Epizoic bryozoans and mobile ephemeral host substrata

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ABSTRACT

Bryozoans are common fouling organisms on immobile permanent substrata. They are epizoic on a variety of mobile living substrata including both nektonic and mobile benthic hosts. Epizoic bryozoans are less common on mobile ephemeral substrata where the host regularly discards its outer surface. Two cheilostomate bryozoans, *Electra angulata* (Levinsen) and *Membranipora savartii* (Audouin), are reported from the seas adjacent to peninsular Malaysia on several hosts that moult or shed. These hosts include one species of horseshoe crab, *Tachypleus gigas* (Müller), and two species of hydrophiid sea snakes, *Lapemis curtus* (Shaw) and *Enhydrina schistosa* Daudin. Results indicate the horseshoe crabs are much more fouled by bryozoans as measured by the percent of hosts fouled, the number of bryozoan colonies per fouled host, and the mean surface area of the bryozoan colonies. The relative fouling rates of the bryozoans on these hosts are controlled by several factors including abrasion by the host and the frequency at which the hosts moult or shed. Despite the problems this type of relationship creates for the epizoans (e.g., unstable substratum, movement of host into stressful environments), bryozoans can accrue benefits (e.g., reduced substratum competition and predation, enhanced gene dispersal and food supply). In contrast, there are more costs (e.g., reduced function of organs, metabolic cost of antifouling behaviour) than benefits for the hosts.

Keywords: Epibiosis, fouling, ephemeral substrata, cheilostomates, sea snakes, horseshoe crabs

INTRODUCTION

Fouling of inert substrata has been well studied compared to living substrata. A variety of organisms form relatively permanent hard substrata in benthic marine environments where hard substrata are typically a limiting resource for sessile organisms. Competition for hard substrata has been well documented (Paine 1974; Jackson 1977; Connell & Keough 1985). Settlement on biological substrata, where the relationship between the host and the fouling organisms is non-symbiotic and facultative (i.e., epibiosis), is a common solution to this competition (Wahl 1989). This study restricts the discussion of epibionts to those sessile fouling organisms (infesters) that use the external surface of another organism principally as a substratum. Endosymbiotic or parasitic epizoans (infecters) are not considered.

In this study, horseshoe crabs and sea snakes act as the host organisms, or basibionts as defined by Wahl (1989). Some hosts are not suitable substrata for epizoans due to their frequent moulting or shedding. This is similar to some seaweed species that periodically shed their epidermis and therefore their epiphytes (Williams & Seed 1992). The ephemeral nature of such substrata reduces the number and density of fouling species.

Most epibionts on ephemeral biological substrata are opportunistic, exhibit early reproduction, have short life cycles, and high growth and reproductive rates (Jackson 1977; Seed 1986). These are traits typical of colonising species (Connell & Slatyer 1977). Many bryozoan species tend to be poor competitors for substratum space (McKinney & Jackson 1989), and as a result they tend frequently to occur on unconventional substrata such as floating plastic debris (Stevens *et al.* 1996, this volume). Ephemeral substrata are dominated by sheet-like, weedy, opportunistic bryozoans (Jackson 1979; McKinney & Jackson 1989). In order to establish breeding colonies on ephemeral substrata, epibiotic bryozoans must have short life cycles and high growth rates and must reproduce early (Seed 1986; Abello *et al.* 1990). Another solution to the ephemeral nature of some biological substrata is exhibited by the bryozoan *Triticella*. Some species of this genus have evolved to the point that sexual reproduction is synchronised with the moulting of the crustacean host so that the bryozoan can recolonise the host soon after moulting (Ström 1969; Eggleston 1971).

The purpose of this study is to: 1) quantitatively describe bryozoan infestation rates on horseshoe-crab and sea-snake hosts from the seas around peninsular Malaysia, 2) compare the fouling rates among the different hosts, and 3) discuss the costs and benefits of epibiosis to the foulers and hosts.

MATERIALS AND METHODS

A variety of mobile organisms with ephemeral exterior surfaces was collected from the seas around peninsular Malaysia. A collection of 75 horseshoe crabs representing two species and two genera was made around Singapore. A collection of 1,364 sea snakes representing 17 species and nine genera was made from the Straits of Malacca and the South China Sea off the coast of the state of Johor. For specific information on the dates, localities, methods, and repositories of collections, see Jeffries *et al.* (1979, 1989) and Key *et al.* (1995, 1996).

Only those host species that were fouled by bryozoans are included in this study. Other hosts and epizoans are discussed elsewhere (Jeffries *et al.* 1979, 1989; Key *et al.* 1995, 1996). Host size was measured to determine age. This was performed using standard morphometric proxies for age which are body length for the sea snakes and prosoma length and width for the horseshoe crabs. The surface area of all the hosts was calculated using the measured relationship between size and surface area for a subset of each of the hosts. The number of hosts that were fouled by bryozoans was counted. Finally, the bryozoans were identified and the sizes of the colonies measured with a PC-based image-analysis system using digitised video images of the colonies.

RESULTS

Of the 75 horseshoe crabs collected, 43 (57.3%) were fouled by bryozoans (Table 1). All the fouled horseshoe crabs belonged to *Tachypleus gigas* (Müller) (family Limulidae, order Xiphosurida, class Merostomata, subphylum Chelicerata, phylum Arthropoda – Yamasaki 1988). It has an Indo-Pacific distribution, including the coastal regions of Southeast Asia from the Bay of Bengal in India to the Malay Peninsula, Singapore, Thailand, Vietnam, Sumatra, Java, Madura, Borneo, and Palawan (Waterman 1958; Sekiguchi *et al.* 1976; Sekiguchi 1988a). Of the 56 specimens of *T. gigas* collected, 43 (76.8%) were fouled by bryozoans (Table 2), with, on average, 8.7 epizoic bryozoan colonies with a mean surface area per colony of 140.0 mm^2 (Table 2). On average, 2.5% of the surface area of each fouled horseshoe crab was covered by bryozoans (Table 2).

Table 1. Bryozoan fouling rates comparing horseshoe crab and sea snake hosts. Numbers in parentheses indicate standard deviation.

Host	horseshoe crabs	sea snakes
No. of host specimens collected	75	1,364
No. of host specimens fouled	43	11
% of host specimens fouled	57.3	0.8
Mean no. of bryozoan colonies per fouled host specimen	8.7 (8.2)	4.0 (5.2)
Mean surface area of individual bryozoan colonies (mm^2)	140.0 (62.12)	3.5 (2.4)
Mean total surface area of bryozoan colonies (cm^2) per fouled host specimen	12.18 (6.42)	0.16 (0.15)
Mean surface area of fouled host specimens (cm^2)	496 (161)	398 (133)
Mean % surface area of fouled host specimens covered by bryozoan colonies	2.46 (3.16)	0.04 (0.07)

Of the 1,364 sea snakes collected, 11 individuals (0.8%) were fouled by bryozoans (Table 1), representing two hydrophiid sea snake species: *Enhydrina schistosa* Daudin and *Lapemis curtus* (Shaw). These are both marine sea snakes with Indo-Pacific distributions (Cogger 1975; Minton 1975; Gritis & Voris 1990). In previous publications, the *Lapemis* sea snakes were assigned to *L. hardwickii* Gray which was considered a separate species from *L. curtus*. In this paper, all specimens of *L. hardwickii* will be referred to as *L. curtus* as suggested by Gritis and Voris (1990). Of the 326 specimens of *E. schistosa* collected, nine (2.8%) were fouled by bryozoans (Table 2), with, on average, 4.7 epizoic bryozoan colonies with a mean surface area per colony of 4.2 mm^2 (Table 2). A mean of 0.05% of the surface area of each fouled sea snake was covered by bryozoans (Table 2). Of the 345 specimens of *L. curtus* collected, two (0.6%) were fouled by bryozoans (Table 2), with an average of 1.0 epizoic bryozoan colony with a mean surface area per colony of 0.6 mm^2 (Table 2). A mean of 0.001% of the surface area of each fouled sea snake was covered by bryozoans (Table 2).

The epizoic bryozoans were identified as the anascan cheilostomates *Membranipora savartii* (Audouin) and *Electra angulata* (Levinsen). The zoarial habits of these bryozoans is generally two dimensional and encrusting (Canu & Bassler 1920; Mawatari 1953).

Host	*Tachypleus gigas*	*Enhydrina schistosa*	*Lapemis curtus*
No. of host specimens collected	56	326	345
No. of host specimens fouled	43	9	2
% of host specimens fouled	76.8	2.8	0.6
Mean no. of bryozoan colonies per fouled host specimen	8.7 (8.2)	4.7 (6.4)	1.0 (0.0)
Mean surface area of individual bryozoan colonies (mm^2)	140.0 (62.12)	4.2 (2.9)	0.6 (0.12)
Mean total surface area of bryozoan colonies (cm^2) per fouled host specimen	12.18 (6.42)	0.19 (0.18)	0.01 (0.001)
Mean surface area of fouled host specimens (cm^2)	496 (161)	377 (160)	491 (10.7)
Mean % surface area of fouled host specimens covered by bryozoan colonies	2.46 (3.16)	0.05 (0.08)	0.001 (0.0003)

Table 2. Bryozoan fouling rates comparing specific host species. Numbers in parentheses indicate standard deviation.

Membranipora savartii currently has a biogeographic distribution incorporating the tropical zones of the Caribbean and Red Seas as well as the Atlantic, Pacific, and Indian Oceans (Ziko & Hamza 1987). This species has also been previously reported from the waters around Singapore (Harmer 1926). *Electra angulata* has a widespread biogeographic distribution, occurring in shallow marine environments throughout the tropical Indo-Pacific and Atlantic Oceans (Mawatari 1974).

DISCUSSION

Both bryozoan species are common fouling organisms that can be found encrusting surface-drift objects such as seeds, wood, and plastic trash. They are also known as epizoans on a variety of nektonic and mobile benthic substrata. *Membranipora savartii* has been reported encrusting the sea snake *Lapemis curtus* (Zann *et al.* 1975) and various crustaceans (Liu 1992). *Electra angulata* is known as an epizoan on the sea snakes *E. schistosa*, *L. curtus*, and *Pelamis platurus* (Linnaeus) (Harmer 1926; Cuffey 1971; Zann *et al.* 1975). *Electra angulata* has also been reported to encrust living shells of cephalopods (Landman *et al.* 1987). Neither bryozoan species has been reported as epizoans on horseshoe crabs, but Rao and Rao (1972) did report an unidentified species of *Membranipora* on the horseshoe crabs *T. gigas* and *Carcinoscorpius rotundicauda* (Latreille). The published occurrences of epizoic bryozoans on horseshoe crabs and other mobile benthic hosts as well as on sea snakes and other nektonic hosts have been recently reviewed elsewhere (Key *et al.* 1995, 1996).

Causes of variation in epizoic bryozoan fouling rates on ephemeral substrates

This study shows that the bryozoans fouled the horseshoe crabs more than the sea snakes. The horseshoe crabs have a larger percentage of specimens fouled, larger number of bryozoan colonies per fouled host specimen, larger mean surface area of individual bryozoan colonies, as well as larger mean percentage surface area of fouled host specimens covered by bryozoan colonies (Table 1). Compared to the sea snakes, why are the horseshoe crabs more fouled by bryozoans? There are several possible causes. Perhaps the physical, chemical, and biological cues that bryozoan larvae need for settlement may not be as prevalent on the sea snakes. Bryozoan larvae do not haphazardly select a substratum. Instead, they show preference for specific substrata (Crisp & Ryland 1960; Woollacott & Zimmer 1971; Hurlbut 1991) which is often based on the presence of a certain microbiota (Soule & Soule 1977; Kitamura & Hirayama 1987).

There may be fewer bryozoans on the sea snakes due to the presence of keratin in the hosts' skin. Keratin in the skin of sea snakes has a low surface energy, and thus has poor adhesiveness for epizoic larvae (Zann *et al.* 1975). Bryozoan larvae may have difficulty settling on the sea snakes due to keratin.

Perhaps the differences in fouling rates among the hosts are due to their different environments. The host sea snakes could carry the bryozoans into environments that lack bryozoan larvae or that are inhospitable for bryozoan colonies (e.g., inhospitable depths, temperatures, and/or salinities). In fact, sea snakes are known to dive to great depths (Heatwole & Seymour 1975; Rubinoff *et al.* 1986). But generally sea snakes live in shallow normal marine water whereas horseshoe crabs live in environments less hospitable to bryozoans. The horseshoe crabs were collected in brackish-water environments (Key *et al.* 1996) while the sea snakes were collected in normal marine conditions (Key *et al.* 1995). The diversity of brackish-water bryozoans is much less than that of marine species (Winston 1977), and *M. savartii*, at least, is known to be restricted to waters with normal marine salinity (Menon 1973; Winston 1977). There are no data on the salinity tolerances of *E. angulata*, but only 3–6% of gymnolaemate bryozoans, to which the two epizoans in this study belong, are known to penetrate into brackish water (Winston 1977). In addition, the horseshoe crabs lay their eggs in beach sand near the high-tide mark (Sekiguchi 1988b), resulting in subaerial exposure which may have a negative impact on the epizoic bryozoans.

The more active nature of the sea snakes may make settlement and/or survival for the bryozoans more difficult. Compared to the horseshoe-crab exoskeleton, sea-snake skin is a less rigid substratum. As a sea snake's body flexes, there can be movement between adjacent scales (Zann *et al.* 1975). As a result, the growth of the epizoic bryozoan colonies on these hosts can be disrupted (Zann *et al.* 1975). In addition, colonies can be damaged by abrasion during copulation, while wedging under corals during feeding, during burrowing, and during knotting. Some sea snakes burrow in supratidal sands as part of their basking routine in colder months (Saint Girons 1990). The unique sea-snake habit of knotting has been interpreted as an antifouling behaviour (Kropach & 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 can result in the removal of unshed skin and barnacles (Zann *et al.* 1975). Horseshoe crabs on the other hand experience abrasion during burrowing, amplexus, and when exposed to moving sediment which may have a negative impact on the epizoic bryozoans. *Tachypleus gigas* has been found to burrow into the sediment during resting, feeding, and the deposition of eggs (Sekiguchi 1988b). Burrowing behaviour in malacostracan crabs has been shown to reduce the incidence of epibiosis (Mori & Zunino 1987; Abello *et al.* 1990).

Perhaps the differences in fouling rates among the hosts is due to their different sizes. It could be that the horseshoe crabs are more fouled than the sea snakes simply because the horseshoe crabs provide a larger "target" for larval settlement. This is doubtful as the mean surface area of the horseshoe crabs (496 cm^2) is only 25% larger than the mean for the sea snakes (398 cm^2). The 25% greater surface area of the horseshoe crabs does not explain the horseshoe crabs' fouling rate being 57% higher, the mean number of bryozoan colonies per fouled host specimen being 118% higher, the mean size of individual bryozoan colonies being 3,900% higher, and the mean percent surface area of fouled host specimens covered by bryozoan colonies being 6,050% higher (Table 1).

Another likely cause for the horseshoe crabs being more fouled is related to the shedding/moulting frequency of the hosts. Sea snakes continue to shed their skin throughout life (Zann et al. 1975) as opposed to horseshoe crabs which stop moulting once sexual maturity is reached (Shuster 1982). 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 other sea snakes ranges from five to 99 days (Shaw 1962; Klemmer 1967; Mays & Nickerson 1968; Zeiller 1969; Zann *et al.* 1975). The main point is that sea snakes continue to shed throughout their lives.

Based on published ontogenetic data on prosoma length and width of *T. gigas* (Sekiguchi et al. 1988; Debnath 1992), most of the *T. gigas* specimens in this study are interpreted to have been older adults in terminal anecdysis (Key *et al.* 1996). This is supported by the measured prosomal dimensions, the presence of modified claspers in males, and the abraded state of the carapaces which all indicate sexual maturity. Thus compared to the sea snakes, the horseshoe crabs provided an older, more stable substratum that had more time to be fouled before they were collected.

Benefits and costs of epibiosis to foulers

Epibiosis presents several potential benefits and costs to epizoans and their hosts. These have been recently reviewed by Wahl (1989) for marine organisms in general, by Key *et al.* (1995, 1996) for bryozoans on nektonic and mobile benthic host substrata in particular, and by Taylor (1994) for bryozoans encrusting gastropod shells inhabited by hermit crabs. There are a variety of potential benefits for epizoans living on mobile ephemeral host substrata (Table 3). First, as most marine communities experience intense competition for substratum space (Paine 1974; Jackson 1977; Connell & Keough 1985), colonisation of unoccupied living substrata may be beneficial to epizoans (Barnes & Bagenal 1951; Wahl 1989).

Second, movement of the host may improve the dispersal and gene flow of the epizoans (Wahl 1989) and expand the biogeographic distribution of the epizoans by increasing the range of larval dispersal. This benefit depends on the relative range of the hosts and the epizoans' larvae. Third, currents generated by the movement, respiration, and/or feeding of the host may

Table 3. Potential benefits and costs of epibiosis for epizoans and mobile ephemeral hosts in general. Asterisks indicate benefits and costs of epibiosis for the epizoans and hosts examined in this study.

	BENEFITS	COSTS
EPIZOAN	Reduced substratum competition* Reduced predation* Enhanced gene dispersal* Enhanced food supply and/or waste removal*	Ephemeral substratum* Food competition with host Vulnerable to host's predators* Exposure to stressful environments due to host's mobility*
HOST	Reduced predation due to camouflage from epizoan Cleaning function of epizoan	Reduced buoyancy Reduced mobility Impaired growth Reduced function of organs* Metabolic cost of antifouling behaviour* Food competion with epizoan Vulnerable to epizoan's predators

improve the food supply to suspension-feeding epizoans as well as improve the removal of wastes produced by the epizoans (Bowers 1968; Wahl 1989; Gili *et al.* 1993). Fourth, epizoans may be protected from slow-moving predators by the activities of the host (Wahl 1989; Abello *et al.* 1990). Predation of epizoic bryozoans on horseshoe crabs or sea snakes has not been observed, but living on a mobile host substratum may remove the bryozoans from their normal predators (e.g., amphipods, annelids, echinoids, isopods, nudibranchs, pycnogonids, and gastropods).

All of the potential benefits to the epizoic bryozoans in this study depend on whether or not the bryozoans were able to sexually reproduce. Unfortunately, *M. savartii* and *E. angulata* do not exhibit any obvious external morphological evidence (e.g., ovicells) of sexual reproduction. The only way to readily ascertain if the colonies were reproducing sexually is to compare the colony sizes with published data relating colony size to age of sexual reproduction. This information is available for *E. angulata* (Mawatari 1953). According to these growth-rate data, the colonies on the sea snakes were probably not sexually mature, while those on the horseshoe crabs were (Key *et al.* 1995, 1996).

There are a variety of potential costs for epizoans living on mobile ephemeral host substrata (Table 3). First, the host may constitute an unstable substratum due to morphological changes through ontogeny (Wahl 1989). The most ephemeral living substrata are those that frequently cast off their external surface. Ephemeral host substrata are created by arthropods moulting (Ross 1983), sea turtles casting off scutes (Frazier *et al.* 1984; Caine 1986), and sea snakes shedding their epidermis (Mays & Nickerson 1968). Substratum stability is a function of the longevity of the host substratum relative to the maturation time of the epizoan (Wahl 1989). As discussed above, all of the fouled horseshoe crabs were in terminal anecdysis, so these hosts provided more stable substrata than the sea snakes which continued to shed throughout their lives. In addition, the host substratum may die and degrade.

Second, epizoans may have to compete with their host for food resources (Wahl 1989). This is not a problem for the plankton-eating epizoic bryozoans and the macroinvertebrate- and vertebrate-eating host species in this study. Third, epizoans may fall victim to the predators of the host (Wahl 1989). Horseshoe crabs and sea snakes are preyed upon by sharks, turtles, birds, and mammals (Shuster 1982; Keinath *et al.* 1987; Debnath & Choudhury 1988, 1991). Fourth, epizoans may be exposed to stressful environmental conditions (e.g., inhospitable depths, salinities, or temperatures) due to the movements of the host into different environments (Wahl 1989). As discussed above, this may have contributed to the different fouling rates between the host substrata.

Benefits and costs of epibiosis to hosts

There are two potential benefits for hosts that are fouled by epizoans (Table 3). First, the epibionts may play a protective role for the host via camouflage (Rasmussen 1973; Ingle 1983; Wahl 1989; Kloc 1993). This phenomenon is best exhibited in the decorator crabs which actively affix to their exoskeleton organisms such as bryozoans, algae, kelp, sponges, hydroids, ascidians, sea anemones, corals, and polychaetes (Wicksten 1980). This potential benefit to hosts probably does not accrue to those in this study as they are too large to be effectively camouflaged by the relatively small encrustations of epizoic bryozoans.

Second, some epizoans may provide a cleaning function for their host (Bauer 1978). Bryozoans have no known cleaning abilities for the host horseshoe crabs and sea snakes.

There are many potential costs for hosts that are fouled by epizoans (Table 3). First, epizoans may reduce the buoyancy of the host (Wahl 1989). This has been suggested for some epizoic barnacles (Overstreet 1983). Due to the thin, sheet-like colonies of the epizoic bryozoans in this study, this is probably not a significant detriment to the host horseshoe crabs.

Second, epizoans may reduce the mobility of hosts. Epizoic barnacles and mussels have been implicated in decreasing the mobility of a variety of hosts (Botton 1981; Shuster 1982; Overstreet 1983). Saha (1989) suggested that the weight of epizoic sea anemones and barnacles on *T. gigas* caused reduced mobility and that this stress ultimately lead to the death of the hosts. Due to the thin, sheet-like bryozoan colonies and small percent cover of the hosts, the epizoans in this study probably do not increase drag on their hosts appreciably.

Third, epibionts may impair the growth of hosts. Epiphytic bryozoans on macroalgae cause decreased growth rates (Woollacott & North 1971), decreased photosynthesis (Oswald *et al.* 1984), and increased blade loss (Dixon *et al.* 1981). Reaka (1978) reported epizoic gastropods on host stomatopod crustaceans where the gastropods had a detrimental effect on the hosts' growth and ability to moult. Mechanical anchoring of epibionts may impair the host's ability to shed. This is common in some epizoic barnacles that impair the ability of their host sea snakes to shed (Zann 1975). As bryozoans do not anchor themselves into the tissue of their host, this is not a problem for the hosts in this study.

Fourth, epizoans may reduce the effectiveness of some of the host's organs. Sea anemones, barnacles, and mussels are known to impair the function of horseshoe crab eyes, appendages, and gills (Shipley 1909; Roonwal 1944; Botton 1981). Kropach and Soule (1973) reported an extensive epizoic bryozoan colony of *M. tuberculata* (Bosc) encrusting one eye and one nostril of the host sea snake *Pelamis platurus* (L.)

Fifth, the hosts' anti-fouling behaviours mentioned above (e.g., knotting and moulting/ shedding) presumably have a metabolic cost to the hosts (Zann *et al.* 1975).

Sixth, competition for food resources between epizoan and host may be a problem (Wahl 1989). As discussed above, this is not a problem for the hosts in this study because they do not have the same trophic requirements as the epizoic bryozoans.

Seventh, hosts may be damaged by predators of epibionts (Bernstein & Jung 1979). Due to their small size, the predators of bryozoans discussed above would probably have little effect on the host horseshoe crabs and sea snakes.

CONCLUSIONS

Overall, epibiosis is less favourable to hosts than epizoans (Wahl 1989; Abello *et al.* 1990; Table 3). As a result, a variety of antifouling structures and behaviours (e.g., tolerance, avoidance, and defense) have evolved in hosts (Wahl 1989). In situations where the host is not significantly negatively impacted by its epizoans, the host will generally tolerate fouling (Wahl 1989). This appears to be the case for the bryozoan-horseshoe crab and bryozoan-sea snake relationships.

The relationship between the epizoic bryozoans and the host horseshoe crabs and sea snakes is best described as phoretic, which refers to a facultative 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. These epizoan-host relationships are accidental as the epizoans are not restricted to this type of substratum. There are no known obligate or host-specific associations known between bryozoans and horseshoe crabs or sea snakes. This is supported by the fact that *M. savartii* and *E. angulata* are commonly found on a variety of other biotic and abiotic as well as mobile and sessile substrata and are not restricted to the hosts discussed here.

The fact that the horseshoe crabs were more fouled by bryozoans than the sea snakes is likely due to a combination of factors. The presence of keratin and the less rigid nature of the sea-snake skin may make it less inviting to settling bryozoan larvae. The antifouling knotting behaviour may further reduce the fouling rate on sea snakes. Finally, the continued shedding of the sea snake throughout its life makes it a less stable substratum for the bryozoans.

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