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BULLETIN OF MARINE SCIENCE. 57(1): 84–93, 1995

ECTOPROCT DIVERSITY OF THE INDIAN RIVER COASTAL LAGOON

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ABSTRACT

Thirty-six species of ectoprocts are known so far from the Indian River Lagoon. The highest diversity occurs where salinities are above 30‰. Only 12 species have been found in the less saline portions of the lagoon. Ectoproct habitats include seagrass meadows, drift algal communities, oyster "rock," docks, pilings, breakwaters, and man-made debris. Ectoproct diversity within the IRL is about one third that of area coastal and offshore habitats, but is probably fairly diverse relative to the available species pool. No ectoprocts are endemic to the IRL. About a third of the species recorded have western Atlantic or western Atlantic/Caribbean distributions. The rest are cosmopolitan fouling or eurytopic species. Species composition of the fauna has remained stable over the last 20 years, but large population fluctuations occur for some species on both a seasonal and year-to-year basis. IRL ectoprocts are somewhat protected from natural disturbance by their physiological tolerance and/or the presence of spatial refuges, but the fact that over a 20-year period many species were observed only at one site indicates that degradation of critical habitats would quickly reduce ectoproct diversity. Most important from a management point of view is the role of these animals in maintaining water quality. Like other suspension feeders, ectoproct colonies act as seawater purifiers—living water treatment plants. For example, colonies of *Zoobotryon verticillatum* found in 1 m^2 of a seagrass bed could clear and recirculate about 48,000 gallons of water per day. Priorities for future work include evaluation and quantification of the role of bryozoans and other suspension feeders in maintaining lagoon water quality, as well a more through taxonomic survey, particularly of the much less well-known northern- and southernmost portions of the lagoon.

STATUS

Original Diversity.—The original ectoproct fauna of the Indian River Lagoon (IRL) can only be surmised on the basis of what is known of its paleoecology. Shallow marine ecosystems with seagrass beds apparently existed on the Florida Peninsula as long ago as the middle Eocene (Ivany et al., 1990). However, the present IRL is only a few thousand years old. Molluscan assemblages found in IRL sediment cores document a change during that period from a limited fauna of stress tolerant euryhaline species, indicative of a restricted lagoonal environment with strong seasonal changes in salinity, to a more diverse euryhaline and stenohaline fauna believed to connote a more open lagoon environment with better water circulation and increased salinity (Bader and Parkinson, 1990). However, as the tidal inlets that existed along this part of the coast were not permanent (McBride, 1987), the pre-modern lagoon probably still received less oceanic input than today's lagoon. Because the number of bryozoans that can tolerate such conditions is very low (about 120 species worldwide; Winston, 1977), the original fauna was probably smaller than today's, perhaps 20 or fewer species.

As coastal settlement and needs for reliable harbors and shipping routes increased over the last 100 years, artificial inlets were cut and natural ones made more permanent by means of jetties (McBride, 1987). In addition, once the lagoon became part of the Intracoastal Waterway, the dredging of deeper channels may have provided refuges from heat or cold for some species, while increasing boat traffic has enhanced the likelihood of non-indigenous species being introduced from further north along the Atlantic coast or from the Caribbean or Gulf of Mexico. Finally, modern commercial shipping traffic has added the possibility of

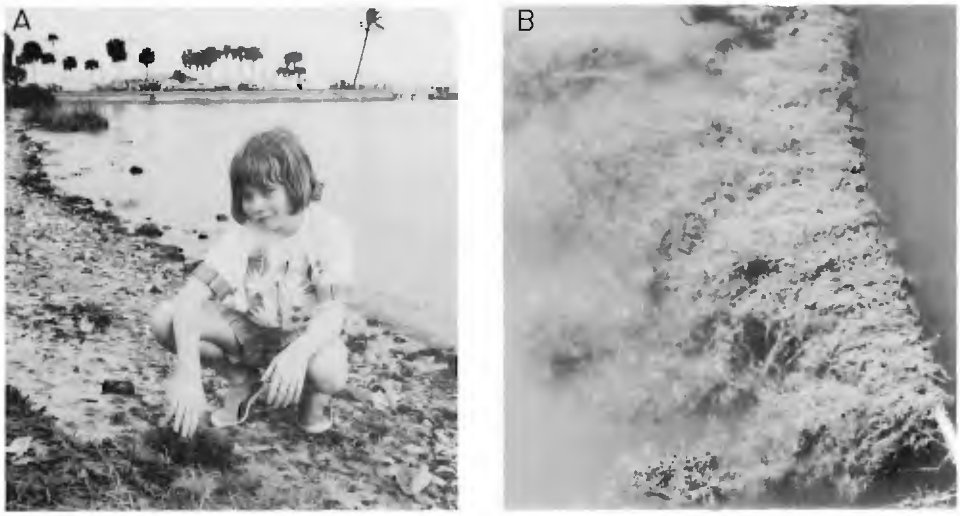

Figure 1. Ectoprocts as dominant elements of Indian River Lagoon communities. A. Winter. Author's daughter points to grapefruit-size colony of *Amathia alternata*. About half of the drift "seaweeds" visible along the strand line are actually colonies of three bryozoan species. [Photographed at the Sebastian Town Beach, February, 1994.] B. Summer. *Zoobotryon verticillatum* here shown growing on a dock line, may also dominate fouling and mangrove root communities and replace drift algae in seagrass beds during the summer months. [Photographed at Little Jim Island Fish Camp, North Beach, Fort Pierce, August, 1989.]

new species being brought in from even farther away as larvae contained in ships' ballast water (Carlton, 1989). It seems likely that these events have resulted in augmentation of the original fauna to its present level.

Present-day Diversity.—Systematic knowledge of the ectoproct fauna of the IRL dates back to the 1970s. My postdoctoral work at the Smithsonian Marine Station in 1974–1975 included a year-long systematic and ecological survey of the ectoprocts of the Indian River area (Winston, 1982). Six stations: Haulover Canal, Titusville, Banana River, Eau Gallie, Sebastian Grass Flat and Back Breakwater, Sebastian Inlet, Link Port Grass Bed and Link Port Canal (Swain et al., 1995, fig. 1), were within the lagoon itself. At that time the Indian River Coastal Zone Study was being carried out at Harbor Branch Foundation (Young and Young, 1977), and I was able to examine some of their quantitatively collected samples for bryozoans. In addition, my own qualitative collections retrieved bryozoans from all substrata available at a site. Bryozoan "traps" (screen fronted slide racks of microscope slides) suspended in the Harbor Branch canal and bryozoans on larger fouling panels being studied by David Mook (Mook, 1976) were also examined periodically.

Since this study was completed I have returned to the area a number of times and collected at some of the original stations, as well as at three new localities: the Little Jim Island Fish Camp docks, the seagrass bed on the north side of Fort Pierce Inlet, and the floating docks at the Fort Pierce Marina. These collections were made to gather material for behavioral studies and not for taxonomic purposes, so were not as comprehensive as those of the original survey. Nevertheless, most of the species originally recorded were collected again in later years. Three new species, *Scrupocellaria bertholetii, Schizoporella* sp., and *Caulibugula* sp. have been added to the fauna from those collections.

Table 1. Ectoprocts recorded from the Indian River Lagoon

Species (* = dominant)	At sta. < 30‰	Distribution	Seasonality	Fouling
1. *Alcyonidium "polyoum"*		1	Sp	X
2. *Amathia alternata**		1	Y-R (W)	
3. *Amathia distans*		2	Y-R	X
4. *Amathia vidovici**		2	Y-R	
5. *Anguinella palmata*		2	W, Sp	X
6. *Bowerbankia gracilis**	X	2	Y-R (W, Sp)	
7. *Bowerbankia maxima**	X	1	(Sp-F)	
8. *Buskia armata*		1	F-W	X
9. *Nolella stipata*		1	Y-R	
10. *Sundanella sibogae*		2	Y-R	
11. *Victorella pavida*	(L)	2	W	X
12. *Zoobotryon verticillatum**	X	2	Sp-Sm	X
13. *Aetea truncata*		2	F	X
14. *Antropora leucocypha*		1	Y-R	
15. *Beania klugei*	X	2	Y-R (W-Sp)	
16. *Bugula neritina**	X	2	Y-R (W)	X
17. *Bugula stolonifera**	X	2	W-Sp	X
18. *Caulibugula* sp.		—	Sm	
19. *Conopeum "seurati"**	X (L)	1	W-Sp	X
20. *Conopeum tenuissimum**	X (L)	1	Y-R (Sp + F)	X
21. *Cryptosula pallasiana*		2	Sp-F	X
22. *Electra bellula*	X	1	Y-R	
23. *Hippoporina verrilli**	X	2	F-Sp (F)	X
24. *Membranipora savartii*		2	Y-R (Sp + F)	X
25. *Savignyella lafontii*		2	Y-R (F)	
26. *Schizoporella cornuta*		2	Sp-F	
27. *Schizoporella floridana**	X	1	W–Sm	X
28. *Schizoporella* sp.		—	Sm	
29. *Scrupocellaria bertholetii*	(L)	2	Sm	X
30. *Scrupocellaria regularis*		1	Y-R (W–Sp)	
31. *Synnotum aegyptiacum*		2	Y-R (Sm)	
32. *Thalamoporella floridana*		1	Y-R (W)	
33. *Vittaticella contei*		2	Y-R	
34. *Watersipora subovoidea**	X	2	Y-R (W)	X
35. *Crisia "eburnea"*		1	Sp	
36. *Crisia elongata*		2	Y-R (W–Sp)	X

Key: * = most abundant species. Salinity: (L) = spp. not found at coastal stations in area. Distribution: 1 = Western Atlantic/Caribbean, 2 = circumtropical or cosmopolitan. Seasonality: Sp = spring, Sm = summer, F = fall, W = winter, Y-R = year-round; parentheses ( ) show most abundant season.

Ecological and Biogeographical Characteristics.—Thirty-six species have been collected at all IRL stations so far (Table 1). One new species, *Bowerbankia maxima,* was described from the lagoon in the original study (Winston, 1982). However, this species also ranges south into the Caribbean (Jamaica), and north as far as Bogue Sound (specimens in VMNH coll.). More than half of the IRL species are known from warm waters around the world. The rest have a more restricted western Atlantic or western Atlantic/Caribbean range.

Diversity was highest at the stations where salinities were above 30‰ during the study period. Only 12 species (Table 1) were collected at localities where the salinity was less than 30‰. Three species, *Victorella pavida, Conopeum tenuissimum,* and *Conopeum "seurati,"* are true estuarine species, found almost entirely in brackish water. The other species occurring in the IRL are warm water, euryhaline species, characteristic of harbors, the mouths of rivers, bays, and coastal waters where salinity is variable, but usually remains above 30‰ (Winston, 1982).

In fact, 20 (56%) of the 36 species have been recorded from other studies of fouling communities.

In comparison with the 103 species recorded from the area so far, the IRL fauna appears quite limited, although it is richer than the fauna recorded for Chesapeake Bay (24 species, Osburn, 1944), for example. A search of the literature for ectoprocts reported from similar low or variable salinity conditions throughout the western Atlantic region (Maine to Argentina) yielded 53 species; eliminating those species found only in cold water, showed that at least 60% of the ectoprocts that could possibly live in the river do occur there, making the IRL ectoproct fauna a fairly rich one. Its relative diversity may, in fact, just be due to the biogeographic setting of the Indian River region at the overlapping boundaries of two fauna provinces, the warm-temperate (Carolinian) and tropical (Caribbean) western Atlantic, as has been hypothesized by workers on several other invertebrate groups, e.g., oligochaetes (Erséus, 1986) and mollusks (Lyons, 1989).

In general, IRL ectoproct communities are at their most luxuriant from fall through spring (about October to May). The peak period of abundance for all species is given in Table 1. Ectoproct populations in the IRL are dominated by a few abundant species (those with an asterisk in Table I). Most are present in the river throughout the year, but have different habitat preferences, and different periods of growth, sexual reproduction, and maximum abundance, cued to seasonal changes in water temperature and salinity. Three arborescent bryozoans: *Amathia alternata, Amathia vidovici,* and *Bugula neritina* can be present in large quantities in winter, where they may make up a large part of the biomass in the drift algal community (Fig. 1A). Another arborescent species, *Zoobotryon verticillatum,* is a dominant in a number of habitats during summer months (Figs. 1B and 2).

Two species of the genus *Bowerbankia, B. maxima* and *B. gracilis,* occur most abundantly on seagrasses, but can also be found on other hard substrata (oyster shells, aluminum cans, etc.) year-round. The other common encrusters of seagrasses in the river are two members of the genus *Conopeum.* Their systematics exemplify some of the questions and uncertainties still remaining in our knowledge of the lagoon's ectoproct fauna.

Conopeum tenuissimum appears to be a native of the western Atlantic-Gulf of Mexico region, where it is found on seagrasses, oyster shells, and other objects. Its distribution extends from Maine to Florida, and the Gulf of Mexico. The species has also been introduced into other areas, such as the Pacific northwest, along with the east coast oyster *Crassostrea virginica* (Lagaaij and Cook, 1973). From at least southern New Jersey to Florida *Conopeum tenuissimum* coexists with another species, *Conopeum "seurati."* The two species occupy the same substrata and closely resemble one another morphologically, but differ in zooid size, initial budding pattern, timing of sexual reproduction, and seasonality, *Conopeum "seurati"* being most common in winter months and *Conopeum tenuissimum* in spring and summer. They also differ in salinity preference with *"seurati"* most common in lower salinity waters (down to 5‰). As part of a study on the East Coast ectoproct fauna, Peter Hayward of the University of Swansea and I are now trying to determine if U.S. material belongs to the European species *Conopeum seurati,* or represents a previously undescribed native species. The largest U.S. populations are located in the James River, adjacent to Jamestown, making a scenario of an early introduction from the southeastern coast of England intriguing. However, the initial growth pattern of U.S. colonies is not quite like that reported for British ones, and the reproductive season also differs. It may take molecular genetic work to solve the problem.

Two *Bugula* species, *Bugula neritina* and *Bugula stolonifera,* dominate during the winter on hard substrata like docks and seawalls. *Bugula neritina* populations show large year to year differences in abundance. In some years its wine colored arborescent colonies line IRL docks and seawalls from November to March; in other years they are only sparsely found. The species is known to be temperature sensitive (Ryland, 1976), and this may explain its fluctuating abundance pattern. In the IRL, colonies on intertidal surfaces senesce and slough off when the water warms, but enough colonies persist in deeper water and in coastal localities over the summer to reseed the lagoon intertidal when cool weather returns. *Bugula stolonifera* colonies are tan in color, have avicularia (which *Bugula neritina* lack), and commonly occur intermingled with colonies of *B. neritina. Bugula stolonifera* is also found at coastal localities and occurs in the IRL from December through April, apparently it is even more sensitive to warm water than *B. neritina.*

The more calcified encrusting bryozoans, *Watersipora subovoidea, Hippoporina verrilli,* and *Schizoporella floridana* are also most abundant during the cooler months of the year. *Schizoporella floridana* colonies are found on seagrasses, particularly *Thalassia.* The other two species occur on various hard surfaces, including fouling panels. In the winter months *Watersipora* colonies can be very abundant, forming a blackish orange crust marking the mid-intertidal zone on jetties and seawalls.

The ctenostome *Zoobotryon* develops very large populations during the summer. This species undoubtedly has the greatest biomass of any bryozoan in the IRL, and may be an important contributor to the overall health of the lagoon.

Role of Zoobotryon *in the Indian River.*—The gelatinous colonies of *Zoobotryon verticillatum* (Fig. 2A) consist of masses of droopy, trifurcately branching stolons, each about half a mm in diameter, with rows of small (0.4 by 0.6 mm) sac-like individual zooids arranged along two sides. The transparent branches of young colonies look like bundles of cellophane noodles (Fig. 2B), while the old colonies, which become coated with greenish-brown diatoms and other epiphytes, resemble masses of drying sauerkraut. Although the species is widely distributed in warm temperate and tropical waters, and frequently found in fouling communities, it was first recorded from Florida in 1914 (Osburn, 1914), and could well be native to the Caribbean since the oldest record of the species there goes back almost 200 years. In the IRL it is found in fouling, mangrove, and seagrass habitats.

Zoobotryon grows best when the water is above 22°C (Bullivant, 1967, 1968b). In the Indian River it flourishes from April through the end of September. When the first cold fronts lower the water temperature, most of the colonies die back, but enough fragments overwinter to produce new growth the next spring. Lagoon area colonies can grow to the size of a fist in a couple of weeks and may become a meter or more in length in 6 to 8 months.

Seagrass beds (shoal, manatee and turtle grass) cover just a small percentage of the total lagoon bottom, but they are extremely important to the health of the lagoon system. The grass beds not only protect the river from erosion, but provide food and shelter for a large number of invertebrates and fish (Gilmore, 1988; Young and Young, 1977). One of these beds lies just south of Little Jim Island on the north side of Fort Pierce Inlet. During the summer of 1989, I did some collecting there and was so impressed with the quantity of *Zoobotryon* (colonies were growing so densely among the seagrasses, that 2–4 m^2 of grass bed yielded enough to fill a 5-gallon bucket, or a wet weight of *Zoobotryon* ranging from 1.4 to 2.7 $kg \cdot m^{-2}$), that I decided to further analyze its role in the seagrass community.

Like all ectoprocts *Zoobotryon* is a suspension feeder. Each *Zoobotryon* zooid

Figure 2. The ctenostome ectoproct *Zoobotryon verticillatum*. A. Sherry Reed (Smithsonian Marine Station) holds amount of *Zoobotryon* collected from 2 m^2 of seagrass bed in August 1989. B. Portion of *Zoobotryon* colony showing trifurcately branching stolons with distal regions lined by minute zooids (scale bar = 5 mm). [Photo by Tom Smoyer, Harbor Branch Oceanographic Institution.] C. Nudibranch *Okenia zoobotryon* feeding on zooids of colony. Egg mass of nudibranch visible in upper left of photograph (scale bar = 0.5 mm). D. Feeding zooids of *Zoobotryon* with tentacles expanded. Each can filter about a third of a milliliter of water per hour (scale bar = 0.5 mm).

(Fig. 2D) extends a funnel of eight ciliated tentacles to filter particles of phytoplankton from the surrounding seawater. Although *Zoobotryon* tentacles are only about 0.3 mm in diameter, their ability to process seawater is impressive. *Zoobotryon* zooids feed on particles 0.045 mm or less in size. The work of Bullivant (1967, 1968a) showed that on good food (such as flagellates), the average zooid can clear 0.368 ml of water per hour (or an average of 33.7 $ml \cdot mg^{-1}$ dry weight, with a range from 0.152–1.05 $ml \cdot zooid^{-1} \cdot h$, or 13.9–96.2 $ml \cdot mg^{-1}$ dry $wt \cdot h^{-1}$). By using this data for clearance rates and by determining the amount of *Zoobotryon* found in a square meter of seagrass bed (above) and its dry weight (avg. 112.2 gm), it was possible to calculate how much the colonies in a square meter of that grass bed could clear. The answer was somewhere between 25,000 and 344,000 liters per day, or an average of 184,728 liters (48,613 gallons) per day. The *Zoobotryon* in 1 m^2 of bottom would thus be processing 184.7 m^3 of seawater daily. Extrapolating those numbers over the total area covered by the grass bed (0.19 $miles^2$ = 0.49 km^2 = 490,000 m^2) would have the total *Zoobotryon* population filtering 90,503,000 m^3 of lagoon water daily—quite a water treatment plant!

Of course, *Zoobotryon* colonies don't feed constantly (although Bullivant reported that his colonies did feed steadily over a 48-h experimental period), nor do they often encounter food particle densities in nature that would induce them to put forth their maximum feeding effort. Obviously, too, the amount of water filtered would depend on the whether the colony was actively growing or senescent, and whether *Zoobotryon* density over the whole grass bed was as high as in the area sampled. But these numbers are given credence by the fact that, in a similar study, benthic filter feeders in the Bay of Brest in France were estimated to be processing 718,000,000 m^3 of water, or about 30% of the total volume of the bay, daily (Hily, 1991). Since this one bed is only a fraction of the seagrass beds found in the IRL, and since *Zoobotryon* is abundant in other lagoon habitats, too, it is apparent that these animals play an important role in keeping lagoon waters clean.

In addition to their role in filtering and recirculating river water, *Zoobotryon* colonies are probably important chiefly as shelter. It is not likely that many organisms actually feed on *Zoobotryon*. Colonies produce bromo-alkaloids, compounds related in structure to drugs like nicotine, morphine, and cocaine (Sato and Fenical, 1983). In *Zoobotryon* tissues, the chemicals probably serve to discourage predation, prevent settlement by larvae of other organisms, or provide protection from viral or bacterial infection. Only a few nudibranch mollusks, including *Okenia zoobotryon* (Fig. 2C), are able to feed on *Zoobotryon* zooids.

Indian River grass beds play a vital role as a nursery ground for fish. Over 200 species occur in the river, 85% of them as juveniles, including a number important in sport or commercial fishing (Gilmore, 1988). The grass beds are rich in species partly because of the variety of microhabitats available. One important microhabitat is the drift seaweed understory. The first surveys of Indian River grass beds in the 1970s, which were based on aerial photographs, concluded that the associated masses of benthic drift algae were densest in the summer (Eiseman and Benz, 1975; Thompson, 1978). However, later direct collections showed that spring and fall were the times of peak algal density (Benz et al., 1979). It is likely that the dense summer "seaweed" growth apparent in the aerial photographs consisted of *Zoobotryon* colonies, which replace much of the grassbed algae during the warmest months of the year. The tangled masses of *Zoobotryon* colonies no doubt function much like the drift algae in providing shelter for other organisms found in the grass bed, especially juvenile fish, and their preferred food, small crustaceans and polychaetes. But in contrast to the algae, which act as current baffles, decreasing grassbed current flow, *Zoobotryon,* by its filtering activities, instead contributes to increased water circulation and renewal within the seagrass bed.

Threats.—From the work on IRL ectoprocts so far it is clear that, at least in the localities studied, the fauna has remained stable over the last 20 years. On the other hand, much of the IRL, especially the northern- and southern-most portions, has never been sampled for ectoprocts.

In addition, some IRL ectoproct species may still be misidentified or have incorrect distribution records. In the nineteenth century, when many of the marine organisms of North America were first studied, they were often identified with the European species that were superficially most similar. Intensive study of ecology, distribution, and genetics may be necessary to determine if such organisms are really conspecific; this work is not yet completed for all IRL species.

The fact that the less common species have been collected in only one locality during the last 20 years suggests that environmental degradation or change at a particular site (such as the Sebastian Inlet breakwater) could greatly reduce species diversity. This is offset by the fact that only 3% of the species found in the lagoon lack a refuge at coastal or offshore stations in the area, a fact which suggests that restored areas would be repopulated by most species.

Any exotic ectoproct species which has already been introduced into the lagoon is probably here to stay. As noted above, about 56% of IRL ectoproct species have been recorded from fouling communities elsewhere in the world. In contrast to places like New Zealand where a number of species have been documented as recent invaders and where invading populations are still limited to urban harbor areas (Gordon and Mawatari, 1992), the southeast coast of the U.S. has experienced boat traffic back and forth between Europe, Africa, the Caribbean for such a long time, that any non-native species now present are well-established within the lagoon. It is unlikely that such species could be eradicated, even if we wished to do so. Within similar climate zones the world's harbors are becoming more and more alike faunistically (Carlton, 1989), and there is little we can do to prevent it. At least five of IRL ectoproct species are found in Genoa Harbor for example (Geraci and Relini, 1970), and at least nine of them occur in Auckland, New Zealand (Gordon and Mawatari, 1992). Some of these cosmopolitan fouling species are the kinds of animals you'd expect in any urban area—aggressive, fast-living, opportunistic pests. But, as suspension feeders, they may still be critical in maintaining water quality and ecosystem functioning.

Management Recommendations.—Since it is impossible to manage the unknown effectively, the first recommendation is to conduct a survey that will systematically collect ectoprocts from every habitat in the entire lagoon, emphasizing the unstudied northern and southern portions.

Most bryozoans in the lagoon are associated in some way with seagrasses. Work on bryozoans should be coordinated with research on seagrass communities. We know quite a bit about the lagoon's seagrass communities, and we understand that their existence and good health is crucial to the life cycles of many other lagoon organisms, from sport and commercial fishes, to sea turtles and manatees. There has been considerable study of the role of algal epiphytes and of motile seagrass associated fauna in such systems, but very little is known about the role of encrusting colonial animal epiphytes. Evidence suggests that 1) the different species of seagrasses are not equally suitable substrata for encrusting organisms (Matthews, 1991), and 2) that colonial suspension feeding organisms play a much different role in such systems than algal epiphytes (see above), but both of these areas need more study.

There has been little research anywhere on the role benthic suspension feeders might play in maintaining the health of shallow water ecosystems. One of the few papers on the subject was actually carried out in the IRL at the Harbor Branch canal. David Mook (1981) showed that the local fouling community efficiently removed particles between 1- and 40-μm in size from lagoon water. Evidence that benthic suspension feeders can reduce or control phytoplankton biomass (which should make them effective in controlling eutrophication) is accumulating (Asmus and Asmus, 1991; Hily, 1991 and refs cited therein). However, there is also evidence that concentrations of suspension feeders (like mussel beds and fouling communities) have the potential to promote primary production both by supplying nutrients (mainly dissolved nitrogen) and by enhancing the rates of water movement and recycling (Doering, 1989; Hily, 1991). Evidence like this strongly implies that suspension feeding benthos are an important part of ecosystem functioning, affecting water circulation and nutrient parameters for better or worse. Their contribution to the management equation cannot be ignored.

ACKNOWLEDGMENTS

My thanks go to all those at the Smithsonian Marine Station and Harbor Branch Oceanographic Institution who have helped me with this project over the years, especially to M. Rice for her unfailing support of basic research, to S. Reed for wading knee-deep in *Zoobotryon*, to K. Metzger for her help with the *Zoobotryon* literature and T. Smoyer for his advice on photography. Contribution no. 358 from the Smithsonian Marine Station at Link Port.

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DATE ACCEPTED: September 1, 1994.

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