

EPIZOIC BRYOZOANS, HORSESHOE CRABS, AND OTHER MOBILE BENTHIC SUBSTRATES

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ABSTRACT

Two species of horseshoe crabs, *Carcinoscorpius rotundicauda* (Latreille) and *Tachypleus gigas* (Müller), were collected from the seas adjacent to Singapore to study the fouling rates of epizoic bryozoans. None of the 19 *C. rotundicauda* specimens were encrusted by bryozoans. Of the 56 individuals of *T. gigas* collected, 77% were infested by the bryozoans *Electra angulata* (Levinsen) and *Membranipora savartii* (Audouin). This difference in fouling rate between the two host species was attributed to several factors including size and age differences of the hosts, morphological differences of the hosts' carapaces, and habitat differences between the hosts. Most importantly, *C. rotundicauda* tends to occupy shallower, more estuarine, brackish water where bryozoans are less abundant. The costs and benefits of epibiosis on mobile benthic substrates such as crustacean carapaces are discussed.

Fouling of inert hard substrates has been well studied compared to living hard substrates. A variety of organisms form hard substrates in benthic marine environments where hard substrates are typically a limiting resource for sessile organisms. Competition for inert hard substrates is often intense (Connell and Keough, 1985; Jackson, 1977; Paine, 1974). As a result, settling on living hard substrates where the relationship between the host and the fouling organisms is non-symbiotic and facultative (i.e., epibiotic) is a common solution to this competition (Wahl, 1989). This study restricts the discussion of epibionts to those sessile fouling organisms that use the external surface of another organism principally as a substrate. Endosymbiotic or parasitic relationships between hosts and their epizoans are not considered.

Most epibionts can be found on sessile organisms. Epibionts are less commonly found on mobile organisms. In this study, bryozoans are the epibionts while horseshoe crabs are the host substrate organisms or basibionts as defined by Wahl (1989). Many arthropod carapaces are not suitable substrates for many epizoans due to their frequent molting in early ontogeny (Gili et al., 1993) and the tendency for some species to burrow in the substrate (Ross, 1983). This is similar to some seaweed species that periodically shed their epidermis and therefore their epiphytes (Williams and Seed, 1992). The ephemeral nature of such substrates reduces the number and density of fouling species. All of the fouled hosts in this study are adults in terminal anecysis. As such, they provide a stable substrate compared to juveniles that molt periodically.

Other than bryozoans, a wide variety of organisms are known as epizoans on mobile benthic hosts. Protists, algae, poriferans, hydrozoans, scyphozoans, sea anemones, anthozoans, cestodes, nematodes, nemertians, annelids, barnacles, molluscs, and echinoderms have been reported as epizoans on copepods, crabs, isopods, lobsters, and shrimp as well as on gastropod shells carried by pagurid (hermit) crabs (Annandale, 1909; Boss, 1965; Botton and Ropes, 1988; Bowers, 1968; Delamare-Deboutteville and Nunes, 1951; Gili et al., 1993; Hastings, 1972; Ingle, 1983; Jeffries and Voris, 1983; Jeffries et al., 1982, 1984; Jensen and Bender, 1973; Lanchester, 1902; Lewis, 1976; Mori and Manconi, 1990; Nilsson-Cantell, 1934; Norse and Estavez, 1977; Overstreet, 1983; Ross, 1983). There is

even a fossil record of these types of epizoic relationship. Clarkson and Tripp (1982) figured a colony of *Corynotrypa* on an Ordovician trilobite, while Tshudy and Feldmann (1988) reported epizoic oysters and worms fouling Cretaceous lobsters.

This study focuses on horseshoe crabs as hosts. The species of horseshoe crabs examined in this study, *Carcinoscorpius rotundicauda* (Latreille) and *Tachypleus gigas* (Müller), are known to be fouled by sea anemones, barnacles, pelecypods, gastropods, amphipods, isopods, and polychaetes (Aurivillius, 1894; Debnath, 1992; Jeffries et al., 1989; Rao and Rao, 1972; Roonwal, 1944; Saha, 1989; Shipley, 1909). The horseshoe crab *Limulus polyphemus* (Linnaeus) is fouled by a wide variety of organisms including green algae, diatoms, coelenterates, flat worms, mussels, oysters, annelids, barnacles, and tunicates (Davis and Fried, 1977; Humm and Wharton, 1942; MacKenzie, 1979; Pearse, 1947, 1949; Shuster, 1982; Verrill, 1893, 1895; Wheeler, 1894).

The purpose of this study is to: 1) quantitatively describe the bryozoan fouling rates on horseshoe crabs from Singapore, 2) compare the fouling rate between the different host species, 3) determine if the epizoic bryozoan-host horseshoe crab relationship permitted sexual reproduction by the bryozoans, and 4) review the costs and benefits of epibiosis on mobile benthic substrates.

The Hosts.—*Carcinoscorpius rotundicauda* and *Tachypleus gigas* belong to the family Limulidae, Order Xiphosurida, Class Merostomata, Subphylum Chelicerata, Phylum Arthropoda (Yamasaki, 1988a). They both have Indo-Pacific distributions (Sekiguchi and Nakamura, 1979; Shuster, 1982). *C. rotundicauda* is found in coastal regions of Southeast Asia from the Bay of Bengal in India to the Malay Peninsula, Singapore, Thailand, Philippines, Sumatra, Java, Madura, Borneo, and Palawan (Sekiguchi, 1988a). *T. gigas* has the same environmental and biogeographic range as *C. rotundicauda* except that *T. gigas* is not found in the Philippines but is found in Vietnam (Sekiguchi, 1988a; Sekiguchi et al., 1976).

The Epizoans.—Two species of anascan, cheilostome, gymnolaemate bryozoans were identified as epizoans on the host horseshoe crabs. These are *Membranipora savartii* (Audouin) and *Electra angulata* (Levinsen). These species are known as epizoans on a variety of nektonic substrates. *M. savartii* has been reported encrusting the sea snake *Lapemis hardwickii* (Gray) (Zann et al., 1975) and various crustaceans (Xi-Xing, 1992). *E. angulata* is known as an epizoan on the sea snakes *Enhydrina schistosa* Daudin, *L. hardwickii*, and *Pelamis platurus* (Linnaeus) (Cuffey, 1971; Harmer, 1926; Key et al., 1995; Zann et al., 1975). *E. angulata* has also been reported to encrust shells of living cephalopods (Landman et al., 1987). Both bryozoan species are common fouling organisms that can also be found encrusting surface-drift objects such as seeds, wood, and plastic trash.

The zoarial habit of *M. savartii* is generally two dimensional and encrusting but it can grow erect (Canu and Bassler, 1920; Cook, 1968; Harmer, 1926; Mawatari, 1974; Osburn, 1940; Xi-Xing, 1992; Ziko and Hamza, 1987). All the specimens in this study were encrusting sheets. Ovicells are lacking (Harmer, 1926; Osburn, 1940; Xi-Xing, 1992), so in the field there is no easy way to determine if the colonies were sexually reproducing. There is no published data on growth rates in this species.

M. savartii has a biogeographic distribution incorporating the tropical zones of the Caribbean and Red Seas as well as the Atlantic, Pacific, and Indian Oceans (Canu, 1912; Canu and Bassler, 1920; Cook, 1968; Harmer, 1926; Mawatari, 1974; Osburn, 1940; Rao and Ganapati, 1974; Xi-Xing, 1992; Ziko and Hamza, 1987). This species has been previously reported from the waters around Singa-

Table 1. Carapace size and bryozoan fouling data for *Carcinoscorpius rotundicauda*

Character	Males	Females	Total
Hosts collected (no.)	13	5	18 + 1 juvenile
Hosts collected (%)	68.4	26.3	100
Mean host prosoma length (mm)	59.1	74.8	63.5
Mean host prosoma width (mm)	106.4	127.9	112.4
Hosts fouled (no.)	0	0	0

pore (Harmer, 1926) where the material for this study came from. The species is generally found in nearshore marine environments in less than 60 m of water (Canu, 1912; Canu and Bassler, 1920; Cook, 1968; Harmer, 1926; Osburn, 1940; Ziko and Hamza, 1987).

The zoarial habit of *E. angulata* is two dimensional and encrusting (Mawatari, 1953, 1974; Rao and Ganapati, 1974). Ovicells are lacking (Mawatari, 1953, 1974; Rao and Ganapati, 1974), so in the field there is no easy way to determine if the colonies were sexually reproducing. The only growth rate data on this species comes from Mawatari (1953). That study measured the growth rate of *E. angulata* colonies on test panels off the coast of Japan. Results indicate a rapid growth rate, with colonies covering 300 mm² within 15 days of larval settlement. At the end of a month, some colonies covered over 1,000 mm². Mawatari (1953) also found that many of the colonies reached sexual maturity in only 3 months.

E. angulata has a widespread biogeographic distribution. It occurs in shallow marine environments throughout the tropical Indo-Pacific and Atlantic Oceans and possibly even the Caribbean Sea (Landman et al., 1987; Mawatari, 1953, 1974; Rao and Ganapati, 1974; Zann et al., 1975).

MATERIALS AND METHODS

All material used in this study is housed in the Zoological Reference Collection (ZRC) in the Department of Zoology of the National University of Singapore. On 9 March 1988, 19 specimens (ZRC.1988.2179–ZRC.1988.2197) of *C. rotundicauda* were collected in the Kranji mangrove swamp, Singapore (1°26'N 103°45'E). The specimens were collected at low tide when they were subaerially exposed or half buried in mud. This collection consisted of 13 males, five females, and one juvenile.

Between December 1985 and May 1987, 56 specimens of *T. gigas* were collected from the shallow marine waters around Singapore. The specimens were collected by trawl nets and drift nets near shore. These specimens consisted of 38 males and 18 females. Four specimens (ZRC.1986.9–ZRC.1986.12) were collected on 2 December 1985 and one specimen (ZRC.1986.13) was collected on 18 December 1985 from the Singapore Straits near Sentosa Island, Singapore (1°15'N 103°50'E). Six specimens (ZRC.1986.3–ZRC.1986.8) were collected on 18 January 1986 and two specimens (ZRC.1986.1–ZRC.1986.2) were collected on 4 April 1986 off Kusu Island, south of Singapore (1°14'N 103°52'E). Three specimens (ZRC.1987.54–ZRC.1987.56) were collected on 14 May 1987 and 40 specimens (ZRC.1987.876–ZRC.1987.915) were collected on 15 May 1987 at Tuas, Singapore (1°19'N 103°40'E).

Host size was measured to determine age. This was performed using prosoma length and width which are standard morphometric proxies for age in these horseshoe crabs (Debnath, 1992; Sekiguchi et al., 1988). The horseshoe crabs were sexed in the field, the degree of abrasion of the carapaces was noted, and the number of horseshoe crabs that were fouled by bryozoans was counted. Finally, the bryozoans were identified.

RESULTS AND DISCUSSION

C. rotundicauda individuals are smaller than those of *T. gigas* (Yamasaki, 1988a, 1988b). In this study, the specimens of *T. gigas* were 160% larger in surface area than those of *C. rotundicauda* (Tables 1, 2). Surface area was estimated by prosoma length times prosoma width. As with all horseshoe crabs,

Table 2. Carapace size and bryozoan fouling data for *Tachypleus gigas*

Character	Males	Females	Total
Hosts collected (no.)	38	18	56
Hosts collected (%)	67.9	32.1	100
Mean host prosoma length (mm)	88.1	123.2	99.4
Mean host prosoma width (mm)	156.7	204.2	172.0
Hosts fouled (no.)	29	14	43
Hosts fouled (%)	76.3	77.7	76.8

sexual dimorphism is most obviously expressed as larger body size in females (Debnath and Choudhury, 1991; Yamasaki, 1988a, 1988b). The *C. rotundicauda* females collected in this study had 52% more surface area than their male counterparts (Table 1, Fig. 1), while the *T. gigas* females had 82% more surface area than the males (Table 2, Fig. 2).

Of the 19 specimens of *C. rotundicauda* examined, none were fouled by bryozoans (Table 1). Of the 56 specimens of *T. gigas* examined, 43 (76.8%) were fouled by bryozoans (Table 2). Jeffries et al. (1989) examined the exact same specimens for barnacles and found that 1) of the *C. rotundicauda* specimens, none were fouled by lepadomorph barnacles and 94.7% were fouled by balanomorph barnacles, and 2) of the *T. gigas* specimens, 69.6% were fouled by lepadomorph barnacles and 50.0% were fouled by balanomorph barnacles.

Why was *T. gigas* fouled by bryozoans, while *C. rotundicauda* was not? There are several possible hypotheses. It may be that the absence of epizoic bryozoans on *C. rotundicauda* is a consequence of it being a smaller target for settling epizoic larvae. As mentioned previously, *T. gigas* on average has 160% more surface area than *C. rotundicauda*, making it an easier target for settling larvae. This pattern of *T. gigas* being more fouled is supported by lepadomorph barnacle data but contradicted by balanomorph barnacle data (Jeffries et al., 1989).

Perhaps the difference in the incidence of fouling in these two host species is due to the fact that unlike *T. gigas*, extensive areas of the *C. rotundicauda* carapace are covered by small bristle-like hairs (Yamasaki, 1988b). Though no con-

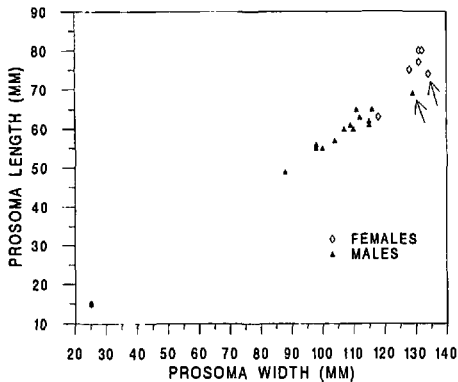


Figure 1 (left). Prosoma size for *Carcinoscorpium rotundicauda* specimens. Arrows point to Sekiguchi et al.'s (1988) data indicating mean size of adult individuals in terminal anecydysis. Juvenile indicated by overlain male and female symbols.

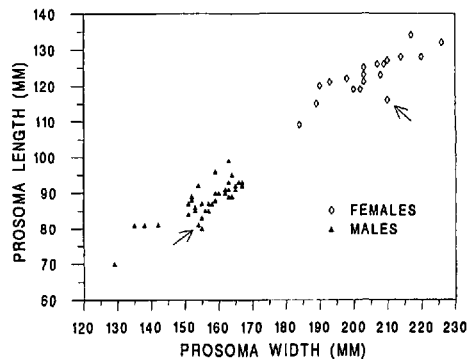


Figure 2 (right). Prosoma size for *Tachypleus gigas* specimens. Arrows point to Sekiguchi et al.'s (1988) data indicating mean size of adult individuals in terminal anecydysis.

trolled study was performed to test this hypothesis, these hairs may deter settlement by epizoic larvae.

An alternative hypothesis for this difference is that these two species spend at least part of their lives in different environments. *T. gigas* is restricted to more coastal environments, while *C. rotundicauda* travels further up estuaries by as far as 145 km to breed (Annandale, 1909; Rao and Rao, 1972; Saha, 1989; Sekiguchi, 1988b). In these upstream environments, the water is less saline than the water in which *T. gigas* lives (Sekiguchi, 1988b). The *T. gigas* specimens were collected in the coastal waters around Singapore where the salinities range from 25.0 to 31.0‰. The *C. rotundicauda* specimens were collected in the Kranji mangrove swamp where the salinities range from 15.0 to 27.5‰.

Perhaps there are fewer epizoic bryozoan larvae in this lower salinity water. It is well known that the diversity of fresh or brackish water bryozoans is much less than that of marine species (Winston, 1977). *M. savartii* is known to be restricted to more normal marine water (Menon, 1973; Winston, 1977). There is no data on the salinity tolerances of *E. angulata*, but only 3–6% of gymnolaemate bryozoans, of which the two epizoans in this study belong, are known to penetrate into brackish water (Winston, 1977). Thus, *E. angulata* is probably also restricted to water with more normal marine salinity.

Bryozoans do not have to spend much time in lower salinity water to be adversely affected. Marine bryozoans often die within several hours of being exposed to lower salinity water (Menon and Nair, 1970). Any of these lightly calcified epizoic bryozoans that may have settled on their host while their host was in more normal marine water may have died and sloughed off their host when exposed to overly brackish water (Menon, 1973). Thus, the trip up the estuaries into the lower salinity water may have removed any epizoic bryozoans from the *C. rotundicauda* hosts.

These same specimens of *C. rotundicauda* were examined for barnacles, and none had lepadomorph barnacles, but 94.7% had balanomorph barnacles (Jeffries et al., 1989). Perhaps since balanomorph barnacles have enclosed body surfaces with less of their tissue directly exposed to their environment, they can withstand lower salinity water compared to the exposed body surfaces of lepadomorph barnacles with their long peduncles. Perhaps, there are no epizoic bryozoans nor lepadomorph barnacles on *C. rotundicauda* because it spends part of its life in brackish water. This hypothesis is supported by specimens collected by Rao and Rao (1972) who reported that *C. rotundicauda* had more than twice as many epizoic balanomorph barnacles as *T. gigas*.

If salinity differences are not the causal factor for the lack of bryozoans on *C. rotundicauda*, temperature may be. Temperature is an important control on the distribution of bryozoans (Gautier, 1962; Ryland, 1970). Perhaps *C. rotundicauda* lacked epizoic bryozoans compared to *T. gigas* because these two species spend at least part of their lives in different temperature environments. In the Kranji mangrove swamp where the *C. rotundicauda* specimens were collected, the temperatures range from 28.5 to 31.0°C. In the coastal waters around Singapore where the *T. gigas* specimens were collected, the temperatures range from 27.0 to 30.0°C. In addition at low tide, the *C. rotundicauda* specimens may be subaerially exposed for a longer period of time than those of *T. gigas*.

Perhaps *C. rotundicauda* lacks epizoic bryozoans because the individuals collected had molted closer to their collection date compared to *T. gigas*. All but one of the *C. rotundicauda* specimens are interpreted to have been younger adults in terminal anecdyosis. This is supported by four reasons. First, all but one of the *C. rotundicauda* specimens cluster closer to published ontogenetic data on pro-

soma length and width of younger adult *C. rotundicauda* males and females (Debnath, 1992; Sekiguchi et al., 1988) than to juveniles (Fig. 1). The use of prosoma size to determine age must be done cautiously as it is affected by both age and geographical habitat differences. The reference points for adults used in Figure 1 may reflect geographical habitat differences of separate populations. Second, the adult age of the males is confirmed by the presence of modified claspers used in amplexus. Third, the carapaces of both sexes are less abraded which is indicative of a shorter time in terminal anecdyosis. Abrasion is caused by burrowing and amplexus. Fourth as mentioned previously, one of the specimens was even a juvenile.

On the other hand based on the same type of published ontogenetic data on prosoma length and width of *T. gigas* males and females (Debnath, 1992; Sekiguchi et al., 1988), most of the *T. gigas* specimens in this study are interpreted to have been older adults in terminal anecdyosis (Fig. 2). This is supported by the prosomal dimensions (Fig. 2), the presence of modified claspers in males, and the more abraded carapaces in both sexes. Thus compared to *C. rotundicauda*, the *T. gigas* specimens may have provided an older substrate that had more time to be fouled before they were collected.

Previously Reported Epizoic Bryozoans on Horseshoe Crabs.—Only three published references have been made to epizoic bryozoans on horseshoe crabs. Pearse (1947) reported the bryozoan *Schizoporella unicornis* (Johnston) as an epizoan on the horseshoe crab *Limulus polyphemus*. Rao and Rao (1972) reported an unidentified species of the bryozoan *M.* on *T. gigas* and *C. rotundicauda*. Butler and Cuffey (1991) reported *Alcyonidium polyoum* (Hassall), *Conopeum tenuissimum* (Canu), *Electra hastingsae* Marcus, *M. tenuis* Desor, and *S. errata* (Waters) on *L. polyphemus*. There have been three unpublished references to epizoic bryozoans on horseshoe crabs. Allee (1922) reported *Bugula turrita* (Desor), *M. crustulenta* Palla, *Membranipora* sp?, *Schizoporella* sp?, on *L. polyphemus*. Watts (1957) listed *M. crustulenta* on *L. polyphemus*. Finally, Debnath (1992) reported an unidentified species of *Membranipora* as an epizoan on both *T. gigas* and *C. rotundicauda*.

Previously Reported Epizoic Bryozoans on other Mobile Benthic Hosts.—Bryozoans are known to encrust a variety of sessile benthic substrates, but their distribution on mobile benthic substrates is less well known. Bryozoans have been reported as epizoans on crabs, isopods, gastropods, and holothurians (Abello et al., 1990; Cadee, 1991; Campbell, 1992; Colodey et al., 1980; Ingle, 1983; Mori and Manconi, 1990; Moyano, 1989; Moyano and Wendt, 1981). See Table 3 for a list of known extant epizoic bryozoan species on a variety of mobile benthic hosts.

There is a scanty fossil record of epizoic bryozoans on mobile benthic substrates. Tetreault (1992) reported epizoic bryozoans on a Silurian trilobite. Whittington (1992) figured an unidentified epizoic bryozoan on an Ordovician trilobite. Kloc (1993) reported epizoic bryozoans encrusting Ordovician and Devonian trilobites. Interpreting the occurrence of fossil epibionts 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.

Epizoic bryozoans are also known to encrust gastropod shells carried by pagurid (hermit) crabs (Baluk and Radwanski, 1984; Bishop, 1987; Cook, 1968, 1970, 1985; Gordon, 1972; Kirkpatrick and Metzelaar, 1922; Morris et al., 1989, 1991; Taylor, 1991; Taylor and Cook, 1981; Taylor et al., 1989). Hermit crab occupied-gastropod shells have been fouled by bryozoans since possibly the De-

Table 3. List of reported extant epizoic bryozoans on mobile benthic hosts (Species names are listed as published)

Bryozoan	Host	Reference
<i>Alcyonidium polyoum</i> (Hassall)	<i>Limulus polyphemus</i> (Linnaeus)	Butler and Cuffey, 1991
<i>Acyonidium verrilli</i> Osburn	<i>Callinectes sapidus</i> Rathbun	Watts, 1957
<i>Bowerbankia caudata</i> Hincks	<i>Hyas coarctatus</i> Leach	Roper, 1913
<i>Bugula avicularis</i> (Linnaeus)	<i>Hyas coarctatus</i> Leach	Roper, 1913
<i>Bugula calathus</i> Norman	<i>Maia squinado</i> Herbst	Richard, 1899
<i>Bugula calathus</i> Norman	<i>Pisa gibbsi</i> Leach	Richard, 1899
<i>Bugula flabellata</i> Thompson	<i>Maia squinado</i> Herbst	Bonnier, 1887; Richard, 1899
<i>Bugula plumosa</i> Pallas	<i>Maia squinado</i> Herbst	Bonnier, 1887; Richard, 1899
<i>Bugula turbinata</i> Alder	<i>Maia squinado</i> Herbst	Richard, 1899
<i>Bugula turbinata</i> Alder	<i>Maia verrucosa</i> Milne-Edwards	Richard, 1899
<i>Bugula turrita</i> (Desor)	<i>Limulus polyphemus</i> (Linnaeus)	Richard, 1899
<i>Bugula</i> sp.	<i>Maia squinado</i> Herbst	Allee, 1922
<i>Carbasea papyrea</i> (Pallas)	<i>Pisa</i> sp.	Stevcic, 1966
<i>Conopeum tenuissimum</i> (Canu)	<i>Limulus polyphemus</i> (Linnaeus)	Prenant and Robin, 1956
<i>Electra hastingsae</i> Marcus	<i>Limulus polyphemus</i> (Linnaeus)	Butler and Cuffey, 1991
<i>Electra pilosa</i> (Linnaeus)	<i>Geryon tridens</i> Kroyer	Butler and Cuffey, 1991
<i>Eucreatea chelata</i> (Linnaeus)	<i>Cancer pagurus</i> Linnaeus	Silen, 1936
<i>Flustra papyracea</i> Ellis et Sol	<i>Cancer pagurus</i> Linnaeus	Renouf, 1932
<i>Flustra papyracea</i> Ellis et Sol	<i>Pisa gibbsi</i> Leach	Bonnier, 1887
<i>Flustra securifrons</i> Pallas	<i>Maia squinado</i> Herbst	Richard, 1899
<i>Flustra securifrons</i> Pallas	<i>Pisa gibbsi</i> Leach	Bonnier, 1887
<i>Hippuraria egeroni</i> Busk	<i>Gonoplax angulatus</i> Pennant	Richard, 1899
<i>Hornera lichenoides</i> Linnaeus	<i>Maia squinado</i> Herbst	Busk, 1874
<i>Membranipora crustulenta</i> Palla	<i>Callinectes sapidus</i> Rathbun	Bonnier, 1887; Richard, 1899
<i>Membranipora crustulenta</i> Palla	<i>Limulus polyphemus</i> (Linnaeus)	Watts, 1957
<i>Membranipora pilosa</i> (Linnaeus)	<i>Carcinus maenas</i> Pennant	Allee, 1922; Watts, 1957
<i>Membranipora savartii</i> (Audouin)	unidentified crustaceans	M'Intosh, 1865
<i>Membranipora tenuis</i> Desor	<i>Limulus polyphemus</i> (Linnaeus)	Xi-Xing, 1992
<i>Membranipora</i> sp.	<i>Carcinoscorpius rotundicauda</i> (Latreille)	Butler and Cuffey, 1991
<i>Membranipora</i> sp.	<i>Tachylepus gigas</i> (Müller)	Rao and Rao, 1972; Debnath, 1992
<i>Membranipora</i> sp?	<i>Limulus polyphemus</i> (Linnaeus)	Rao and Rao, 1972; Debnath, 1992
<i>Microporella impressa</i> Audouin	<i>Cancer pagurus</i> Linnaeus	Allee, 1922
<i>Nolella annexens</i> Harmer	<i>Bathynectes pipertius</i> Manning and Holthuis	Renouf, 1932
<i>Schizoporella errata</i> (Waters)	<i>Limulus polyphemus</i> (Linnaeus)	Gili et al., 1993
		Butler and Cuffey, 1991

Table 3. Continued.

Bryozoan	Host	Reference
<i>Schizoporella sanguinea</i> Mont.	<i>Maia squinado</i> Herbst	Richard, 1899
<i>Schizoporella sanguinea</i> Mont.	<i>Maia verrucosa</i> Milne-Edwards	Richard, 1899
<i>Schizoporella unicornis</i> (Johnston)	<i>Limulus polyphemus</i> (Linnaeus)	Pearse, 1947
<i>Schizoporella</i> sp?	<i>Limulus polyphemus</i> (Linnaeus)	Allee, 1922
<i>Scrupocellaria reptans</i> Linnaeus	<i>Maia verrucosa</i> Milne-Edwards	Richard, 1899
<i>Scrupocellaria scruposa</i> Linnaeus	<i>Stenorhynchus longirostris</i> Fabricius	Richard, 1899
<i>Terminoflustra tenella</i> (Hincks)	<i>Pisa</i> sp.	Prenant and Bobin, 1956
<i>Triticella boeckii</i> Sars	<i>Calocaris macandreae</i> (Bell)	Roper, 1913
<i>Triticella boeckii</i> Sars	<i>Geryon tridens</i> Kroyer	Sars, 1873
<i>Triticella boeckii</i> Sars	<i>Portunus depurator</i> Linnaeus	Duerden, 1893
<i>Triticella boeckii</i> Sars	<i>Xantho rivulosus</i> Risso	Winther, 1877
<i>Triticella elongata</i> (Osburn)	<i>Callinectes sapidus</i> Rathbun	Osburn, 1944; Watts, 1957
<i>Triticella flava</i> Dalyell	<i>Sacculina carcini</i> Thompson	Richard, 1899; Hayward, 1985
<i>Triticella flava</i> Dalyell	unidentified crustacean	Silen, 1936
<i>Triticella flava</i> Dalyell	<i>Calocaris macandreae</i> (Bell)	Hayward, 1985
<i>Triticella flava</i> Dalyell	<i>Carcinus maenas</i> Pennant	Hayward, 1985
<i>Triticella flava</i> Dalyell	<i>Goneplax rhomboides</i> Heller	Hayward, 1985
<i>Triticella flava</i> Dalyell	<i>Liocarcinus</i> sp.	Hayward, 1985
<i>Triticella flava</i> Dalyell	<i>Nephrops norvegicus</i> Linnaeus	Hayward, 1985
<i>Triticella flava</i> Dalyell	<i>Upogebia</i> sp.	Eggleston, 1969, 1971, 1972; Richard, 1899; Roper, 1913; Silen, 1936
<i>Triticella koreni</i> Sars	<i>Calocaris macandreae</i> (Bell)	Silen, 1936
<i>Triticella koreni</i> Sars	<i>Geryon tridens</i> Kroyer	Eggleston, 1969, 1972
<i>Triticella koreni</i> Sars	<i>Nephoplax rhomboides</i> Heller	Eggleston, 1969, 1972
<i>Triticella koreni</i> Sars	<i>Nephrops norvegicus</i> Linnaeus	Duerden, 1893
<i>Triticella koreni</i> Sars	<i>Portunus arcuatus</i> Leach	Duerden, 1893; Richard, 1899
<i>Triticella koreni</i> Sars	<i>Sacculina carcina</i> Thompson	Duerden, 1893
<i>Triticella koreni</i> Sars	<i>Xanthia rivulosa</i> Risso	Eggleston, 1969
<i>Triticella koreni</i> Sars	<i>Upogebia deltaura</i> (Leach)	Hyman, 1959
<i>Triticella</i> sp.	unidentified crustacean	Mori and Manconi, 1990
<i>Turbicellopora</i> sp.	<i>Paromola cuvieri</i> (Risso)	Mori and Manconi, 1990
<i>Turbicellopsis</i> sp.	<i>Paromola cuvieri</i> (Risso)	Mori and Manconi, 1990
<i>Tubulipora</i> sp.	<i>Paromola cuvieri</i> (Risso)	Mori and Manconi, 1990

vonian (Morris et al., 1991), but definitely since the Jurassic (Buge and Fischer, 1970; Glaessner, 1969; Morris et al., 1989; Palmer and Hancock, 1973; Roger and Buge, 1947; Taylor, 1976; Taylor and Cook, 1981; Walker, 1988; Walter, 1969).

Previously Reported Epizoic Bryozoans on Nektonic Hosts.—Epibiont communities are also known on nektonic substrates. Bryozoans are occasional epizoans on sea snakes (Cantor, 1841; Cuffey, 1971; Harmer, 1926; Key et al., 1995; Kharin, 1981; Kropach and Soule, 1973; Zann et al., 1975). Bryozoans have also been reported on sea turtles (Annandale, 1912; Frazier et al., 1992; Jackson and Ross, 1975) and cephalopods (Landman et al., 1987).

Benefits of Epibiosis to Epizoans.—There are a variety of potential benefits to epizoans living on mobile benthic host substrates. As most marine communities experience intense competition for substrate space (Connell and Keough, 1985; Jackson, 1977; Paine, 1974), colonization of unoccupied living substrates may be beneficial to epizoans (Barnes and Bagenal, 1951; Wahl, 1989). Laterally growing epizoans (e.g., encrusting bryozoan colonies) may benefit from the growth of their hosts as they can colonize the newly emerging surface of the host (Wahl, 1989). This only applies to hosts that grow by accretion, not to those that grow by molting as in this study.

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.

Currents generated by the movement, breathing, and/or feeding of the host may improve the food supply to suspension feeding epizoans as well as improve the removal of wastes produced by the epizoans (Bowers, 1968; Gili et al., 1993; Wahl, 1989).

Epizoans may be protected from slow moving predators by the activities of the host (Abello et al., 1990; Wahl, 1989). Predation of epizoic bryozoans on horseshoe crabs has not been observed, but bryozoans are known to be predated by a variety of organisms such as amphipods, annelids, echinoids, fishes, isopods, nudibranchs, pycnogonids, and gastropods (McKinney and Jackson, 1989). This may not be a significant benefit to the epizoic bryozoans as horseshoe crabs are quiescent for varying lengths of time while awaiting the tidal change or the return of warm weather months.

All of these potential benefits to the epizoic bryozoans in this study depend on whether or not the bryozoans were able to sexually reproduce. Unfortunately as discussed above, *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 data is only available for *E. angulata* (Mawatari, 1953). According to this growth rate data, these colonies were probably not sexually mature. But since the hosts were in terminal anecdyosis, the colonies would probably eventually be able to sexually reproduce. Thus, the relationship between the epizoic bryozoans and the host horseshoe crabs is facultative. This is supported by the fact that *M. savartii* and *E. angulata* are commonly found on a variety of other mobile and sessile substrates and are not restricted to this species of horseshoe crab. Many epizoic bryozoans are unspecific random settlers (Ross, 1983).

Costs of Epibiosis to Epizoans.—There are a variety of potential costs to epizoans living on mobile benthic host substrates.

Host substrates may be unstable due to morphological changes of hosts through ontogeny (Wahl, 1989). The most ephemeral living substrates are those that frequently cast off their external surface. Many arthropods molt, and ecdysis helps keep the host's exoskeleton free from epizoans (Ross, 1983). This is similar to sea turtles casting off scutes (Caine, 1986; Frazier et al., 1984) and sea snakes shedding their epidermis (Mays and Nickerson, 1968). Substrate stability is a function of the longevity of the host substrate relative to the maturation time of the epizoan (Wahl, 1989). As discussed above, all of the fouled horseshoe crabs were in terminal anecdyosis, so these hosts provided stable substrates.

Substrate stability is not only a problem for epizoans on animal hosts. Some seaweed species periodically shed their epidermis and therefore their epiphytes (Filion-Myklebust and Norton, 1981; Williams and Seed, 1992). It has been hypothesized that epidermis shedding evolved as an antifouling behavior in response to fouling pressure due to the longevity of the host species. For most seaweeds, shedding is not cost effective because their branches are shorter lived. Metabolically expensive antifouling behaviors such as shedding are more cost effective for longer lived hosts (Wahl, 1989).

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 macro-invertebrate-eating host horseshoe crabs of this study.

Epizoans may fall victim to the predators of the host (Wahl, 1989). Horseshoe crabs are preyed upon by sharks, turtles, birds, and mammals (Debnath and Choudhury, 1988, 1991; Keinath et al., 1987; Shuster, 1982).

Epizoans may be exposed to stressful environmental conditions (e.g., inhospitable depths, salinities, or water temperatures) due to the movements of the host into different environments (Wahl, 1989). This has been suggested as a problem for epizoans on sea snakes (Key et al., 1995) and sea turtles (Caine, 1986) both of which may carry their epizoans into water of radically differing temperatures, salinities, etc. This was implicated above as a possible reason for the lack of epizoic bryozoans on the *C. rotundicauda* specimens.

The host horseshoe crab *T. gigas* lays its eggs in beach sand near the high tide mark (Sekiguchi, 1988b). This may have a negative impact on the epizoic bryozoans due to subaerial exposure. This species also burrows into the sediment during resting, feeding, and the deposition of eggs (Sekiguchi, 1988b). This may have a negative impact on the epizoic bryozoans due to abrasion from burrowing. Burrowing behavior in other crabs has been shown to reduce the incidence of epibiosis (Abello et al., 1990; Mori and Zunino, 1987).

Benefits of Epibiosis to Hosts.—Epibionts can provide two possible benefits to their host. The epibionts may play a protective role for the host via camouflage (Wahl, 1989). This phenomenon is best exhibited in the decorator crabs which actively affix bryozoans, algae, kelp, sponges, hydroids, ascidians, sea anemones, corals, and polychaetes (Wicksten, 1980). Ingle (1983) and Rasmussen (1973) argued that epibionts on crabs serve a protective value to the host via camouflage. Kloc (1993) interpreted the fouling of some Paleozoic trilobites as providing a benefit to the hosts by breaking up the outlines of the hosts and making them less conspicuous to predators. This potential benefit to hosts probably does not accrue to the horseshoe crabs in this study as they are too large to be effectively camouflaged by the relatively small encrustations of epizoic bryozoans.

Some epizoans may provide a cleaning function for their host. This has been

suggested for epizoic decapods that actually reduce the fouling of their hosts through their cleaning activities (Bauer, 1978). Bryozoans have no known cleaning abilities for the host horseshoe crabs.

Costs of Epibiosis to Hosts.—In some epizoan-host relationships, the hosts are known to be negatively impacted. Epizoans may negatively affect the function of their host through a variety of ways. 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.

Epizoans may reduce the mobility of hosts. Epizoic protozoans and diatoms on pelagic crustacean zooplankton impede the hosts' ability to avoid and escape predators, to obtain food, and to maintain their position in the water column (Chiavelli et al., 1993). Epizoic barnacles that encrust their crustacean host's appendages hamper their host's movement (Overstreet, 1983). Mussel infestations on the ventral surface of the horseshoe crab *Limulus polyphemus* can impair movement of the host's appendages (Botton, 1981; Shuster, 1982). Saha (1989) suggested that the weight of epizoic sea anemones and barnacles on *T. gigas* and *C. rotundicauda* causes reduced mobility and that this stress ultimately leads to the death of the hosts. Erect, branching epizoans may increase the drag of mobile hosts. Due to the thin sheet-like colonies and small percent cover of the epizoic bryozoans in this study, this is probably not a significant detriment to the host horseshoe crabs. Epizoans may reduce the flexibility of hosts. This is especially true of rigid, encrusting epizoans. Due to the relatively rigid nature of the carapaces of the host horseshoe crabs and the thin, flexible nature of the bryozoan colonies, the bryozoans are probably not a significant detriment to the hosts in this respect.

Epibionts may impair the growth of hosts. Epiphytic bryozoans on macroalgae cause decreased growth rates (Woollacott and 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 molt. 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 substrate, this is not a problem for the host horseshoe crabs in this study.

Epizoans may reduce the effectiveness of some of the host's organs. Mussel infestations on the branchial appendages of the horseshoe crab *Limulus polyphemus* can impair aeration of the host's gills (Botton, 1981). Epizoic bryozoans have been reported to encrust the eyes and antenna of their host crabs (Cadee, 1991; Renouf, 1932). This often leads to the loss of function of the organ (Cadee, 1991). Epizoic hydroids are known to penetrate the eyes of shrimp (Overstreet, 1973). Roonwal (1944) and Shipley (1909) reported that the eyes of some host horseshoe crabs were covered by epizoic sea anemones and barnacles.

Competition for food resources between epizoan and host may be a problem (Wahl, 1989). As discussed above, it is not a problem for the host horseshoe crabs because they do not have the same trophic requirements as the epizoic bryozoans.

Hosts may be damaged by predators of epibionts. The predators of bryozoans discussed above would probably have little affect on the host horseshoe crabs. This is not true for all epizoan-host relationships. Epizoic protozoans and diatoms on pelagic crustacean zooplankton increase the hosts' vulnerability to planktivo-

rous fish (Chiavelli et al., 1993). Marine macroalgae that are encrusted by epiphytic bryozoans are more readily damaged by carnivorous fish (Bernstein and Jung, 1979).

Overall, epibiosis is less favorable to hosts than epizoans (Abello et al., 1990; Wahl, 1989). As a result, a variety of antifouling structures and behaviors (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 relationship.

Some morphological structures and behavioral patterns of the host horseshoe crabs may serve antifouling functions, but these are probably secondary/fortuitous functions. As mentioned above, small hair-like bristles on the carapace of the horseshoe crabs (Yamasaki, 1988b) may hinder colony growth in the encrusting, sheet-like bryozoans. As discussed above, the subaerial egg laying, burrowing into sediment, and molting all have negative impacts on the epizoic bryozoans. Undoubtedly, these behaviors evolved primarily for reasons other than defense against fouling.

CONCLUSIONS

Seventy five horseshoe crabs belonging to two species were collected from the seas adjacent to Singapore. None of the *C. rotundicauda* horseshoe crabs were fouled by epizoic bryozoans while 77% of the *T. gigas* horseshoe crabs were fouled. The bryozoans belonged to the species *E. angulata* and *M. savartii*. The differences in fouling rate between the two host horseshoe crab species was attributed to several factors including the fact that *C. rotundicauda* spends part of its life in shallower, brackish water which is detrimental to the fouling bryozoans.

The pattern of bryozoan-horseshoe crab relationships that emerges from this and previous studies is that *E. angulata* and *M. savartii* have adapted to a wide range of substrates and are not restricted to horseshoe crabs. These species are able to exploit an extremely diverse range of mobile benthic hosts. As such, the relationship between the host horseshoe crabs and the epizoic bryozoans is non-symbiotic and facultative. The bryozoans were probably able to sexually reproduce while on the adult host horseshoe crabs. The host horseshoe crabs are minimally impacted by the fouling bryozoans. Thus, they seem to tolerate the bryozoans and do not actively defend themselves against fouling.

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