheetham and W. A. Oliver, Jr., eds. *Animal colonies*. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pennsylvania.
- Hyman, L. H. 1955. *The invertebrates: Echinodermata*. Volume IV. McGraw-Hill Book Company, New York. 763 pp.
- . 1959. *The invertebrates: smaller coelomate groups*. Volume V. McGraw-Hill Book Company, New York. 783 pp.
- Lang, J. 1973. Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. *Bull. Mar. Sci.* 23: 260-279.
- MacArthur, R. H. and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey. 203 pp.
- Maturo, F. J. S., Jr. 1968. The distributional pattern of the Bryozoa of the east coast of the United States exclusive of New England. *Atti. Soc. It. Sc. Nat. e Mus. Civ. St. Nat. Milano* 108: 261-284.
- Palumbi, S. R. and J. B. C. Jackson. 1982. Ecology of cryptic coral reef communities. II. Recovery from small disturbance events by encrusting Bryozoa: the influence of "host" species and lesion size. *J. Exp. Mar. Biol. Ecol.* 64: 103-115.
- Ryland, J. S. 1976. Physiology and ecology of marine bryozoans. *Adv. Mar. Biol.* 14: 285-443.
- Winston, J. E. 1988. Life histories of free-living bryozoans. *Nat. Geogr. Res.* 4: 528-539.
- and A. W. Bernheimer. 1986. Haemolytic activity in an Antarctic bryozoan. *J. Nat. Hist.* 20: 369-374.

—— and E. Håkansson. 1986. The interstitial bryozoan fauna from Capron Shoal, Florida. *Amer. Mus. Novitates* no. 2865: 1–50.

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