# BRYOZOAN FOULING OF THE BLUE CRAB *CALLINECTES SAPIDUS* AT BEAUFORT, NORTH CAROLINA

*Marcus M. Key, Jr., Judith E. Winston, Jared W. Volpe, William B. Jeffries and Harold K. Voris*

## ABSTRACT

This study examines the prevalence, intensity, abundance, and spatial distribution of fouling bryozoans on 168 blue crabs, *Callinectes sapidus,* taken from an estuarine environment in the area of Beaufort, North Carolina. Three epizoic bryozoan species were found on the host crabs. These include *Alcyonidium albescens* Winston and Key, *Membranipora arborescens* (Canu and Bassler), and *Triticella elongata* (Osburn). The proportion of blue crabs fouled was 16%. Results indicate female crabs were significantly more fouled than males. This suggests that the prevalence and intensity of bryozoans are dominantly controlled by the migratory habits of the host, since female crabs spend more time in deeper waters of higher salinity where they are more likely to be fouled by bryozoan larvae. The ventral surface was significantly more fouled than the dorsal. The *A. albescens* colonies were significantly more abundant on the hosts' lateral spines, *M. arborescens* dominated the subhepatic sector, and *T. elongata* was most common around the mouth. The costs and benefits of epibiosis are reviewed. The bryozoan/blue crab relationship described here appears to be phoretic. This means there is minimal negative impact on the crab, the relationship is more beneficial to the bryozoans, and there is no special symbiotic relationship between the crab and the bryozoan.

Biofouling of surfaces found in marine environments is a common phenomenon. Those that foul ships and pipes are a problem as a result of the increased operating costs resulting from drag and increased corrosion, costs to prevent fouling, and costs to remove epizoans (Woods Hole Oceanographic Institution, 1952). Studies on epibiosis and antifouling mechanisms can provide valuable insight into antifouling technology (Davis et al., 1989; Wahl, 1989). Most studies of natural antifouling mechanisms have focused on soft-bodied hosts; however hosts with hard exoskeletons (as in this study) are more similar to manmade structures (e.g., ship hulls, heat exchangers, water intake pipes) than soft-bodied organisms (Becker, 1996).

Studies of fouling marine organisms may provide insight into controlling biofouling of marine technology. Next to barnacles, bryozoans are the most common invertebrates fouling anthropogenic marine surfaces (Christie and Dalley, 1987). In addition, bryozoans are common epizoans on planktonic (Taylor and Monks, 1997), nektonic (Key et al., 1995, 1996a), and motile benthic host substrates (Key et al., 1996a,b).

This paper uses the terminology of Overstreet (1979) and Margolis et al. (1982) with a symbiont being defined as an organism living in special association with a host. The degree of benefit or harm to either partner is irrelevant. Ectosymbionts (i.e., epizoans and epiphytes) live on the external surface of their host and are said to infest their hosts. The prevalence of fouling refers to the proportion of infested hosts. Abundance is the number of symbionts per host, and intensity is the number of symbionts per infested host.

The goals of this study are: (1) to quantitatively describe the prevalence, abundance, and intensity of ectosymbiotic bryozoans on blue crabs at Beaufort, North Carolina; (2) to quantitatively describe the number and size of bryozoan colonies on the host blue crabs; (3) to compare the prevalence of bryozoans on male and

female blue crabs; (4) to quantitatively describe the spatial distribution of bryozoans on the host blue crabs; and (5) to review the costs and benefits of the bryozoan/blue crab relationship for both the host and the epizoans.

THE HOST.—The blue crab *Callinectes sapidus* Rathbun is a common portunid, brachyuran, decapod (Rathbun, 1896; Millikin and Williams, 1984), ranging from Nova Scotia to Argentina including Bermuda and the Antilles. It has, however, recently been introduced into Europe and Japan (Rathbun, 1896, 1930; Hay, 1905; Van Engel, 1958; Williams, 1974; Millikin and Williams, 1984; Williams, 1984).

The blue crab is one of the most euryhaline estuarine organisms (Odum, 1953). Larval stages occur in higher salinity waters (e.g., greater than 20‰) (Dudley and Judy, 1971; Millikin and Williams, 1984). Juveniles and adult stages can survive and grow in almost any salinity from fresh (0‰) to hypersaline (117‰) water (Churchill, 1919; Williams, 1974; Millikin and Williams, 1984; Guerin and Stickle, 1992). Ovigerous females usually migrate to waters with salinities higher than 17‰ (Millikin and Williams, 1984).

The habitat of the blue crab includes depths from 0–90 m, but the crab is mainly found in shallower (i.e., <35 m) water (Franks et al., 1972; Williams, 1974). In the Beaufort area it is the most common crab (Dudley and Judy, 1971). It can be found in brackish water, intertidal salt marshes, mud flats, sand flats, eel-grass beds, subtidal soft bottoms of the Newport River estuary, and in the normal marine water of Onslow Bay of the Atlantic Ocean (Kirby-Smith and Gray, 1977). In the Beaufort area, it has been reported in salinities from 0.05–34.1‰ (Pearse, 1936).

The life history of the blue crab has been well reviewed by Harris (1979), Millikin and Williams (1984), and Williams (1984). Males and females reach maturity after 18–20+ postlarval molts (Churchill, 1919; Truitt, 1939; Van Engel, 1958; Costlow and Bookhout, 1959). As with most crustaceans, the intermolt period increases with age and size (Churchill, 1919; Van Engel, 1958; Tagatz, 1968a; Millikin and Williams, 1984). Males molt three or four more times after reaching sexual maturity (Van Engel, 1958). It was formerly thought that females went into terminal anecdysis after their pubertal molt (Truitt, 1939; Tagatz, 1968a), but it is now thought that some go into a diapause stage (Havens and McConaugha, 1990) and rarely molt again (Churchill, 1919; Van Engel, 1958; Millikin and Williams, 1984). Time to maturity from hatching ranges from 10 mo in areas with longer growing seasons to 20 mo in areas with shorter growing seasons (Churchill, 1919; Millikin and Williams, 1984). Males may mate several times after reaching maturity, whereas females generally mate only once following their pubertal molt (Tatum, 1979; Millikin and Williams, 1984). Most mating occurs in low salinity waters, since males usually remain in low salinity areas during the adult stage (Millikin and Williams, 1984). Few individuals survive more than 1 yr after reaching maturity, which equals a total of 2 yrs of postlarval age at death (Tagatz, 1968b). Females typically die soon after their last batch of eggs is hatched (Churchill, 1919). The estimated maximum age of blue crabs is 4 yrs in Florida (Tagatz, 1968b), but in the Beaufort area, it is only 1–3 yrs (Pearson, 1951; Judy and Dudley, 1970).

Following larval development, early juvenile stages migrate upstream during summer months into estuaries with lower salinity and shallower waters (Costlow and Bookhout, 1959; Millikin and Williams, 1984; Williams, 1984). Later they move to slightly deeper channels to hibernate during colder months when growth ceases or decreases appreciably. During winter, females concentrate more in deeper channels, whereas males generally overwinter in lower salinity waters. In spring, immature females approaching their pubertal molt migrate to lower salinity

Table 1. List of reported epizoic bryozoans on the blue crab *Callinectes sapidus*. Species names are listed as published.

| Bryozoan | Reference(s) |
| --- | --- |
| *Alcyonidium mytili* Dalyell | Pearse, 1947 |
| *Alcyonidium polyoum* (Hassall) | Williams and Porter, 1964 |
| *Alcyonidium verrilli* Osburn | Watts, 1957 |
| *Conopeum tenuissium* (Canu) | Overstreet, 1979 |
| *Membranipora crustulenta* Palla | Watts, 1957 |
| *Membranipora (Acanthodesia) tenuis* Desor | Scrocco and Fabianek, 1969; Overstreet, 1979 |
| *Triticella elongata* (Osburn) | Osburn, 1912, 1932, 1944; DeTurk, 1940; Maturo, 1957; Watts, 1957; Rogick, 1964; Overstreet, 1979 |

waters to seek out mature males for mating. Soon after mating in the summer to early fall, mature females migrate back to higher salinity waters at the mouths of estuaries or in the ocean to spawn and hatch their eggs or to overwinter and spawn the following spring. In this study area, the spawning grounds are downstream near Beaufort Inlet (Williams, 1965). The larvae are less euryhaline than the adults and they hatch in higher salinity waters which are required for their development.

The two following prevailing patterns of (1) males generally occupying the shallower, lower salinity waters farther upstream with females dominating the deeper, higher salinity waters downstream and (2) the similar but less well-defined pattern exhibited within sexes with juveniles in shallower waters and adults in deeper waters, have been documented in Chesapeake Bay (Hay, 1905; Churchill, 1919; Truitt, 1939; Van Engel, 1958; Hines et al., 1987; van Montfrans et al., 1991), North Carolina including the Beaufort area (Pearson, 1951; Judy and Dudley, 1970; Dudley and Judy, 1971, 1973), South Carolina (Lunz, 1951; Eldridge and Waltz, 1977; Archambault et al., 1990), Georgia (Fitz and Wiegert, 1992), Florida (Tagatz, 1968b), Alabama (Tatum, 1979), Mississippi (Perry, 1975; Perry and Stuck, 1979), Louisiana (Darnell, 1959; Adkins, 1979), and Texas (Gunter, 1950; Daugherty, 1952; More, 1969).

THE SYMBIONTS.—Because the blue crab supports a valuable commercial fishery, its symbionts have received much attention. *C. sapidus* is known to be infested by several parasitic endosymbionts (Overstreet, 1979). Various nonparasitic symbionts have also been reported on blue crab gills. These include trematodes (Pearse, 1932), the branchiobdellid annelid worm *Cambarincola vitreus* Ellis (Perry, 1975; Overstreet, 1979; Perry and Stuck, 1979), the egg predator *Carcinonemertes carcinophila* (Kölliker) (Humes, 1942; Hopkins, 1947; Pyle and Cronin, 1950; Williams and Porter, 1964; Scrocco and Fabianek, 1969; Perry, 1975; Overstreet, 1979; Perry and Stuck, 1979), the lepadomorph barnacle *Octolasmis mülleri* (Coker) (Coker, 1902; Pilsbry, 1907; DeTurk, 1940; Humes, 1941; Pearse, 1947, 1952; Causey, 1961; More, 1969; Walker, 1974; Perry, 1975; Lang, 1976; Perry and Stuck, 1979; Jeffries and Voris, 1983; Millikin and Williams, 1984; Gannon, 1990; Gannon and Wheatly, 1992, 1995), and most importantly for this study, the bryozoan *T. elongata* (Osburn) (Table 1).

*T. elongata* (Osburn) is a ctenostomate gymnolaemate bryozoan that is restricted to the warm-temperate waters of the Atlantic coast where it extends from Massachusetts to North Carolina (Winston, 1977). It has been previously reported at Beaufort, North Carolina (Maturo, 1957; Kirby-Smith and Gray, 1977; Winston, 1977). As a pleiomesohaline organism, *T. elongata* is limited to salinities from

Table 2. List of reported host crab species fouled by the bryozoan *Triticella elongata*. Species names are listed as published.

| Host Crab | Reference(s) |
| --- | --- |
| *Hepatus epheliticus* (Linnaeus) | DeTurk, 1940 |
| *Libinia dubia* Milne-Edwards | DeTurk, 1940 |
| *Libinia emarginata* Leach | DeTurk, 1940 |
| *Libinia* sp. | Osburn, 1912, 1932; Rogick, 1964 |
| *Pinnixia chaetopterana* Stimpson | Osburn, 1912, 1932, 1944; Maturo, 1957; Rogick, 1964; Kirby-Smith and Gray, 1977; Overstreet, 1979 |

brackish (i.e., 8–18‰) to normal marine (i.e., 35‰) (Winston, 1977), but it is more abundant at the higher end of this range (Osburn, 1944; Overstreet, 1979).

Like other triticellids, *T. elongata* is an obligate symbiont of crustaceans and is found infecting the branchial chamber and occasionally infesting the pereiopods and carapace of various crab species (Table 2). *T. elongata* is best known as a symbiont of the blue crab, where it is found infecting the branchial chamber and occasionally spreading out onto the carapace and infesting the bases of the pereiopods (Osburn, 1912, 1932, 1944; DeTurk, 1940; Maturo, 1957; Watts, 1957; Rogick, 1964; Overstreet, 1979). Watts (1957) and DeTurk (1940) argued that the site of initial infestation was within the branchial chamber and from there it spread to the surface of the body because the external occurrence of *T. elongata* seemed to be always associated with a heavy gill chamber infestation.

Many epizoans are known as nonparasitic ectosymbionts on the carapace of the blue crab. They include corals, amphipods, tunicates (Pearse, 1947), oysters, polychaetes, sponges (Overstreet, 1979), mussels (Hay, 1905; Perry, 1975), hydroids (Williams and Porter, 1964), leeches (Pearse, 1936; Meyer and Barden, 1955; Hutton and Sogandares-Bernal, 1959; Daniels and Sawyer, 1975; Perry, 1975; Sawyer et al., 1975; Overstreet, 1979), barnacles (Key et al., 1997 and references therein), and most importantly for this study, various bryozoans (Table 1).

The fouling community of Beaufort has been well studied, particularly the bryozoans (Verrill, 1878; DeTurk, 1940; Pearse, 1936; McDougall, 1943; Pearse and Williams, 1951; Maturo, 1957, 1959; Wells, 1961; Sutherland and Karlson, 1973, 1977; Sutherland, 1974, 1977, 1978; Kirby-Smith and Gray, 1977; McKinney, 1996). Of importance to this study are the two bryozoans *A. albescens* and *M. arborescens*.

*A. albescens* Winston and Key is a non-calcified, fleshy ctenostome bryozoan with a western Atlantic geographic distribution (Winston and Key, 1999). This species has been previously reported as *A. polyoum* on the blue crab (Table 1). It has been previously reported as *A. polyoum* (Hassall) from Chesapeake Bay (Osburn 1932, 1944), and Beaufort, North Carolina (Maturo, 1959; Wells, 1961). Wells (1961) reported this species as *A. polyoum* in the Newport estuary both up- and down-stream of our study site.

*M. arborescens* (Canu and Bassler) is a moderately calcified cheilostome bryozoan with a temperate to tropical geographic distribution (Winston, 1982). Along the southeastern U.S. coast, it has been reported from Beaufort, North Carolina (Maturo, 1959), the New River Inlet reefs (Pearse and Williams, 1951), and Florida (Winston, 1982). Although it has not been previously reported from the blue crab (Table 1), some reports of *M. tenuis* Desor may actually refer to this very similar species. In the Beaufort area it has been found on shells and alcyonarian
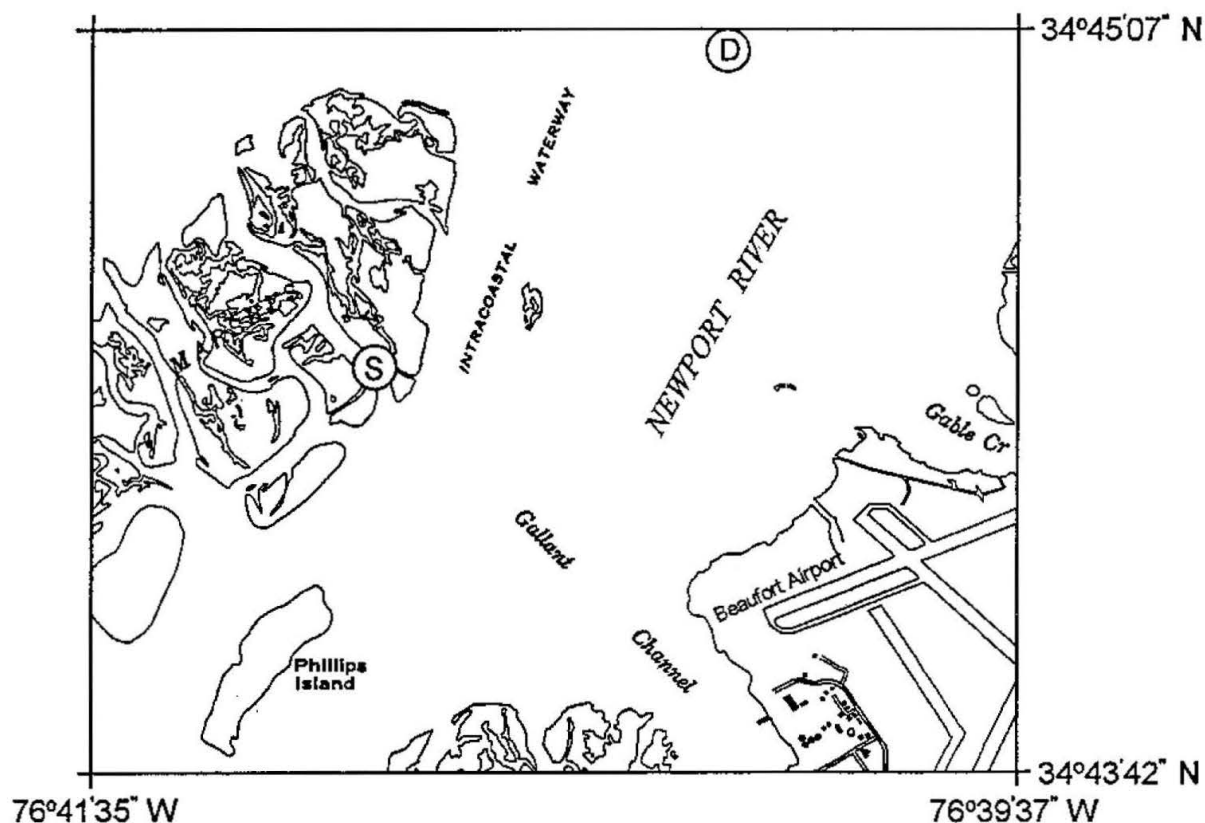
Figure 1. Map of collection localities. S = shallow collection. D = deep collection. Scale: 25 mm = 1 km. Modified from the U.S.G.S. Beaufort and Core Creek 7.5 minute series topographic quadrangle maps.

stems (Maturo, 1957). This species occurs in euryhaline marine environments with salinities from 18–33‰ (Winston, 1977).

## MATERIALS AND METHODS

Blue crabs were collected from the Newport River estuary in Carteret County immediately north of Beaufort, North Carolina. Beaufort is situated at the northeast end of the cuspate Onslow Bay along the southeast Atlantic coast of North Carolina, approximately 125 km southwest of Cape Hatteras. Cape Hatteras is the boundary between the subtropical Carolinian and the temperate Virginian zoogeographic faunal subprovinces (Ekman, 1953). As a result, the fauna in the Beaufort area is more closely related to the southern, Carolinian Province rather than northern, Virginian Province (Pearse and Williams, 1951; Maturo, 1968).

Two collections of blue crabs were made on 22 August 1980 using baited commercial crab pots set the previous day. The collections came from the Newport River estuary 7 km upstream from the mouth of the river at Beaufort Inlet (Fig. 1). The "shallow" collection was made from three crab pots set in a 1–2 m deep, 10–15 m wide channel between two small islands in the Newport Marshes (34°44'30"N, 76°41'00"W). The "deep" collection was made from three crab pots set in 4–5 m deep open water in the Newport River on the eastern edge of the Intracoastal Waterway (34°45'00"N, 76°40'15"W). The two collections are combined in this study as they are only 2–4 m different in depth and in the Newport River estuary, the water is vertically well-mixed due to currents from tides and wind (Kirby-Smith and Costlow, 1989).

The Newport River is the main estuarine channel in the Beaufort area connecting the brackish water upstream environments to the normal marine environments of the Atlantic Ocean. Both collections are from soft-bottom estuarine habitats typical of the Beaufort area where tides range from 0.7–2.0 m, salinities range from 0–40‰, and water temperatures range from 3–30°C (McDougall, 1943; Kirby-Smith and Gray, 1977; Kirby-Smith and Costlow, 1989). At the time of collection, the temperatures at the Duke University Marine Laboratory dock, 4 km to the south, were 26.0–26.7°C.

The crabs were stored in 70% ethanol. Each crab was sexed and its stage of maturity determined by the sexually dimorphic external differences in the shape of the abdominal outline. Females were
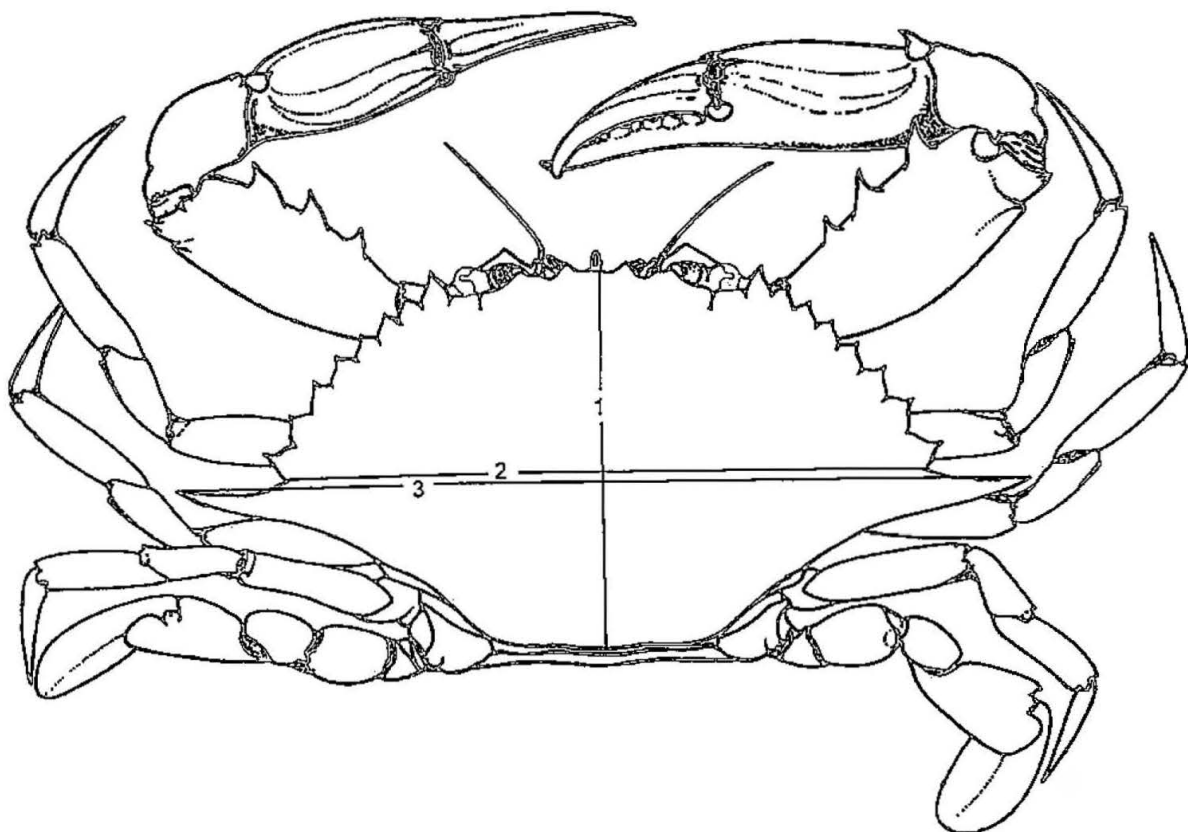
Figure 2. Dorsal surface of *Callinectes sapidus* showing the carapace dimensions measure. 1 = length. 2 = inner width. 3 = outer width. Modified from Williams (1974: fig. 1).

classified as either immature or mature and, if mature, as either ovigerous or nonovigerous. Since there are no readily discernible external indicators of sexual maturity in males (Churchill, 1919; Tagatz, 1968a,b), no effort was made to discriminate sexually immature juvenile males from sexually mature adult males.

Crab size was measured using carapace length and width, which are standard morphometric proxies for age in blue crabs (Gray and Newcombe, 1938a; Newcombe et al., 1949a,b; Tagatz, 1968a; Williams, 1974). Length was measured as the distance across the carapace from the median anterior notch on the face of the crab to the anterior end at the first segment of the abdomen (Fig. 2). The outer width was measured as the distance, perpendicular to the length, between the ends of the ninth pair of anterolateral spines of the carapace (Fig. 2). Because of the problem of variation in spine length for a given size crab and because of the frequency of broken spines (Gray and Newcombe, 1938a; Williams, 1974; Olmi and Bishop, 1983), an inner width was also measured between the bases of the notches between the spines and the preceding anterolateral teeth (Fig. 2). Inner and outer width were significantly correlated (Pearson correlation coefficient = 0.85, P < 0.001), and either one can be used as a measure of size. Total surface area was defined as the combined surface area of the dorsal and ventral surfaces excluding the appendages, calculated as the product of carapace inner width, length, and the constant 1.53. This relationship was empirically determined by measuring the areas of Figures 3 and 4.

The number of missing appendages for each crab was noted. The dorsal and ventral external surfaces of the carapace of each crab were examined for bryozoans. The type, location, number, and size (i.e., surface area) of bryozoan colonies were noted on templates showing the various sectors of the ventral (Fig. 3) and dorsal surfaces (Fig. 4). Measuring the colony size of *A. albescens* and *M. arborescens* was facilitated by their encrusting zoarial habit, but measuring colony size was more difficult with *T. elongata* as it grows in tuft-like patches. All measurements were made with a personal computer-based image analysis system using digitized video images of the crabs. Repeatability experiments indicate a measurement error of less than 4.0%.

## RESULTS AND DISCUSSION

THE HOSTS.—A total of 168 crabs was collected, consisting of 37 (22%) males and 131 (78%) females (Table 3). Of the females, 104 (79%) were mature but
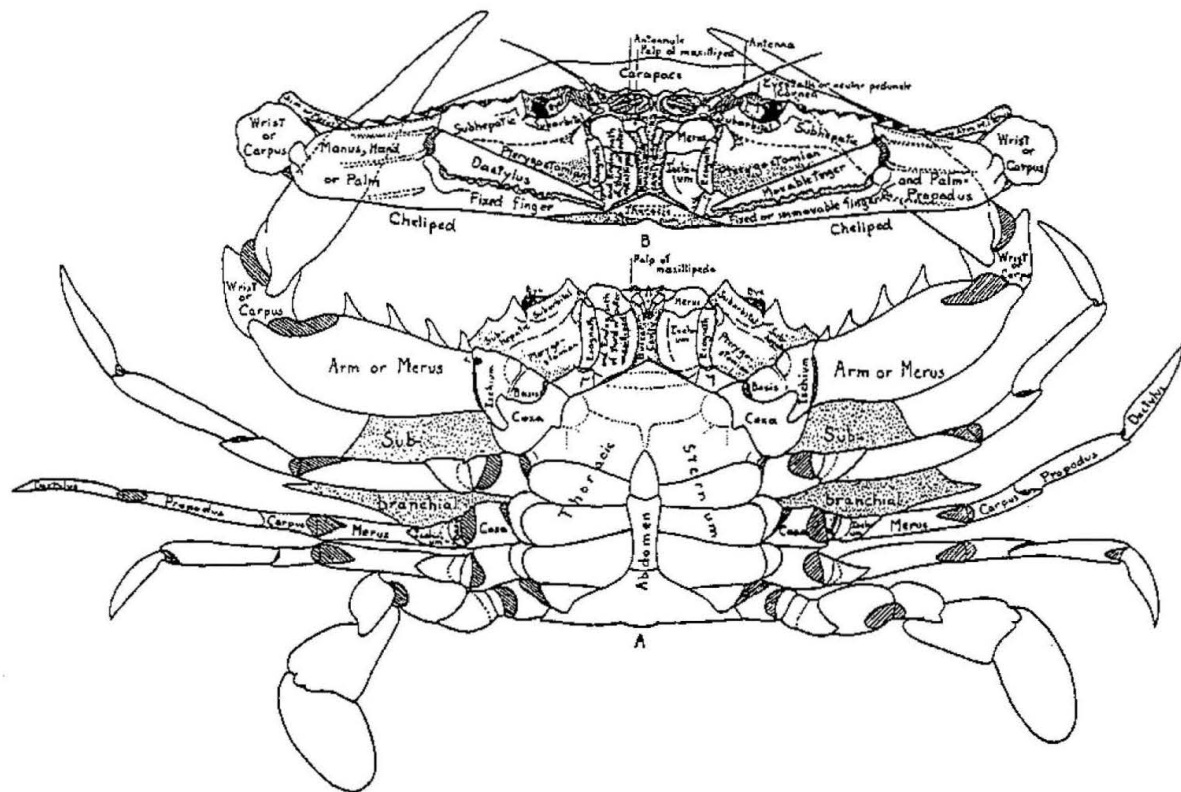
Figure 3.   Ventral (A) and frontal (B) surfaces of a male *Callinectes sapidus* showing the various sectors examined for epizoans. From Rathbun (1930: fig. 2).

nonovigerous and 27 (21%) ovigerous. No sexually immature juvenile females were collected. Based on previous studies on the size of males at maturity (Gray and Newcombe, 1938b; Van Engel, 1990), all of the male crabs in the present study were probably adults.

All of the crabs were missing at least two appendages because the chelipeds were removed for sale by the commercial collector. The percentage of appendages missing ranged from 100% for the first pereiopod to 13% for the fifth (swimming) pereiopod (Table 4). The other missing appendages are attributed to autotomy presumably caused by damage to the appendages (Churchill, 1919), sudden decrease in temperature (Hay, 1905), or handling (Kennelly et al., 1990). Because of the high frequency of missing appendages, this study excludes the appendages.

The crabs ranged in size from 112–180 mm outer carapace width, from 96–133 mm inner carapace width and from 49–72 mm carapace length. The summary carapace dimensions for all the crabs are given in Table 3. There were no significant differences in terms of total surface area between the male and female crabs nor between the nonovigerous mature and ovigerous female crabs (t-test, $P > 0.05$).

Blue crabs often exhibit sexual dimorphism in size. Some studies have found that adult males tend to be larger in carapace length and width than adult females (Rathbun, 1896, 1930; Churchill, 1919; Williams, 1974, 1984), whereas others have found the opposite (Tagatz, 1968a; Eldridge and Waltz, 1977). The fact that no significant difference was found in the size of the male and female crabs suggests that the sample may represent crabs of various ages that have previously lived in various geographic locations with different water depths, dissolved oxygen levels, temperatures, salinities, and food availability, all of which affect blue
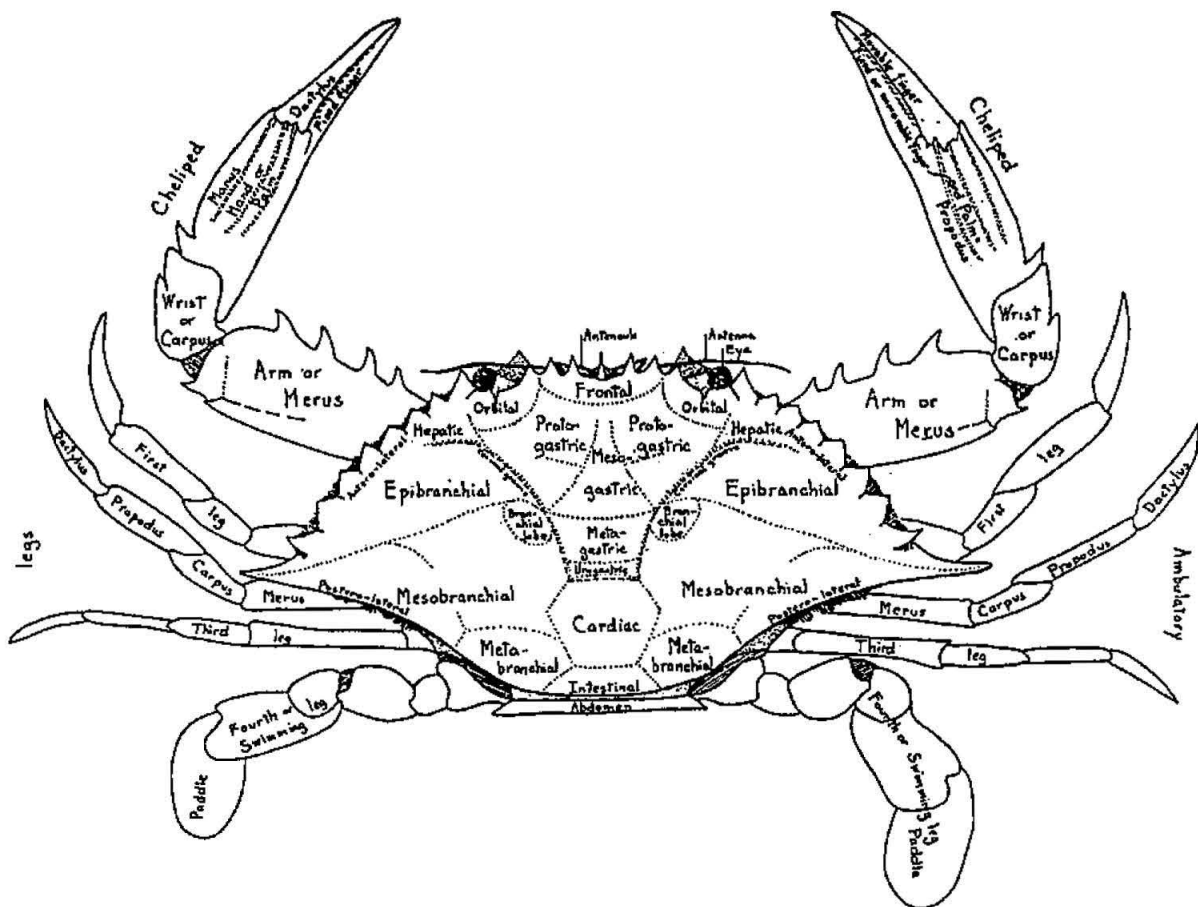
Figure 4.   Dorsal surface of *Callinectes sapidus* showing the various sectors examined for epizoans. From Rathbun (1930: fig. 1).

crab growth rates (Newcombe, 1945; Porter, 1956; Cargo, 1958a,b; Van Engel, 1958; Fischler, 1959; Haefner and Shuster, 1964; Tagatz, 1965, 1968a,b).

THE ECTOSYMBIONTS.—The external surfaces of the crabs were infested by the following ectosymbionts: several hydroid colonies, two species of barnacles (*Chelonibia patula* and *Balanus amphitrite*), six serpulid worms, two slipper shells (*Crepidula plana*), a colonial ascidian, and three species of bryozoans (*A. albescens, M. arborescens* and *T. elongata*). The positions of the barnacles are described in Key et al. (1997). The serpulid worms were most common on the ventral subbranchial sectors. The hydroids were most common on the ventral subbranchial sectors. The slipper shells occurred on the ventral subhepatic and subbranchial sectors. The ascidian was found on the eye stalk of one crab.

A total of 27 (16%) of the 168 crabs were fouled by bryozoans (Table 3). This number is much lower than the only other study on the fouling of blue crabs by bryozoans which revealed a prevalence of 97% from Delaware Bay (Watts, 1957). This difference may simply reflect differing water conditions during the two studies. The 16% prevalence of bryozoans in this study is much lower than that for barnacles (67%) on the same crabs (Key et al., 1997). In another study, Negreiros-Fransozo et al. (1995) also reported that barnacles were more frequent and abundant than bryozoans on two different species of *Callinectes* from Brazil.

The total number of bryozoan colonies found on these 27 crabs was 53 with a range of 1–7 colonies per crab and a mean intensity of 2.0. The number of bryozoan species per fouled host crab ranged from one to three (mean = 1.3). Colony sizes ranged from 4–372 mm² (mean = 89 mm²) with a mean percentage

Table 3. Size data for the crab *Callinectes sapidus* and fouling data for all bryozoan species combined (± SD).

| Character | Males | Nonovigerous mature females | Ovigerous females | Total females | Total |
|---|---|---|---|---|---|
| Number of crabs collected | 37 | 104 | 27 | 131 | 168 |
| % of crabs collected | 22.0 | 61.9 | 16.1 | 78.0 | 100.0 |
| Mean carapace outer width of crabs (mm) | 134 ± 13 | 147 ± 16 | 151 ± 13 | 148 ± 15 | 145 ± 16 |
| Mean carapace inner width of crabs (mm) | 113 ± 10 | 111 ± 10 | 113 ± 8 | 112 ± 10 | 112 ± 10 |
| Mean carapace length of crabs (mm) | 61 ± 5 | 60 ± 5 | 61 ± 4 | 61 ± 5 | 61 ± 5 |
| Mean total surface area of crabs (mm²) | 10,526 ± 1,789 | 10,170 ± 1,855 | 10,528 ± 1,285 | 10,432 ± 1,752 | 10,435 ± 1,766 |
| Number of crabs fouled by bryozoans | 0 | 22 | 5 | 27 | 27 |
| Prevalence of bryozoans (%) | 0 | 21.2 | 18.5 | 20.6 | 16.1 |
| Mean # of bryozoan species per fouled host | 0 | 1.3 ± 0.7 | 1.2 ± 0.5 | 1.3 ± 0.6 | 1.3 ± 0.6 |
| Total number of bryozoan colonies | 0 | 44 | 9 | 53 | 53 |
| Mean abundance of bryozoans | 0 | 0.4 ± 1.0 | 0.3 ± 0.8 | 0.4 ± 1.0 | 0.3 ± 0.9 |
| Mean intensity of bryozoans | 0 | 2.0 ± 1.6 | 1.8 ± 0.8 | 2.0 ± 1.5 | 2.0 ± 1.5 |
| Mean bryozoan colony surface area (mm²) | 0 | 81 ± 78 | 132 ± 64 | 89 ± 80 | 89 ± 80 |
| Mean total surface area of all bryozoan colonies per fouled crab (mm²) | 0 | 161 ± 174 | 239 ± 129 | 176 ± 167 | 176 ± 167 |
| Mean % cover of fouled crabs | 0 | 1.6 ± 1.8 | 2.2 ± 1.3 | 1.7 ± 1.7 | 1.7 ± 1.7 |

Table 4. Percentage of pereiopods missing from *Callinectes sapidus*.

| Pereiopod # | % Missing |
|:-----------:|:---------:|
| 1 | 100.0 |
| 2 | 34.2 |
| 3 | 32.2 |
| 4 | 30.9 |
| 5 | 13.1 |
| 1–5 LEFT | 40.0 |
| 1–5 RIGHT | 41.9 |
| 1–5 TOTAL | 40.9 |

cover of the host of 1.7. Other studies have reported bryozoans covering a much larger percentage of their host blue crab (Watts, 1957; Williams and Porter, 1964; Norse and Estevez, 1977).

There was no significant difference in the prevalence of bryozoan fouling between the shallow (15.9%) and deep collections (16.1%) (t-test, $P > 0.05$). The two collections were also not distinguishable in terms of the number of bryozoan colonies per crab, cumulative surface area of bryozoan colonies per crab, percentage cover per crab, and the number of bryozoan species per crab (t-tests, $P > 0.05$). This similarity in fouling of the crabs from the shallow and deep collections suggests that the salinities in the two collections were similar due to their similar depths (1–2 vs 4–5 m), or that the crabs inhabiting these two environments previously shared an environment elsewhere (e.g., higher salinity waters toward the mouth of the estuary) where they were fouled by bryozoan larvae. Thus, they brought the same prevalence of fouling into their respective environments.

Whereas none of the male crabs were fouled (Table 3), the female crabs were significantly more fouled in terms of the prevalence of bryozoans (20.6% vs 0.0%), the intensity of bryozoan colonies (2.0 vs 0.0), mean surface area of bryozoan colonies (89 mm$^2$ vs 0.0 mm$^2$), percentage cover per crab (1.7 vs 0.0), and the number of bryozoan species per fouled crab (1.3 vs 0.0) (t-tests, $P < 0.001$). The same crabs were examined in another study on barnacle fouling, and the relative prevalence of epizoans on male and female crabs was similar (Key et al., 1997).

Why would the female crabs be more fouled than the males? Previous studies have found similar differences in the fouling of male and female blue crabs. Most of the bryozoan colonies on the females were *A. albescens*, and they preferentially occurred on the ventral subbranchial sector. In males, the ventral subbranchial sector has thousands of small "hairs" which may impede bryozoan larval settlement in the area compared to the females which have many fewer of these hairs. It has been reported that epizoans are especially common on aged female blue crabs in their final postlarval molt and who have spawned two or more times (Tagatz, 1968b; Perry and Stuck, 1979; Tatum, 1979; Crisp, 1983; Millikin and Williams, 1984). Previous workers hypothesized that females were more fouled than males because the females enter terminal anecdysis after their pubertal molt, whereas the males continued to molt (Truitt, 1939; Van Engel, 1958; Tagatz, 1968b; Perry, 1975; Overstreet, 1979, 1983; Crisp, 1983). As the incidence of epibiosis is directly proportional to the time elapsed since the last molt (Abelló et al., 1990; Negreiros-Fransozo et al., 1995), then the females would be more fouled. If females molt as frequently as males after the pubertal molt, females must be more heavily fouled for other reasons. (1) Female crabs may be older and, hence, would be exposed to settling bryozoan larvae over a longer period.

This can be discounted as was discussed previously; the females were not significantly larger (and, therefore, not presumably older) than the males. (2) Females may be more attractive to settling bryozoan larvae, but it has never been suggested that bryozoan larvae prefer female blue crabs. (3) Females spend more time in higher salinity waters and, hence, they are more likely to be exposed to settling bryozoan larvae. As mentioned above, female blue crabs typically migrate offshore after mating to higher salinity water, where they carry their egg masses and deposit larvae. It may be here that the females are fouled by the bryozoans which develop in high salinity water. In contrast, most males remain in low salinity estuaries where infestation by bryozoans occurs less frequently because of fewer bryozoan larvae.

There was no significant difference in the prevalence of fouling bryozoans on ovigerous (21.2%) and nonovigerous mature female crabs (18.5%) (t-test, P > 0.05). The two types of females were also indistinguishable in terms of the number of bryozoan colonies per crab, mean surface area of bryozoan colonies, percentage cover per crab, and the number of bryozoan species per crab (t-tests, P > 0.05). This is in contrast to the barnacles where the nonovigerous mature females were fouled significantly more than ovigerous females (Key et al., 1997).

There was no significant correlation (P > 0.05) between crab size (i.e., carapace inner width × length) and the mean abundance, intensity, size, or percentage cover of bryozoan colonies per crab. There was a significant positive correlation (P < 0.05) between crab size and the mean number of bryozoan species per crab. Other studies have suggested a positive correlation between fouling prevalence and host size, especially with older adult females (Churchill, 1919; Newcombe, 1945; Hopkins, 1947; Van Engel, 1958; Williams and Porter, 1964; Perry, 1975; Eldridge and Waltz, 1977). In fact, the fouling prevalence and abundance of different epizoans have been used as an indication of the physiological age of blue crabs (Williams and Porter, 1964; Scrocco and Fabianek, 1969). These studies suggest there should be a positive correlation between crab size and the prevalence of bryozoans for two reasons: (1) larger crabs make a larger target for larval settlement and (2) larger crabs are generally older, molt less frequently, and tend to be more fouled.

Of the three bryozoan species, *A. albescens* was the most common with the highest prevalence, abundance, colony size, and percentage cover (Tables 5–8). Of the 27 crabs fouled by bryozoans, 23 (85%) contained *A. albescens* and four (15%) contained only *M. arborescens* or *T. elongata*. Of the 53 bryozoan colonies found, 34 (64%) were *A. albescens* and 19 (36%) were *M. arborescens* or *T. elongata*.

In addition to the analysis of the prevalence, abundance, and intensity of bryozoan fouling, the spatial distribution of the bryozoan colonies on the crabs was also analyzed. Bryozoan colonies from the appendages were excluded from this analysis as mentioned above. There were significantly more bryozoan colonies on the ventral surface of the crabs (mean = 1.6) than on the dorsal surface (mean = 0.6) (t-test, P < 0.005). The colonies on the ventral (mean = 111 mm²) side were larger than the dorsal (mean = 92 mm²), but it was not significant (t-test, P > 0.05). This is in contrast to the epizoic barnacles which were more common on the dorsal side (Key et al., 1997).

Why would the ventral surface of the crabs be more fouled? (1) The settling bryozoan larvae may prefer the ventral surface because it is exposed to less light. Bryozoans tend to be more successful foulers on cryptic rather than exposed surfaces (Eggleston, 1972; Jackson, 1977; Bishop, 1988; Ward and Thorpe, 1989, 1991; Martindale, 1992; Lescinsky, 1993) as they typically lose competitive in-

Table 5. Fouling data for the bryozoan *Alcyonidium albescens* on the crab *Callinectes sapidus* (± SD).

| Character | Males | Nonovigerous mature females | Ovigerous females | Total females | Total |
|---|---|---|---|---|---|
| Number of crabs collected | 37 | 104 | 27 | 131 | 168 |
| Mean total surface area of crabs (mm²) | 10,526 ± 1,789 | 10,170 ± 1,855 | 10,528 ± 1,285 | 10,432 ± 1,752 | 10,435 ± 1,766 |
| Number of crabs fouled by bryozoans | 0 | 18 | 5 | 23 | 23 |
| Prevalence of bryozoans (%) | 0 | 17.3 | 18.5 | 17.6 | 13.7 |
| Total number of bryozoan colonies | 0 | 26 | 8 | 34 | 34 |
| Mean abundance of bryozoans | 0 | 0.3 ± 0.6 | 0.3 ± 0.7 | 0.3 ± 0.6 | 0.2 ± 0.6 |
| Mean intensity of bryozoans | 0 | 1.4 ± 0.6 | 1.6 ± 0.6 | 1.4 ± 0.6 | 1.4 ± 0.6 |
| Mean bryozoan colony surface area (mm²) | 0 | 130 ± 81 | 147 ± 55 | 134 ± 80 | 134 ± 80 |
| Mean total surface area of all bryozoan colonies per fouled crab (mm²) | 0 | 188 ± 173 | 235 ± 128 | 198 ± 163 | 198 ± 163 |
| Mean % cover of fouled crabs | 0 | 1.9 ± 1.8 | 2.2 ± 1.2 | 2.0 ± 1.6 | 2.0 ± 1.6 |

Table 6. Fouling data for the bryozoan *Membranipora arborescens* on the crab *Callinectes sapidus* (± SD).

| Character | Males | Nonovigerous mature females | Ovigerous females | Total females | Total |
|---|---|---|---|---|---|
| Number of crabs collected | 37 | 104 | 27 | 131 | 168 |
| Mean total surface area of crabs (mm²) | 10,526 ± 1,789 | 10,170 ± 1,855 | 10,528 ± 1,285 | 10,432 ± 1,752 | 10,435 ± 1,766 |
| Number of crabs fouled by bryozoans | 0 | 7 | 1 | 8 | 8 |
| Prevalence of bryozoans (%) | 0 | 6.7 | 3.7 | 6.1 | 4.8 |
| Total number of bryozoan colonies | 0 | 10 | 1 | 11 | 11 |
| Mean abundance of bryozoans | 0 | 0.1 ± 0.4 | 0.0 ± 0.2 | 0.1 ± 0.4 | 0.1 ± 0.3 |
| Mean intensity of bryozoans | 0 | 1.4 ± 0.8 | 1.0 ± 0.0 | 1.4 ± 0.8 | 1.4 ± 0.8 |
| Mean bryozoan colony surface area (mm²) | 0 | 7 ± 4 | 21 ± 0 | 8 ± 5 | 8 ± 5 |
| Mean total surface area of all bryozoan colonies per fouled crab (mm²) | 0 | 10 ± 5 | 21 ± 0 | 12 ± 6 | 12 ± 6 |
| Mean % cover of fouled crabs | 0 | 0.1 ± 0.1 | 0.2 ± 0.0 | 0.1 ± 0.1 | 0.1 ± 0.1 |

Table 7. Fouling data for the bryozoan *Triticella elongata* on the crab *Callinectes sapidus* ($\pm$ SD).

| Character | Males | Nonovigerous mature females | Ovigerous females | Total females | Total |
|---|---|---|---|---|---|
| Number of crabs collected | 37 | 104 | 27 | 131 | 168 |
| Mean total surface area of crabs (mm²) | 10,526 $\pm$ 1,789 | 10,170 $\pm$ 1,855 | 10,528 $\pm$ 1,285 | 10,432 $\pm$ 1,752 | 10,435 $\pm$ 1,766 |
| Number of crabs fouled by bryozoans | 0 | 4 | 0 | 4 | 4 |
| Prevalence of bryozoans (%) | 0 | 3.8 | 0 | 3.1 | 2.4 |
| Total number of bryozoan colonies | 0 | 8 | 0 | 8 | 8 |
| Mean abundance of bryozoans | 0 | 0.1 $\pm$ 0.4 | 0 | 0.1 $\pm$ 0.4 | 0.1 $\pm$ 0.3 |
| Mean intensity of bryozoans | 0 | 2.0 $\pm$ 0.8 | 0 | 2.0 $\pm$ 0.8 | 2.0 $\pm$ 0.8 |
| Mean bryozoan colony surface area (mm²) | 0 | 11 $\pm$ 7 | 0 | 11 $\pm$ 7 | 11 $\pm$ 7 |
| Mean total surface area of all bryozoan colonies per fouled crab (mm²) | 0 | 22 $\pm$ 11 | 0 | 22 $\pm$ 11 | 22 $\pm$ 11 |
| Mean % cover of fouled crabs | 0 | 0.2 $\pm$ 0.1 | 0 | 0.2 $\pm$ 0.1 | 0.2 $\pm$ 0.1 |

Table 8. Spatial distribution of bryozoans colonies per fouled sector of the crab's exoskeleton ($\pm$ SD). Unlisted sectors were not fouled by any bryozoan species.

| Sector | *Alcyonidium albescens* | | *Membanipora arborescens* | | *Triticella elongata* | | All species combined | |
|---|---|---|---|---|---|---|---|---|
| | Mean # of colonies | Mean size of colonies (mm²) | Mean # of colonies | Mean size of colonies (mm²) | Mean # of colonies | Mean size of colonies (mm²) | Mean # of colonies | Mean size of colonies (mm²) |
| Dorsal epibranchial | 0.4 $\pm$ 0.3 | 145 $\pm$ 102 | 0.6 $\pm$ 0.0 | 16 $\pm$ 0 | 0.4 $\pm$ 0 | 19 $\pm$ 0 | 0.4 $\pm$ 0.3 | 129 $\pm$ 110 |
| Dorsal mesobranchial | 0.4 $\pm$ 0.2 | 162 $\pm$ 132 | 0 | 0 | 0 | 0 | 0.4 $\pm$ 0.2 | 162 $\pm$ 132 |
| Dorsal total | 0.6 $\pm$ 0.3 | 152 $\pm$ 117 | 0.6 $\pm$ 0.0 | 16 $\pm$ 0 | 0.4 $\pm$ 0 | 19 $\pm$ 0 | 0.6 $\pm$ 0.3 | 141 $\pm$ 122 |
| Ventral subhepatic | 1.0 $\pm$ 0.0 | 6 $\pm$ 0 | 2.0 $\pm$ 1.4 | 5 $\pm$ 2 | 0 | 0 | 1.7 $\pm$ 1.2 | 5 $\pm$ 2 |
| Ventral pterygostomian | 0 | 0 | 1.0 $\pm$ 0 | 21 $\pm$ 0 | 3.0 $\pm$ 0.0 | 3 $\pm$ 2 | 2.0 $\pm$ 1.4 | 7 $\pm$ 4 |
| Ventral mouthparts | 1.0 $\pm$ 0.0 | 9 $\pm$ 0 | 0 | 0 | 2.0 $\pm$ 0.0 | 15 $\pm$ 6 | 1.7 $\pm$ 0.6 | 14 $\pm$ 6 |
| Ventral thoracic sternum | 1.0 $\pm$ 0.0 | 62 $\pm$ 0 | 0 | 0 | 0 | 0 | 1.0 $\pm$ 0.0 | 62 $\pm$ 0 |
| Ventral subbranchial | 0.9 $\pm$ 0.4 | 140 $\pm$ 101 | 1.1 $\pm$ 0.6 | 8 $\pm$ 5 | 0.6 $\pm$ 0.0 | 18 $\pm$ 8 | 0.9 $\pm$ 0.4 | 109 $\pm$ 102 |
| Ventral Total | 1.0 $\pm$ 0.6 | 124 $\pm$ 120 | 1.3 $\pm$ 0.9 | 8 $\pm$ 5 | 1.9 $\pm$ 1.0 | 10 $\pm$ 6 | 1.6 $\pm$ 1.6 | 73 $\pm$ 66 |
| Total | 1.4 $\pm$ 0.6 | 134 $\pm$ 73 | 1.4 $\pm$ 0.8 | 8 $\pm$ 5 | 2.0 $\pm$ 0.8 | 11 $\pm$ 7 | 2.0 $\pm$ 1.6 | 89 $\pm$ 80 |

teractions with encrusting algae on well-lighted surfaces (Martindale, 1992). (2) The settling bryozoan larvae may prefer the ventral surface because it is downward facing. Some bryozoan larvae exhibit initial geopositive behavior followed by geonegative behavior which results in more settlement on downward facing (i.e., ventral) surfaces (Pomerat and Reiner, 1942; Maturo, 1959). On the crabs examined here, *M. arborescens* was twice as common on the ventral surface as the dorsal (Table 8). (3) The settling bryozoan larvae may prefer the ventral surface because it has a more attractive biofilm. The presence of a microfloral film is known to affect settlement of bryozoan larvae (Brancato and Woollacott, 1982; Maki et al., 1989; Scholz and Krumbein, 1996). (4) The prevalence of barnacle settlement on the dorsal surface (Key et al., 1997) may preclude bryozoan larvae from settling there.

The final analysis involved comparing the relative prevalence of bryozoan fouling on the various sectors of the dorsal and ventral surfaces of the crabs. The percentage and mean size of bryozoan colonies on each sector of the carapace (Table 8) was compared to the relative surface area of each sector (Figs. 3,4). The only two dorsal sectors fouled by bryozoans were the epibranchial and mesobranchial. The ventral surface had five different sectors fouled (Table 8). The results indicate that *M. arborescens* preferred the ventral subhepatic sector, *T. elongata* preferred the ventral pterygostomian and mouthpart sectors, and *A. albescens* preferred the dorsal epibranchial and mesobranchial sectors and the ventral subbranchial sector ($X^2$ tests, $P < 0.05$). The proximity of *T. elongata* to the mouth probably is a reflection of its primary infestation within the branchial chambers (DeTurk, 1940; Watts, 1957). The preference of *T. elongata* for the ventral surfaces of blue crabs was also reported by Watts (1957).

*A. albescens* was most commonly found as single colonies encrusting both dorsal and ventral sides of the lateral spines. Williams and Porter (1964) reported this species as *A. polyoum* on the ventral subhepatic and subbranchial sectors. It is not known why this species' larvae prefer this area for settlement. This relative lack of bryozoans on the medial sectors was also noted with the epizoic barnacles (Key et al., 1997). It may reflect relatively more abrasion during burrowing (Becker, 1996). Blue crabs often burrow into the substrate and hide with only their antennae exposed (Hay, 1905; Churchill, 1919; Thomas et al., 1990; Williams et al., 1990; van Montfrans et al., 1991; Auster and Degoursey, 1994). Blue crabs may burrow to avoid predators (Orth and van Montfrans, 1982; Wilson et al., 1987) or to hibernate during the winter months (Millikin and Williams, 1984). This has been observed during the winter in the Beaufort area (Dudley and Judy, 1971). This burrowing activity may abrade bryozoans more on the medial sectors, since the medial sectors are topographically higher than the lateral sectors (Fig. 3B).

COSTS AND BENEFITS OF EPIBIOSIS.—The costs and benefits of epibiosis have recently been reviewed for ephemeral substrates in general (Key et al., 1995, 1996a) and crustaceans in particular (Key et al., 1996a,b) and will not be reviewed here. Comments will be restricted to the blue crab/bryozoan relationship addressed in the present study.

There are potential costs for the host blue crabs that are fouled by bryozoans. Epizoans can negatively impact blue crabs when the weight becomes a burden, swimming ability is impaired due to increased drag, or movement of encrusted appendages is hampered, all of which make the crab more vulnerable to predators (Tatum, 1979; Overstreet, 1979, 1983). This is especially true of female crabs which often after spawning gradually become debilitated under epizoic attack (Williams, 1984; Becker, 1996).

Fouling of the blue crabs' gills by *T. elongata* (which was not addressed in this study) may negatively affect blue crabs in the same ways as some barnacles that live nonparasitically on the host's gills (Walker, 1974). This type of fouling results in (1) reduced efficiency of the respiratory process of the host blue crab, (2) accumulation of debris in gills which may further reduce the efficiency of the respiratory process of the crab, (3) reduced oxygen available to the crab due to oxygen demands of the epizoans (Walker, 1974).

Other epizoans can also negatively affect the host blue crabs. An unidentified colonial ascidian was found on the left ocular peduncle of one crab, possibly impairing its vision. In some host/epizoan relationships, the ectosymbionts may compete with their host for food resources (Wahl, 1989). This is not likely to be a problem for the blue crab, which is an omnivorous predator/scavenger/cannibal whose diet consists mostly of molluscs, crustaceans, and fish (Darnell, 1958; Tagatz, 1968b; Laughlin, 1982). The large-prey consuming blue crabs do not obviously compete with the plankton-eating epizoic bryozoans.

The only potential benefit to the host blue crabs is if the bryozoans provided a protective role for the host via camouflage (Wahl, 1989). Rasmussen (1973) and Ingle (1983) argued that some epibionts on crabs serve just such a function. This phenomenon is best exhibited in the decorator crabs which actively affix a variety of organisms to their carapaces (Wicksten, 1980). This potential benefit to the hosts probably does not accrue to the blue crabs in the present study for three reasons. (1) The bryozoans only cover a small percentage of the their hosts (Tables 5–7). (2) Many of the bryozoan colonies are on the ventral surface where they would not be visible to a sighted predator above. (3) The colonies are sloughed off after each molt, unless the hosts are anecdysial.

The potential costs of epibiosis to the bryozoans are few. The motile host blue crabs may expose the bryozoans to environments where the temperature, salinity, and/or dissolved oxygen are suitable for the crab, but harmful to the bryozoans. As mentioned above, the ecological range of the blue crab is much greater than that of the bryozoans. The bryozoan colonies may also be abraded by a variety of host activities such as burrowing and copulation (Abelló et al., 1990). Epizoans may be killed when their host crab is preyed upon. Blue crabs are preyed upon by a variety of animals including other blue crabs, starfish, fish (including eels and sharks), alligators, birds, and mammals (Gunter, 1945; Darnell, 1959; Adkins, 1972; Wenner and Musick, 1975; Millikin and Williams, 1984; Wilson et al., 1987; Hunt and Slack, 1989; Platt et al., 1990; Stillwell and Kohler, 1993; Auster and Degoursey, 1994).

The main cost to the bryozoans is obviously the molting of the host crab, which removes the bryozoans from their living host (Negreiros-Fransozo et al., 1995). Crustaceans expose a new body surface during molting, epibionts attached to the exuviae are removed, and recolonization can begin again (Becker, 1996). This has been documented for *T. elongata* which has been found in molted blue crab exoskeletons (Osburn, 1944). This may lead to their demise if the molted shell is eaten or buried.

There are a variety of potential benefits for epizoans living on motile benthic host substrates (Wahl, 1989; Key et al., 1995, 1996a,b). All of the following potential benefits to the bryozoans in the present study obviously depend on whether or not the bryozoans are able to sexually reproduce before the host blue crabs molt. Maturo (1957) reported that some *T. elongata* colonies on blue crabs from Beaufort Inlet were sexually reproducing on their hosts. (1) Since most marine communities experience intense competition for hard, stable substrate space (Connell, 1961; Paine, 1974; Jackson, 1977; Connell and Keough, 1985),

colonization of living substrates may be beneficial to epizoans. (2) Movement of the host may improve the dispersal and gene flow of the epizoans 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 larvae of the epizoans. (3) 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. (4) Epizoans may be protected from their predators by the activities of the host.

These potential gains that may accrue from epibiosis are to some degree offset by the short life spans associated with ephemeral substrates such as the exoskeletons of decapod crustaceans. The fact that these bryozoan/crab relationships have repeatedly evolved (Key et al., 1996b) suggests that there is a real benefit to the bryozoans. In summary, the potential costs of epibiosis to the host blue crabs appear to be greater than any benefits which may accrue. On the contrary the potential benefits of epibiosis to the symbionts appear to be greater than any costs.

The bryozoan/blue crab relationship is best deemed phoretic, (1) with the bryozoans acting as hitch-hikers, (2) with a minimal negative impact on the crab, and (3) with no special symbiotic relationship between the crab and the bryozoan. Others have also interpreted bryozoan/blue crab relationships as phoretic (Scrocco and Fabianek, 1969).

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ADDRESSES: (M.M.K., J.W.V.) *Department of Geology; P.O. Box 1773; Dickinson College; Carlisle, Pennsylvania 17013–2896; E-mail: key@dickinson.edu.* (J.E.W.) *Virginia Museum of Natural History; 1001 Douglas Avenue; Martinsville, Virginia 24112; E-mail: jwinston@leo.vsla.edu.* (W.B.J.) *Department of Biology; P.O. Box 1773; Dickinson College; Carlisle, Pennsylvania 17013–2896; E-mail: jeffries@dickinson.edu.* (H.K.V.) *Division of Amphibians and Reptiles; Roosevelt Road at Lake Shore Drive; Field Museum of Natural History; Chicago, Ilinois 60605; E-mail: voris@fmppr.fmnh.org.*