EPIZOIC BRYOZOANS, SEA SNAKES, AND OTHER NEKTONIC SUBSTRATES

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ABSTRACT

A total of 1,364 sea snakes were collected from the seas adjacent to peninsular Malaysia to study the fouling rates of epizoic bryozoans and the spatial distribution of the epizoans on the hosts. Only a single bryozoan species, the cheilostome *Electra angulata* (Levinsen), was found encrusting two species of hydrophid sea snakes: *Lapemis hardwickii* Gray and *Enhydrina schistosa* Daudin. Eight tenths percent of the sea snakes examined were infested. The epizoic bryozoan colonies on *L. hardwickii* were significantly smaller than those on *En. schistosa*. Other than a preference for the dorsal surface, the epizoic bryozoan colonies did not show a lateral or a head-tail preference for settlement. Evidence is presented that suggests the colonies were not sexually reproductive and that the fouler-host relationship is "accidental." The costs and benefits to the host and fouler are also discussed.

Sessile substrates are typical sites for larval settlement. Such substrates often include rocks, piers, algae, and exoskeletons of living or dead benthic or dead nektonic organisms. Living nektonic substrates are less common sites for larval settlement. Living nektonic species that shed or molt are even more ephemeral substrates for settling larvae. Thus, sea snakes are seemingly unconventional substrates for epizoan settlement. As nektonic animals, they do not provide a stationary substrate. But sea snakes are not the only nektonic substrates for epizoans. The epizoan communities of whales, dugongs, sea turtles, and cephalopods are quite diverse.

Sea snakes are encrusted by diatoms, foraminiferans, hydrozoans, serpulids, pelecypods, bryozoans, parasitic ticks, and barnacles (Bennett, 1971; Cantor, 1841; Cuffey, 1971; Darwin, 1851; Dean, 1938; Gotto, 1969; Harmer, 1926; Jeffries and Voris, 1979; Kropach and Soule, 1973; Lanchester, 1902; Pilsbry, 1916; Wall, 1921; Wilson, 1970; Zann, 1975; Zann et al., 1975). Whales and dugongs are encrusted by barnacles (Zann, 1975). Sea turtles are encrusted by algae, barnacles, bryozoans, isopods, crabs, amphipods, tunicates, hydrozoans, gastropods, and pelecypods (Annandale, 1912; Caldwell, 1968; Frazier et al., 1984, 1992; Jackson and Ross, 1975; Zann, 1975). Cephalopods are encrusted by bryozoans, foraminiferans, polychaetes, barnacles, corals, scyphozoans, pelecypods, sponges, diatoms, and coccoliths (Landman et al., 1987).

Due to their mobile nature, nektonic hosts tend generally to have a low percentage of total surface area encrusted by epizoans. Compared to other nektonic hosts, there is a general lack of fouling on sea snakes which suggests they have some antifouling properties. These include the presence of keratin in their skin as well as behaviors such as periodic shedding of skin, knotting, and diving (Zann et al., 1975). Keratin in the skin of sea snakes has a low surface energy, and thus has poor adhesiveness for epizoic larvae (Zann et al., 1975). This is similar to the grease-impregnated integument of sea turtles that has been linked to the low degree of encrustation on sea turtles (Frazier et al., 1984).

Bryozoans are common fouling organisms. They are known as epibionts on a variety of substrates. They commonly attach themselves to hard substrates and even nektonic organisms. Of particular interest to this study are the documented cases of epizoic bryozoans on nektonic host substrates. Epizoic bryozoans have been found encrusting living sea turtles (Annandale, 1912; Frazier et al., 1992;

Jackson and Ross, 1975) as well as cephalopods (Landman et al., 1987). Bryozoans are also known as epizoans on sea snakes. Sea snakes have been reported to be encrusted by the bryozoans *Cellepora pertusa* (*Hippodiplosia pertusa*) (Smitt) (Cantor, 1841), *Electra angulata* (Levinsen) (Cuffey, 1971; Harmer, 1926), *Membranipora tuberculata* (Bosc) (Kropach and Soule, 1973), *Membranipora savartii* (Audouin) (Zann et al., 1975), and *Monoporella* sp. (Zann et al., 1975; Kharin, 1981).

Epizoic bryozoans on nektonic host substrates also have an abundant fossil record which indicates bryozoans have a long evolutionary history of fouling nektonic substrates. Fossil nektonic hosts that have been fouled by bryozoans include Ordovician and Devonian cephalopods (Baird et al., 1989), Mississippian cephalopods (Boston et al., 1988), Jurassic cephalopods (Seilacher, 1982), Cretaceous turtles (Zangerl, 1948), and Cretaceous cephalopods (Dunbar, 1928; Landman et al., 1987). Most of the above examples provide strong morphologic evidence that the epizoic bryozoans fouled their nektonic hosts while the hosts were alive. Interpreting the occurrence of fossil epizoans is problematic in some cases as it is difficult to determine if the host was alive or dead at the time of attachment and growth of the epifauna (Seilacher, 1960, 1982). Fossil epizoic bryozoans have never been reported on host sea snakes as the sea snakes' skin is not readily preserved in the fossil record.

This study was undertaken to: 1) quantitatively describe the bryozoan fouling rates on sea snake hosts around peninsular Malaysia, 2) quantitatively describe the bryozoans' spatial recruitment pattern on the host sea snakes, and 3) determine if the epizoic bryozoan-host sea snake relationship permitted sexual reproduction by the bryozoan.

MATERIALS AND METHODS

In late 1974 and in 1975, 1,364 sea snakes representing 17 species and 9 genera were collected and examined for epizoans (Jeffries and Voris, 1979). The collections were made in the Straits of Malacca and the South China Sea off the coast of the state of Johor in peninsular Malaysia. The sea snakes were collected by local fishermen using stake nets and otterboard trawls. The collections were made in water at depths from 6 to 18 m with salinities of 28 to 31‰ and temperatures of 28 to 30°C. For more detail on the collecting, transport, and storage process see Jeffries and Voris (1979).

RESULTS

Epizoic bryozoans were only occasionally found on the sea snakes. Eleven (0.8%) of the 1,364 sea snakes were documented to have epizoic bryozoan colonies. The epizoic bryozoan colonies were found on the external surface of the scales of two host sea snake species: *Enhydrina schistosa* Daudin and *Lapemis hardwickii* Gray. Of the 326 specimens of *En. schistosa,* nine (2.8%) were fouled by bryozoans. Of the 345 specimens of *L. hardwickii,* two (0.6%) were fouled by bryozoans. The specimens of *En. schistosa* came from the mouth of the Muar River at 2°3'20"N 102°34'20"E. The specimens of *L. hardwickii* came from Parit Botak at 1°41'45"N 103°6'15"E. Both of these localities are in the Straits of Malacca.

En. schistosa and *L. hardwickii* are both marine sea snakes with Indo-Pacific distributions (Cogger, 1975; Minton, 1975). *En. schistosa* grows to an average length of 1.2 m, and *L. hardwickii* is slightly smaller with an average length of 1.0 m (Cogger, 1975). The 11 specimens of these two sea snake species found with epizoic bryozoan colonies were smaller than this, which may indicate they were juveniles. The nine specimens of *En. schistosa* had a mean length of 49.9 cm, and the two specimens of *L. hardwickii* had a mean length of 65.0 cm (Table

Table 1. Lengths of two species of host sea snakes

FMNH # of host	Length (cm)	Host species
19693	66.0	*Lapemis hardwickii*
19763	64.0	*Lapemis hardwickii*
197971	32.5	*Enhydrina schistosa*
197972	37.4	*Enhydrina schistosa*
197973	35.0	*Enhydrina schistosa*
197974	36.8	*Enhydrina schistosa*
197975	36.8	*Enhydrina schistosa*
197976	36.8	*Enhydrina schistosa*
197981	75.7	*Enhydrina schistosa*
197982	80.0	*Enhydrina schistosa*
197983	78.5	*Enhydrina schistosa*
Minimum	32.5	
Mean	52.6	
Maximum	80.0	

1). *En. schistosa* prefers shallow (0–20 m), nearshore, and more estuarine conditions (Cogger, 1975; Dunson, 1975). *L. hardwickii* prefers deeper (0–30 m) and more turbid conditions (Cogger, 1975; Dunson, 1975).

This study is the fist report of epizoic bryozoans on the sea snake *En. schistosa*. In contrast, the sea snake *L. hardwickii* is a common host for other epizoans in addition to the bryozoan species reported in this study. Zann et al. (1975) reported the bryozoan *Membranipora savartii* on *L. hardwickii*. Lanchester (1902) and Zann (1975) both reported specimens of *L. hardwickii* that were encrusted by the barnacle *Platylepas ophiophilus* Lanchester. In fact, Zann (1975) found that 54% of the collected specimens of *L. hardwickii* were encrusted by barnacles.

All of the colonies found encrusting on the sea snakes belonged to the anascan, cheilostome, gymnolaemate bryozoan *Electra angulata* Levinsen. *E. angulata* has elongate quadrangular autozooids (Fig. 1). Avicularia and ovicells are lacking (Mawatari, 1953; Rao and Ganapati, 1974). Zann et al. (1975) reported that epizoic bryozoans on sea snakes do not show any morphologic adjustments at the zooidal level to the host sea snake substrate except that the colonies tend not to be heavily calcified.

E. angulata is geographically widespread. It occurs throughout the tropical Indo-Pacific and possibly even the Caribbean (Landman et al., 1987; Mawatari, 1953; Rao and Ganapati, 1974; Zann et al., 1975). It tends to be a shallow water species. This is supported by the depths at which it has been found as epizoans on various nektonic hosts.

This species forms two dimensional encrustations attached to a substrate (Mawatari, 1953). Jackson (1979) referred to this type of colony as having a sheet colony growth habit. Sheet-like colonies are generally opportunistic and reproduce early in colony astogeny and exhibit high fecundity (Jackson, 1979). They tend to dominate on unstable substrates (Jackson, 1979) like sea snakes. Epizoic bryozoan colonies on host sea snakes are fast growing and tend not to reach large sizes or be as heavily calcified as those colonies on more conventional substrates (Zann et al., 1975). These opportunistic traits are beneficial on the short-lived substrate of a sea snake skin because of the periodic shedding of skin. Frazier et al. (1992) reported that the epizoic bryozoan colonies on host sea turtles exhibit fast growth rates and short life spans of roughly 1 month. These traits are necessary on the host sea turtles because of the periodic flaking away of scutes (Frazier et al., 1984).

Figure 1.   Autozooids of an epizoic *Electra angulata* colony on the host sea snake *Enhydrina schistosa* (FMNH 197975). Note opercula covering some orifices and lophophore tentacles extending from others. Magnification: 88.4.

Mawatari (1953) measured the growth rate of *E. angulata* colonies on test panels off the coast of Japan. Results indicate a rapid growth rate, with colonies containing over 4,000 zooids and covering 300 mm^2 within 15 days of larval settlement. At the end of a month, some colonies covered over 1,000 mm^2. Mawatari (1953) also found that many of the colonies reached sexual maturity in only 3 months.

E. angulata has been previously reported as an epizoan on host sea snakes. Harmer (1926) reported this species on an unidentified sea snake. Cuffey (1971) found this species fouling the sea snake *Pelamis platurus* (Linnaeus) off the Pacific coast of Costa Rica at the surface in 180 m of water.

E. angulata is not restricted to sea snake hosts. It is a common fouling organism found encrusting surface-drift objects such as seeds, wood, and plastic trash. In fact when the species was first described, the type material came from a piece of drift wood (Levinsen, 1909). *E. angulata* has also been reported to encrust living shells of cephalopods (Landman et al., 1987) and oysters (Mawatari, 1953).

Two separate analyses were performed. The first examined the size of the epizoic bryozoan colonies. The second focused on the spatial distribution of the epizoic bryozoan colonies on the host sea snakes. All measurements in the first analysis were made with a PC-based image analysis system using digitized video images of the colonies. Repeatability experiments indicate a measurement error of less than 2.4%. All specimens are housed at the Field Museum of Natural History (FMNH).

The size of 16 *E. angulata* colonies were measured. Size was measured as the

Table 2. *Electra angulata* colony sizes from 16 colonies found on five host sea snakes. The # of zooids refers to the number of complete zooids in a colony. The # of scales represents the number of host sea snake scales partially or completely covered by a colony.

FMNH # of host	Colony area (mm²)	# of zooids in colony	# of scales	Host species
19693	0.52	14	1	*Lapemis hardwickii*
19763	0.69	16	1	*Lapemis hardwickii*
197971	3.94	63	6	*Enhydrina schistosa*
197971	2.86	48	4	*Enhydrina schistosa*
197971	6.41	101	12	*Enhydrina schistosa*
197971	2.65	55	4	*Enhydrina schistosa*
197971	2.83	56	4	*Enhydrina schistosa*
197971	1.01	19	2	*Enhydrina schistosa*
197971	2.31	45	5	*Enhydrina schistosa*
197971	7.51	121		*Enhydrina schistosa*
197971	1.95	37	8	*Enhydrina schistosa*
197971	5.24	87	14	*Enhydrina schistosa*
197971	1.05	21	7	*Enhydrina schistosa*
197971	2.14	42	10	*Enhydrina schistosa*
197974	10.30	156	17	*Enhydrina schistosa*
197975	7.96	117		*Enhydrina schistosa*
Minimum	0.52	14	1	
Mean	3.71	62.4	6.8	
Maximum	10.30	156	17	

amount of area of the substrate covered by a colony as well as the number of complete zooids in a colony (Table 2). The colonies came from five sea snakes representing both species of hosts. Of the 16 colonies, two were from *L. hardwickii* and 14 from *En. schistosa*. The size of the bryozoan colonies ranged from 0.52 mm² to 10.30 mm² (mean = 3.71 mm²). The bryozoan colonies on *L. hardwickii* were smaller (mean = 0.61 mm²) than those on *En. schistosa* (mean = 4.15 mm²). The bryozoan colonies contained from 14 to 156 zooids (mean = 62.4). Once again, the bryozoan colonies on *L. hardwickii* were smaller (mean = 15.0 zooids) than those on *En. schistosa* (mean = 69.1 zooids).

According to the growth rate data from Mawatari (1953) presented above, these colonies are very young. Using Mawatari's data and assuming an exponential increase in colony size (colony radius increases linearly while colony area increases exponentially), the largest colonies on these sea snakes are at most only a few days old. This assumption may not be exactly justified for two reasons. First, Mawatari's *E. angulata* colonies may have had faster growth rates because of a more stable substrate (test panels) compared to an active host sea snake with moving scales. Second, Mawatari's test environment may have been more conducive to the growth of the bryozoans than the Straits of Malacca where the sea snakes were collected.

With such a small sample of epizoic bryozoan colonies from *L. hardwickii*, it is impossible to determine the robustness of the difference in colony size between the two species of host sea snakes. Perhaps this difference is because of a higher frequency of shedding in *L. hardwickii*. Unfortunately there are no published data on the relative frequency of shedding in these two species of host sea snakes, but there are data on other species. The average time interval between shedding in the sea snake *Pelamis* is roughly 20 days with a range of 5–65 days (Shaw, 1962; Zann et al., 1975; Zeiller, 1969). For the sea snake *Laticauda* the range if 90–99 days (Klemmer, 1967; Mays and Nickerson, 1968).

Perhaps the difference in the size of the epizoic bryozoan colonies is because

of interscale movement in *L. hardwickii*. In some host sea snakes (e.g., *Astrotia stokesii* (Grey)) the scales are imbricate (overlapping) which results in movement between adjacent scales when the snake's body flexes (Zann et al., 1975). As a result, the epizoic bryozoan colonies on these host sea snakes are broken into sections, one on each adjacent scale (Zann et al., 1975).

To determine if the 16 *E. angulata* colonies were restricted to a single scale on the host sea snakes, the number of host sea snake scales that were partially or completely covered by the epizoic bryozoan colonies were counted (Table 2). The number of partially or completely covered scales ranged from 1–17 (mean = 6.8). The two epizoic bryozoan colonies on the host sea snake *L. hardwickii* covered only a single scale each. This is in contrast to the host sea snake *En. schistosa* (Fig. 2) where the 14 epizoic bryozoan colonies covered from 2–17 scales (mean = 7.8 scales). This could be because of the presence of imbricate scales as discussed above and/or differences in the size of host sea snake scales between the two species and/or differences in the size of epizoic bryozoan colonies.

En. schistosa has slightly imbricate scales, while those on *L. hardwickii* are simply juxtaposed (Cogger, 1975). Thus in this study, the imbricate nature of the scales does not affect the size of the colonies as the host sea snake with the imbricate scales has colonies encrusting multiple contiguous scales while the sea snake without imbricate scales has colonies encrusting single scales. The ventral scales of *L. hardwickii* have a unique spinuous shape (Cogger, 1975; Zann, 1975) for which bryozoan larvae show a preference for settlement (Zann, 1975). These spines may affect the bryozoans' ability to encrust adjacent scales (Zann et al., 1975). Perhaps this factor limits the size of the epizoic bryozoan colonies on the host *L. hardwickii*.

The scales of *L. hardwickii* are an order of magnitude larger than those of *En. schistosa* (Table 3). The mean size of scales on *L. hardwickii* is 5.30 mm^2 (N = 2) while that of *En. schistosa* is 0.63 mm^2 (N = 18). Perhaps the epizoic bryozoan colonies on *L. hardwickii* are restricted to single scales because the scales on this host sea snake are so large, whereas those colonies on *En. schistosa* encrust several scales because the scales on this host are so small. This hypothesis must be rejected as the epizoic bryozoan colonies on *L. hardwickii* are smaller than the scales (0.61 mm^2 vs. 5.30 mm^2 respectively). This is in contrast to the epizoic bryozoan colonies on *En. schistosa* which are larger than the scales (4.15 mm^2 vs. 0.63 mm^2 respectively).

Perhaps the epizoic colonies of *E. angulata* on *L. hardwickii* are smaller and cover fewer scales because, by chance, the two specimens of *L. hardwickii* were younger substrates due to having recently shed prior to being caught. In this scenario, the epizoic bryozoan colonies on *L. hardwickii* would have been smaller than those on *En. schistosa* simply because there was not sufficient time for larger colonies to grow on *L. hardwickii* since the larvae settled.

There is no evidence that these colonies were sexually reproducing. Unfortunately *E. angulata* does not exhibit any obvious external morphological evidence (e.g., ovicells) of sexual reproduction (Mawatari, 1953). If the above estimates of colony age derived from colony size based on Mawatari's (1953) data are correct, then these epizoic bryozoan colonies may not have been sexually mature. In contrast, epizoic bryozoan colonies living on more stable nektonic hosts have been found to be sexually reproductive (Landman et al., 1987).

It is often assumed that one of the benefits to epizoans on nektonic hosts is reduced substrate competition. Undoubtedly there is less larval recruitment on a nektonic substrate. This apparent lack of spatial competition is magnified on nektonic hosts that periodically shed or molt. One would think that epizoic bryozoan
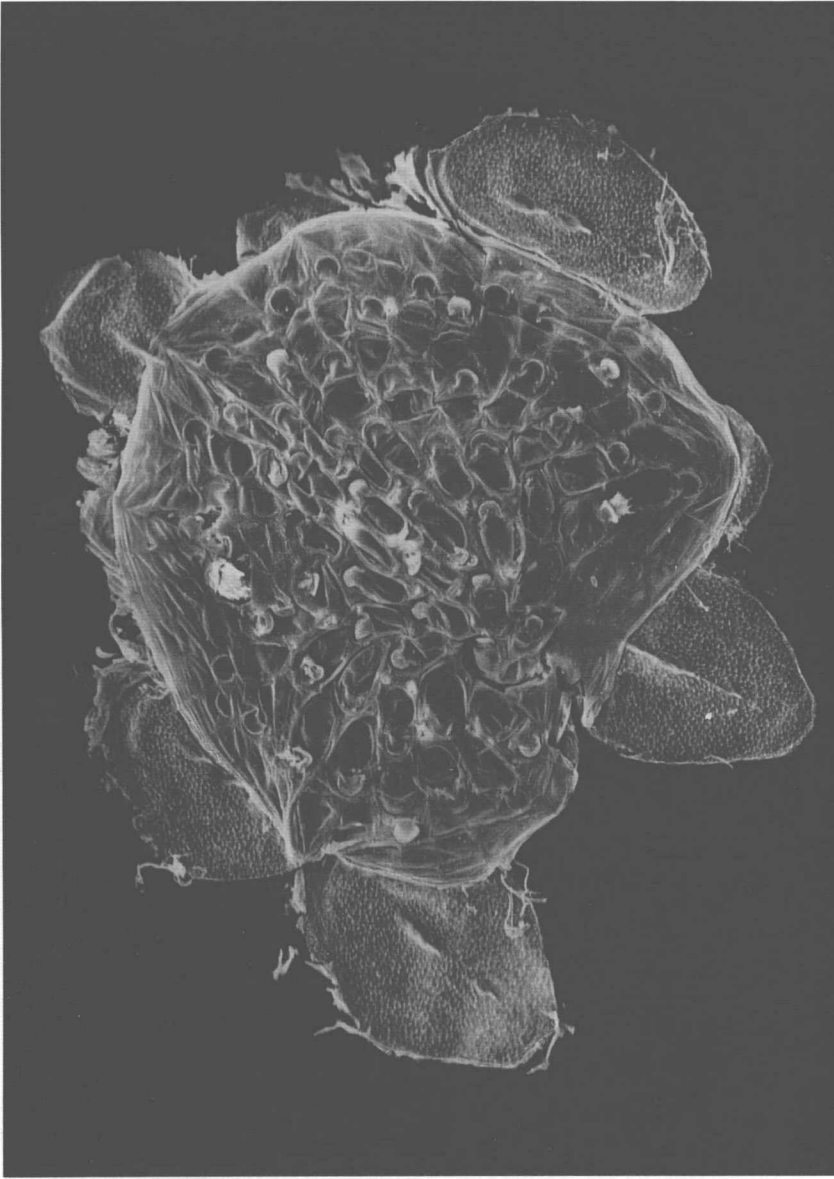
Figure 2. Epizoic *Electra angulata* colony on the host sea snake *Enhydrina schistosa* (FMNH 197975). Note the bryozoan colony covers several contiguous sea snake scales. Magnification: 32.

colonies on host sea snakes are too rare and short-lived to exhibit spatial competition. But on one sea snake specimen (*En. schistosa,* FMNH 197971), three adjacent colonies of *E. angulata* were found together on a single cluster of scales. The three epizoic bryozoan colonies were abutting on their margins. There was no evidence of overgrowth (sensu Jackson, 1977; Stebbing, 1973; Taylor, 1979) or fusion (sensu Chaney, 1983). This suggests there may be some minimal competition for space on sea snakes. This competition must be limited though because of the periodic shedding of skin by the host sea snakes.

Table 3. Scale sizes on two species of host sea snakes

FMNH # of host	# of scales measured	Mean scale area (mm²)	Host species
19763	2	5.30	*Lapemis hardwickii*
197971	2	0.69	*Enhydrina schistosa*
197971	3	0.63	*Enhydrina schistosa*
197971	3	0.67	*Enhydrina schistosa*
197971	7	0.41	*Enhydrina schistosa*
197974	3	0.73	*Enhydrina schistosa*
Minimum	2	0.41	
Mean	3.3	1.41	
Maximum	7	5.30	

In the second analysis, the distribution of 118 *E. angulata* colonies was mapped on six specimens of the host sea snake *En. schistosa* (FMNH 197971–197976). The number of bryozoan colonies found on these six snakes ranged from 1–54 (mean = 19.7). The data on their distribution are shown in Table 4. The surface of each sea snake was arbitrarily divided up into four equal length sections from the head to the tail. Each of these four sections was further divided into four separate quadrants: dorsal, ventral, left, and right. Thus, the surface of each snake was divided up into 16 sections.

As expected, a chi-squared test revealed that there was no statistically significant (at $P = 0.05$) difference in the left-right (i.e., lateral) distribution of the epizoic bryozoan colonies on the host sea snakes. A chi-squared test revealed no statistical difference (at $P = 0.05$) in the spatial distribution of the bryozoan colonies between the four sections from anterior (head) to posterior (tail). Nor did a chi-squared test reveal any significant difference (at $P = 0.05$) in the distribution of colonies between the anterior and posterior halves of the sea snakes. This is similar to the findings of Zann et al. (1975) who reported that epizoic bryozoans occurred on all parts of the sea snakes' bodies.

This is in contrast to the work of Zann (1975) who examined the distribution of epizoic barnacles on six species of host sea snakes (including *L. hardwickii*). In a qualitative analysis, he found that most epizoic barnacles occurred toward the tail end of the sea snakes. Jeffries and Voris (1979) examined the distribution

Table 4. Number of bryozoan colonies counted per quadrant on six specimens of the host sea snake *Enhydrina schistosa*. 1/4 = head quadrant, 2/4 = proximal mid-quadrant, 3/4 = distal mid-quadrant, 4/4 = tail quadrant, DL = dorsal left quadrant, DR = dorsal right quadrant, VL = ventral left quadrant, VR = ventral right quadrant.

FMNH #	1/4 DL	1/4 DR	1/4 VL	1/4 VR	2/4 DL	2/4 DR	2/4 VL	2/4 VR	3/4 DL	3/4 DR	3/4 VL	3/4 VR	4/4 DL	4/4 DR	4/4 VL	4/4 VR
197971	10	4	4	2	3	5	1	0	4	5	1	1	6	5	0	3
197972	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
197973	2	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0
197974	5	2	2	3	1	4	2	6	1	0	1	0	3	1	6	1
197975	1	2	0	1	0	0	0	0	0	0	0	1	0	0	0	0
197976	4	2	0	1	1	1	0	1	1	0	0	1	1	0	1	1
Total	23	11	6	7	5	11	3	7	6	5	3	3	10	6	7	5
%	19	9	5	6	4	9	3	6	5	4	3	3	8	5	6	4
Min.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mean	3.8	1.8	1.0	1.2	0.8	1.8	0.5	1.2	1.0	0.8	0.5	0.5	1.7	1.0	1.2	0.8
Max.	10	4	4	3	3	5	2	6	4	5	1	1	6	5	6	3

of epizoic barnacles on 17 species of host sea snakes (including *En. schistosa* and *L. hardwickii*). In a qualitative analysis, they also found that most epizoic barnacles occurred toward the tail end of the sea snakes. Zann (1975) attributed the tendency for more epizoans to occur toward the tail end of host sea snakes to the knotting behavior of sea snakes which may be more efficient in removing epizoans toward the head end.

A chi-squared test did reveal a statistically significant (at $P = 0.05$) difference between the relative abundance of *E. angulata* colonies on the dorsal versus ventral surfaces of the sea snakes. Seventy-seven (65%) of the 118 bryozoan colonies occurred on the dorsal surface of the sea snakes. As expected, most of the epizoic bryozoan colonies were found on the dorsal surface of the host sea snakes.

DISCUSSION

It is not known what aspect(s), if any, of the sea snakes' skin attracts bryozoans. Morphological, textural, and compositional characteristics of substrates are known to affect the recruitment of epizoic bryozoan larvae. It has been documented that bryozoan larvae do not haphazardly select a substrate. Instead, they show preference for specific substrates (Crisp, 1973, 1974; Crisp and Ryland, 1960; Hulbert, 1991; Pinter, 1969; Rogick and Croasdale, 1949; Ryland, 1959, 1962, 1976; Winston and Eiseman, 1980; Woollacott and Zimmer, 1971) which is often based on the presence of a certain microflora (Cancino, 1986; Kitamura and Hirayama, 1987; Soule and Soule, 1977; Stebbing, 1972).

The relationship between the epizoic colonies of *E. angulata* and the host sea snake is described as phoretic (Zann, 1975) which refers to a hitchhiking association (Gotto, 1969). This relationship is not mutualistic (i.e., mutually beneficial) as the host does not gain anything from this relationship, and the relationship is not parasitic. The epizoan-host relationship discussed in this study is best considered accidental for three reasons. First, the epizoan is not restricted to this type of substrate. There are no known obligate or host-specific associations known between bryozoans and sea snakes. This is in contrast to the findings by Landman et al. (1987) and Frazier et al. (1992) who suggested that certain epizoic bryozoans may be species specific on different species of cephalopods and sea turtles. Second, less than 1% of the collected sea snakes in this study had epizoic bryozoans. Zann et al. (1975) reported that few of the sea snakes they collected had epizoic bryozoan colonies as well. This is in contrast to other epizoans. For example, the epizoic barnacle *Octolasmis grayii* (Darwin) was found on 17.2% of the sea snakes collected (Jeffries and Voris, 1979) as compared to this study's findings of 0.8% for the bryozoans. Considering there are only two species of sea snakes involved in this study, it highlights the rarity of epizoic bryozoans on these hosts. Forty-two of the 326 specimens (12.9%) of *En. schistosa* and 87 of the 345 specimens (25.2%) of *L. hardwickii* were fouled by *O. grayii* (Jeffries and Voris, 1979). The epizoic bryozoan *E. angulata* was found on nine of the 326 specimens (2.8%) of *En. schistosa* and on two of the 345 specimens (0.6%) of *L. hardwickii*. The paucity of epizoic bryozoans on the sea snakes in this study also suggests an accidental relationship. Third, the host sea snakes are probably not a useful substrate. For such a substrate to be useful, the growth of the epizoic bryozoan colonies via asexual zooid replication must be rapid enough to allow sexual reproduction before the host sea snake sheds its skin. As discussed above, the colonies in this study probably had not reached sexual maturity.

Encrusting host sea snakes has several potential benefits for the epizoic bryozoans. First, this relationship can expand the biogeographic distribution of the

epizoans by increasing the range of larval dispersal, depending on the range of the host. This is only true if the epizoans are able to sexually reproduce while on the host. As discussed above, this probably was not true for the epizoans examined in this study. Second, the epizoans may be exposed to a better food supply because of the snakes' mobility. The currents resulting from the sea snakes' swimming may provide an aid to the bryozoan's feeding. Based on the presence of lophophores (Fig. 1), it is known that the zooids in the epizoic colonies of *E. angulata* were feeding while on the host sea snakes. Third, the host sea snake substrate may provide protection from predation. Living on a nektonic substrate removes the epizoans from the normal benthic predators (e.g., amphipods, annelids, echinoids, fishes, isopods, nudibranchs, pycnogonids, and gastropods). Fourth, the host sea snakes can provide unoccupied substrate space. Competition for substrate space is intense, so exploitation of the sea snake skin can lessen the competition for substrate. This study documented intraspecific substrate competition among the colonies of *E. angulata,* but intraspecific overgrowth is rare in bryozoans. Abutment or fusion is more common among conspecific colonies (Chaney, 1983; Poluzzi and Coppa, 1991).

In addition to the benefits to the epizoic bryozoans, there are potential costs. Certain behaviors of the host sea snakes could damage the epizoic bryozoan colonies. Such potential behaviors include diving, flexure of tail, copulation, wedging in crevices, knotting, and obviously shedding. Many such behaviors may serve an antifouling function. The host sea snakes could carry the epizoan to unfavorable environments (e.g., inhospitable depths, salinities, or water temperatures). For example, sea snakes are known to dive to great depths (Heatwole and Seymour, 1975). Damage to the bryozoan colonies from flexure of the sea snake skin during swimming is probably not a major problem for three reasons. First, some of the colonies in this study are restricted to single sea snake scales. This is true for the colonies on the host sea snake *L. hardwickii* where the colonies are small and the scales large. Second, the colonies in this study that cover multiple scales are so small relative to the size of the sea snakes that probably only minor bending of the colonies occurs (Kropach and Soule, 1973; Zann et al., 1975). This is true for the colonies on the host sea snake *En. schistosa* where the colonies are small, but they cover multiple scales because of the small size of the scales. Third, the low degree of calcification of the colonies facilitates bending. As a result, even though the host sea snake substrate is somewhat flexible, the colonies probably are not broken because of the swimming action of the host. On the other hand, colonies can be damaged by abrasion during copulation, while wedging under corals during feeding, and during knotting.

The unique sea snake habit of knotting has been categorized as a cleaning behavior (Pickwell, 1971), a shedding behavior (Pickwell, 1971), and an antifouling behavior (Kropach and Soule, 1973; Zann et al., 1975). Knotting has been observed in the natural habitat, and it is often performed vigorously and sometimes for several hours (Zann et al., 1975). Knotting was observed to result in the removal of unshed skin, barnacles, and pieces of adhesive tape from sea snakes (Zann et al., 1975). Adhesive tape is a good analog for a sheet-like epizoic bryozoan colony like *E. angulata.*

The frequent sloughing of skin during shedding may also serve as an antifouling mechanism (Kropach and Soule, 1973). Epizoans presumably die when removed from the host by shedding. Epizoic bryozoan colonies are defenseless against removal by shedding. This is in contrast to barnacles. The barnacle *Platylepas ophiophilus* can occasionally withstand shedding on the sea snake *L. hardwickii* because of the barnacles ability to penetrate the host's skin with downward-

extending ribs (Zann, 1975). Perhaps this is why Zann (1975) found that epizoic barnacles are more common than bryozoans on host sea snakes.

In addition to the potential costs to the epizoic bryozoans, there are potential costs to the host sea snakes. These include increased drag, impairment of sight, and additional metabolic costs of antifouling behavior. First, the presence of epizoans with a large cross-sectional profile like barnacles may increase the drag on a small host. The small sheet-like epizoic bryozoan colonies in this study probably do not increase the drag appreciably. Second, epizoic bryozoan colonies can impair the vision of the host sea snakes. Kropach and Soule (1973) reported an extensive epizoic bryozoan colony of *Membranipora tuberculata* encrusting the head of the host sea snake *Pelamis platurus*. The colony covered half of the sea snake's head including one eye and one nostril. Finally, the antifouling behaviors mentioned above (especially the high frequency of shedding in *Pelamis*) presumably have a metabolic cost to the host sea snakes (Zann et al., 1975).

CONCLUSIONS

Sea snakes are not a common substrate for epizoans. This is especially true for bryozoan larvae that must settle, metamorphose, asexually reproduce, and finally sexually reproduce before the host sea snake sheds its skin. Such a relationship between the epizoic bryozoan *E. angulata* and the host sea snakes *L. hardwickii* and *En. schistosa* is reported from the Straits of Malacca. Based on the lateral extent of the colonies and their constituent number of zooids, the colonies in this study were small. These colonies probably had not reached sexual maturity. As a result, the relationship between the epizoic bryozoans and the host sea snakes is probably accidental. This is supported by the fact that *E. angulata* is commonly found on a variety of other mobile and sessile substrates and is not restricted to either of these species of sea snakes. The rarity of epizoic bryozoans on these two species of sea snakes also suggests an accidental relationship.

ACKNOWLEDGMENTS

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