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

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A B S T R A C T

This study examines the barnacle symbionts on 168 blue crabs, *Callinectes sapidus,* taken from both shallow and deep estuarine environments in the area of Beaufort, North Carolina. The purpose of the study was to quantify the prevalence, intensity, abundance, and spatial distribution of the ectosymbiotic barnacle *Chelonibia patula* on blue crabs. The proportion of blue crabs fouled was 67%. There was no difference in the prevalence of barnacles on crabs from the shallow versus the deep environment. Results indicate female crabs were significantly more fouled than males. This suggests that the prevalence and intensity of barnacles 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 barnacle larvae. The spatial distribution of barnacles on the crab carapaces was controlled by the surface topography of the carapace with more barnacles on the lateral regions than medial. The orientation of the carinal to rostral axes of the barnacles on the carapaces of the host crabs was measured, but no preferred orientation was found. The costs and benefits of epibiosis are reviewed and the barnacle/blue crab relationship appears to be more beneficial to the barnacles than to the host blue crabs.

Biofouling of surfaces found in marine environments is a common phenomenon. Marine organisms that foul ships and pipes are a problem due to the increased operating costs resulting from drag and increased corrosion, costs to prevent fouling, and costs to remove epizoans (Woods Hole Oceanographic Institution, 1952). Barnacles (Cirripedia) are one of the most common groups of invertebrates responsible for fouling (Christie and Dalley, 1987).

This paper uses the terminology of Overstreet (1979) and Margolis *et al.* (1982). A symbiont is 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 barnacles on blue crabs at Beaufort, North Carolina, (2) to quantitatively describe the spatial distribution of barnacles on the host blue crabs, (3) to quantitatively describe the orientation of barnacles on the host blue crabs, (4) to compare the prevalence of barnacles between shallow and deep estuarine environments, (5)

to compare the prevalence of barnacles on male and female blue crabs, and (6) to review the costs and benefits of the barnacle/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,

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1971). It can be found in brackish water intertidal salt marshes, mud flats, sand flats, and eel-grass beds as well as the subtidal soft bottoms of the Newport River estuary and 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 to 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 months in areas with longer growing seasons to 20 months 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 one year after reaching maturity, which equals a total of two years 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 four years in Florida (Tagatz, 1968b), but in the Beaufort area, it is only one to three years (Pearson, 1951; Judy and Dudley, 1970). In adult crabs, when molting is very infrequent or absent, ectosymbionts such as barnacles colonize the crabs (Williams, 1984).

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 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), and Texas (Gunter, 1950; Daugherty, 1952; More, 1969).

The Ectosymbionts

Because the blue crab supports a valuable commercial fishery, its symbionts have received much attention. *Callinectes 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 bryozoan *Triticella elongata* (Osburn) (Osburn, 1912, 1932, 1944; DeTurk, 1940; Maturo, 1957; Watts, 1957; Rogick, 1964; Overstreet, 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), and 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).

Many epizoans are known as nonparasitic ectosymbionts on the carapace of the blue crab, such as corals, amphipods, and 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), various bryozoans (Pearse, 1947; Watts, 1957; Williams and Porter, 1964; Scrocco and Fabianek, 1969; Overstreet, 1979), several species of the balanomorph barnacle *Balanus* (DeTurk, 1940; Williams, 1965, 1984; Scrocco and Fabianek, 1969; Kirby-Smith and Gray, 1977; Overstreet, 1978, 1979, 1983; Adkins, 1979; Zullo, 1979), and the barnacle *Chelonibia patula* (Ranzani) (McDougall, 1943; Pearse, 1947, 1952; Williams and Porter, 1964; Williams, 1965; Tagatz, 1968b; Ross and Jackson, 1972; Lang, 1976; Eldridge and Waltz, 1977; Overstreet, 1978, 1979, 1983; Zullo, 1979; Crisp, 1983; Millikin and Williams, 1984; Williams, 1984; Gannon, 1990).

Chelonibia patula is a coronulid balanomorph barnacle (Newman and Ross, 1976; Zullo, 1979; Newman, 1987; Frazier and Margaritoulis, 1990) that is commonly referred to as a turtle barnacle. It has a global distribution in tropical to warm temperate waters (Darwin, 1854; Pilsbry, 1916; Stubbings, 1967; Newman and Ross, 1976; Zullo, 1979). Laboratory studies on *C. patula* taken from blue crabs in the Beaufort Inlet reveal a tolerance to a wide range of salinities (15–50‰) and temperatures (15–30°C) (Crisp and Costlow, 1963), but their cyprid larvae generally require slightly higher salinity water (Lang, 1976).

Chelonibia patula occurs on a wider variety of substrates compared to other turtle barnacles (Ross and Newman, 1967). It has been reported infesting the xiphosurans *Limulus polyphemus* (Linnaeus) and *Tachypleus gigas* (Müller) (Pilsbry, 1916; Hiro, 1936; McDougall, 1943; Ross and Jackson, 1972; Zullo, 1979) as well as various decapod crustaceans (Darwin, 1854; Ross and Newman, 1967; Overstreet, 1979; Zullo, 1979) such as *Callinectes marginatus* (A. Milne Edwards) (Stubbings, 1967), *Portunus pelagicus* (Linnaeus) (Phillips and Cannon, 1978; Shields, 1992), and several species of *Libinia* (Pearse, 1952). It is occasionally reported on gastropods, stomatopods, turtles, sea snakes, buoys, and ship anchors and hulls (Darwin, 1854; Hentschel, 1923; Woods Hole Oceanographic Institution, 1952; Ross and Newman, 1967; Stubbings, 1967; Ross and Jackson, 1972).

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 the 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 3 crab pots set in a 1–2 m deep, 10–15 m wide channel between 2 small islands in the Newport Marshes (34°44′30″N, 76°41′00″W). The "deep" collection was made from 3 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 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. Since the deep collection came from the main channel of the Newport River, it most likely was from water of higher salinities. Both environments are 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). 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 ab-
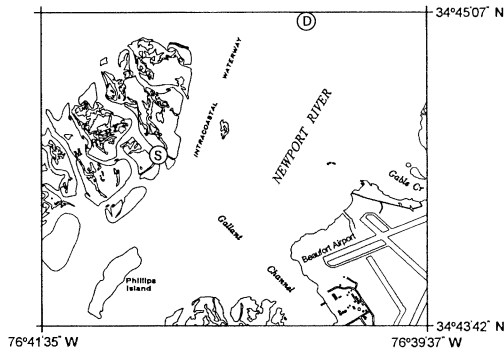
Fig. 1. Map of collection localities. S = shallow collection. D = deep collection. Scale: 1 km = 33 mm. Modified from the U.S.G.S. Beaufort and Core Creek 7.5 minute series topographic quadrangle maps.

dominal outline. Females were 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). The outer

width was measured as the distance 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. Length was measured as the distance perpendicular to the width, 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). 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. The relationship was empirically determined by measuring the areas of Figs. 3, 4.

The number of missing appendages for each crab was noted. The dorsal and ventral external surfaces of the carapace and appendages of each crab were examined for epizoans. The type, location, and number of epizoans were noted on templates showing the various sectors of the dorsal (Fig. 3) and ventral surfaces (Fig. 4). The number of barnacles that settled directly on a crab was counted separately from those that settled on other barnacles. Unless otherwise indicated, all barnacle data refer only to those barnacles that settled directly on their host and not another barnacle (e.g., Fig. 5). All measurements were made with a personal computer-based image analysis sys-
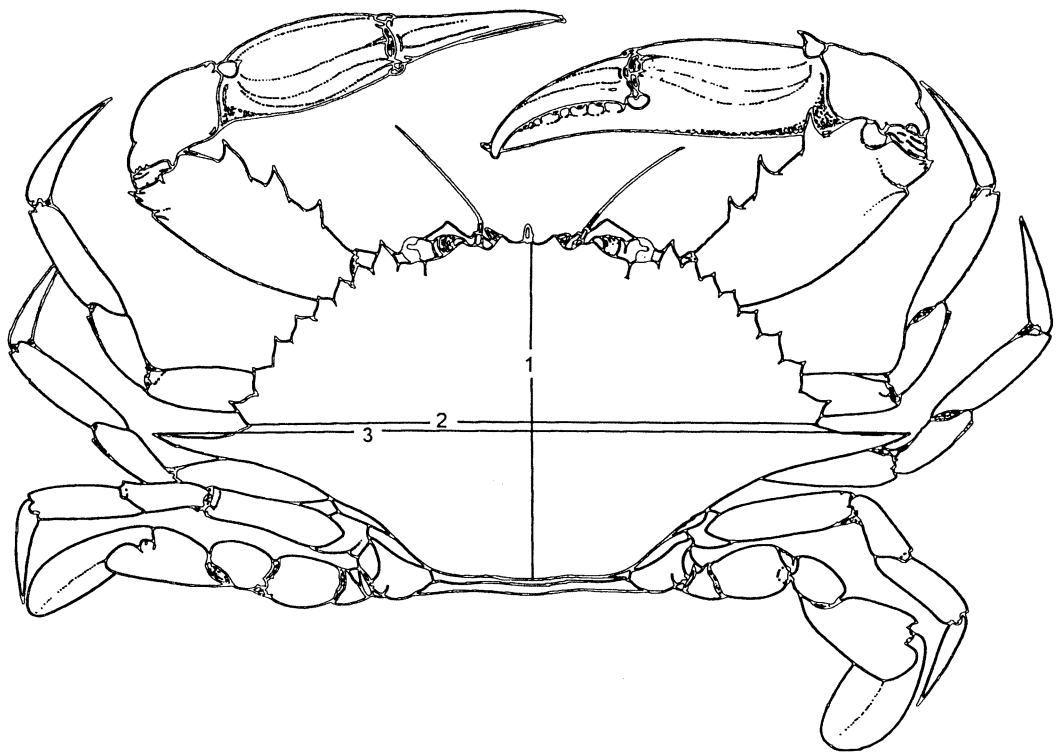

Fig. 2. Dorsal surface of *Callinectes sapidus* showing the carapace dimensions measured. 1 = length. 2 = inner width. 3 = outer width. Modified from Williams (1974, fig. 1).
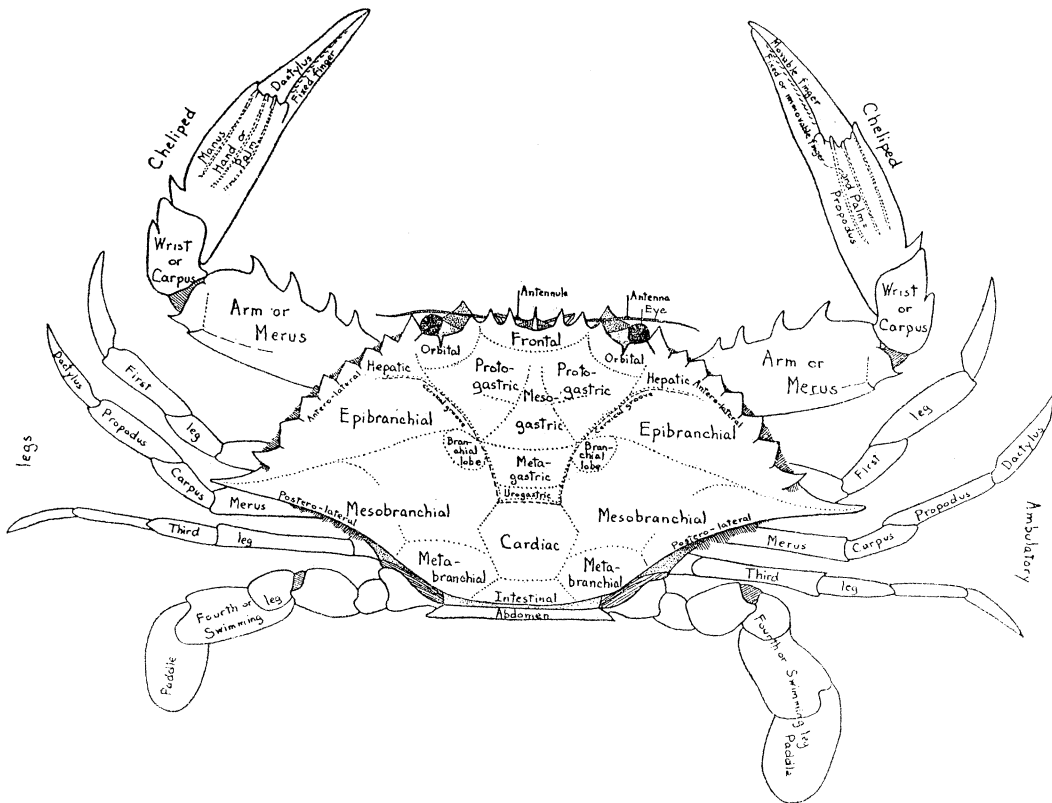
Fig. 3.   Dorsal surface of *Callinectes sapidus* showing the various sectors examined for epizoans. From Rathbun (1930, fig. 1).

tem using digitized video images of the crabs. Repeatability experiments indicate a measurement error of less than 2.9%.

The orientation of the carinal to rostral axis of *C. patula* was measured relative to the long axis of the width of the crab through the lateral spines. Only those barnacles that settled directly on the carapace were measured. Barnacles growing on other barnacles and/or the appendages were excluded. Barnacle orientation was measured in 33.3° fields from 90° at the head of the crab to 0° at the lateral spines to −90° at the abdomen.

RESULTS AND DISCUSSION OF THE HOSTS

A total of 168 crabs was collected, consisting of 37 (22%) males and 131 (78%) females (Table 1). Of the females, 104 (79%) were mature but 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. Of the 168 crabs, 69 (41%) were collected from the shallow environment and 99 (59%) came from the deep environment (Tables 2, 3). As mentioned, females tend to

be more common in deeper, higher salinity water (Tagatz, 1968b; Williams, 1974). This was confirmed here with the deep collection consisting of 95% females compared to only 54% in the shallow collection. This may reflect salinity differences in the two collection sites.

All of the crabs were missing at least two appendages because the chelipeds were removed for sale by the commercial collector. When combining the data from both collections, the percentage of appendages missing ranged from 100% for the first pereiopod to 13% for the fifth (swimming) pereiopod. 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 (e.g., Fig. 5), all surface area calculations exclude the appendages.

The crabs ranged in size from 112–180-mm outer carapace width, from 96–133-mm inner

Fig. 4.   Ventral (A) and frontal (B) surfaces of a male *Callinectes sapidus* showing the various sectors examined for epizoans. From Rathbun (1930, fig. 2).

carapace width, and from 49–72-mm carapace length. The summary carapace dimensions for all the crabs are given in Table 1 and for the shallow and deep collections in Tables 2, 3, respectively. There were no significant differences in terms of total surface area be-

Fig. 5.   Dorsal surface of an ovigerous female *Callinectes sapidus* from the shallow collection fouled by the barnacle *Chelonibia patula*. The distance between the ends of the ninth pair of anterolateral spines of the carapace is 141 mm. Note: (1) the missing pereiopods (i.e., left first, second, and fifth; right first); (2) the gregarious nature of the barnacle settlement pattern; and (3) the lack of barnacles on the medial sectors of the carapace.

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

The crabs from the shallow collection were significantly larger in terms of their total surface area than those from the deep collection (*t*-test, $P < 0.01$). Typically, smaller individuals, regardless of sex, are more common in

Table 1. Size data for the crab *Callinectes sapidus* and fouling data for the barnacle *Chelonibia patula* from both the shallow and deep collections 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)	10,796 ± 1,789	10,342 ± 1,855	10,528 ± 1,285	10,435 ± 1,752	10,435 ± 1,766
Number of crabs fouled by barnacles	20	78	14	92	112
Prevalence of barnacles (%)	54.1	75.0	51.9	70.2	66.7
Total number of barnacles	50	565	86	651	701
Mean abundance of barnacles	1.4 ± 2.1	5.4 ± 6.9	3.2 ± 4.5	5.0 ± 6.5	4.2 ± 6.0
Mean intensity of barnacles	2.5 ± 2.4	7.2 ± 7.1	6.1 ± 4.6	7.1 ± 6.8	6.3 ± 6.5

shallower water (Hay, 1905; Churchill, 1919; Tagatz, 1968b; Dudley and Judy, 1973; Perry, 1975; Orth and van Montfrans, 1987). The results from the present study do not support this, perhaps because the shallow and deep collections differ in depth from only two to four meters.

RESULTS AND DISCUSSION OF THE ECTOSYMBIONTS

The external surfaces of the crabs were infested by the following ectosymbionts: two species of balanomorph barnacles (*Chelonibia patula* (Ranzani) and *Balanus amphitrite* Darwin), a colonial ascidian, several ctenostome and cheilostome bryozoan colonies, and serpulid worms. Since more than 99% of the epizoans were *C. patula,* this barnacle will be the focus of the remainder of the paper.

A total of 112 (67%) of the 168 crabs were fouled by *C. patula.* There was no significant difference in the prevalence of barnacle fouling between the shallow (70%) and deep collections (65%) (*t*-test, *P* > 0.05).

Previous work on fouling of blue crabs by *C. patula* revealed prevalences of 22% in Florida (Gannon, 1990) to 85% in North Carolina (Crisp, 1983). Norse and Estevez (1977) reported that the prevalence of *C. patula* fouling blue crabs in Colombian estuaries increased in a seaward (i.e., higher salinity) direction. The results from the present study do not support this, but longer-term data are needed for confirmation. This similarity in the prevalence of fouling between the shallow and deep collections suggests that the salinities in the two collections were similar due to their similar depths (1–2 versus 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 barnacle larvae. Thus, they brought the same prevalence of fouling into their respective environments. This shared seaward en-

Table 2. Size data for the crab *Callinectes sapidus* and fouling data for the barnacle *Chelonibia patula* from the shallow collection (± SD).

Character	Males	Nonovigerous mature females	Ovigerous females	Total females	Total
Number of crabs collected	32	26	11	37	69
% of crabs collected	46.4	37.7	15.9	53.6	100.0
Mean carapace outer width of crabs (mm)	136 ± 13	152 ± 14	145 ± 16	150 ± 15	144 ± 16
Mean carapace inner width of crabs (mm)	115 ± 10	115 ± 11	110 ± 8	113 ± 10	114 ± 10
Mean carapace length of crabs (mm)	63 ± 5	62 ± 6	60 ± 4	62 ± 5	62 ± 5
Mean total surface area of crabs (mm²)	11,066 ± 1,716	10,890 ± 1,921	10,081 ± 1,347	10,701 ± 1,804	10,796 ± 1,761
Number of crabs fouled by barnacles	18	22	8	30	48
Prevalence of barnacles (%)	56.3	84.6	72.7	81.1	69.6
Total number of barnacles	40	156	54	210	250
Mean abundance of barnacles	1.3 ± 5.4	6.0 ± 5.9	4.9 ± 4.4	5.7 ± 5.4	3.6 ± 4.7
Mean intensity of barnacles	2.2 ± 1.9	7.1 ± 5.7	6.8 ± 3.7	7.0 ± 5.2	5.2 ± 4.9

Table 3. Size data for the crab *Callinectes sapidus* and fouling data for the barnacle *Chelonibia patula* from the deep collection (± SD).

Character	Males	Nonovigerous mature females	Ovigerous females	Total females	Total
Number of crabs collected	5	78	16	94	99
% of crabs collected	5.1	78.8	16.2	94.9	100.0
Mean carapace outer width of crabs (mm)	125 ± 14	145 ± 16	155 ± 8	147 ± 16	145 ± 16
Mean carapace inner width of crabs (mm)	105 ± 8	110 ± 10	116 ± 7	111 ± 10	111 ± 10
Mean carapace length of crabs (mm)	58 ± 5	60 ± 5	62 ± 3	60 ± 5	60 ± 5
Mean total surface area of crabs (mm^2)	9,302 ± 1,453	10,081 ± 1,787	10,985 ± 1,142	10,172 ± 1,721	10,172 ± 1,717
Number of crabs fouled by barnacles	2	56	6	62	64
Prevalence of barnacles (%)	40.0	71.8	37.5	66.0	64.6
Total number of barnacles	10	409	32	441	451
Mean abundance of barnacles	2.0 ± 3.9	5.2 ± 7.3	2.0 ± 4.3	4.7 ± 6.9	4.6 ± 6.8
Mean intensity of barnacles	5.0 ± 5.7	7.3 ± 7.6	5.3 ± 5.9	7.1 ± 7.5	7.0 ± 7.4

vironment hypothesis is supported by the very presence of *C. patula* (see Overstreet, 1979) whose cyprid larvae require high salinity water (Lang, 1976) and are present throughout the summer in the coastal waters of North Carolina (Crisp, 1983).

Female crabs had a higher prevalence of *C. patula* (70%) than males (54%) (*t*-test, $P < 0.05$). Previous studies have found similar results, and they noted that *C. patula* is 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). If females molt as frequently as males after the pubertal molt, females may be more heavily fouled for several other reasons. (1) Female crabs may be older, and, hence, would be exposed to settling barnacle 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 barnacle larvae, but it has never been suggested that larvae of *C. patula* prefer female blue crabs. (3) Females spend more time in higher salinities, and, hence, they are more likely to be exposed to settling barnacle larvae. As mentioned above, female blue crabs typically migrate offshore after mating to higher salinity water, where they carry their egg masses and de-

posit larvae. As hypothesized by Crisp (1983) and Overstreet (1983), it is here that the females are fouled by the barnacles which develop in high salinity water. In contrast, most males remain in low salinity estuaries where infestation by barnacles occurs less frequently because of fewer barnacle larvae.

The nonovigerous mature females (75%) were fouled significantly more than ovigerous females (52%) (*t*-test, $P < 0.05$). The only other study of the prevalence of fouling of *C. patula* on crabs of differing sexual condition was by Shields (1992). That study, involving a different host species, found that nonovigerous females were not significantly fouled more than ovigerous females, but this may simply reflect inclusion of immature females in that study.

There was no significant correlation ($P > 0.05$) between crab surface area and the mean abundance or mean intensity of barnacles per crab. This was confirmed for all crabs combined, shallow collection crabs, deep collection crabs, males, females, nonovigerous mature females, and ovigerous females. This same result has been found with *C. patula* on the crab *Portunus pelagicus* (L.) (see Shields, 1992). 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 pos-

itive correlation between crab size and the prevalence of barnacles 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.

In addition to the analysis of the prevalence, abundance, and intensity of barnacle fouling, the spatial distribution of barnacles was also analyzed. A total of 812 barnacles was found on the crabs. Of those, 701 (86%) were attached directly to the crab, and 111 (14%) were growing on previously settled barnacles. Of the 701 barnacles attached directly to the crabs, 15 (2%) were fouled by other barnacles. These 15 tended to be the largest barnacles (Fig. 5). On these 15 barnacles, the number of epizoic barnacles ranged from 1–14 (mean = 7.4).

The restriction of epizoic barnacles to the few largest host barnacles suggests that there is a minimum host barnacle size at which other barnacles will settle on, or that barnacle larvae are selective settlers. Where hard substrates are rare, many balanomorph species settle epizoically on their own species, forming clumps attached to the substrate through the basis of only the first settled individual (Hui and Moyse, 1987). *Chelonibia patula* exhibits this gregarious style of larval settlement (Williams and Porter, 1964; Crisp, 1983), probably in response to settlement-inducing proteins from conspecifics (Crisp, 1983; Gabbott and Larman, 1987). Gregarious settling may also be a response to certain crabs being more attractive or having greater exposure to barnacle larvae (Gannon, 1990). The remaining discussion of the results from the barnacle data will be restricted to those barnacles that settled directly on crabs.

The abundance of barnacles that were attached directly to each host ranged from 0–44 (mean = 4.2 ± 6.0), whereas the fouling intensity ranged from 1–44 (mean = 6.3 ± 6.5). This is lower than both the 10–20 *C. patula* reported on blue crabs in North Carolina by Crisp (1983) and the mean of 11.9 *C. patula* reported on *Portunus pelagicus* (see Shields, 1992). There was no significant difference in the fouling intensity between the shallow (mean = 5.2 ± 4.9) and deep collections (mean = 7.0 ± 7.4) nor between ovigerous (mean = 6.1 ± 4.6) and nonovigerous mature females (mean = 7.2 ± 7.1) (*t*-test, $P > 0.05$). The females (mean = 7.1 ± 6.8), how-

ever, had a significantly higher fouling intensity than the males (mean = 2.5 ± 2.4) (*t*-test, $P < 0.001$). These relative intensities of fouling are similar to the prevalences mentioned above.

In addition to the analysis of the abundance and intensity of barnacle fouling, the orientation of the carinal to rostral axis of the turtle barnacles attached directly to their host was analyzed relative to the long axis of the width of the crab through the lateral spines. There was no preferential orientation of the barnacles for any of six 33.3° fields from 90° at the head of the crab to 0° at the lateral spines to –90° at the abdomen (χ^2 test, $P > 0.05$). Even when combining the six fields into three groups (i.e., 90.0° to 66.7°, 66.7° to 33.3°, 33.3° to 0.0°, 0.0° to –33.3°, –33.3° to –66.7°, and –66.7° to –90.0°), there was no preferred orientation (χ^2 test, $P > 0.05$).

This lack of orientation of the barnacles contradicts the qualitative findings of Ross and Jackson (1972) who argued that the carinal to rostral axes of *C. patula* on blue crabs tend to be oriented parallel to the long axis of the width of the crab through the lateral spines. They suggested that this orientation probably serves to maximize the feeding capabilities of the barnacles since the cirral net would be oriented parallel to the sideways direction of movement of the crab. Several factors have been suggested as controls on the initial orientation of settling barnacle larvae. In order of decreasing importance (Crisp, 1975; Crisp and Bourget, 1985), these factors include substrate topography (Crisp and Barnes, 1954), light (Barnes *et al.*, 1951), and water currents (Crisp and Stubbings, 1957; Forbes *et al.*, 1971). In regard to surface topography, there seemed to be a preference for the barnacles to settle on surface irregularities, such as wounds and the subtle furrows between the sectors on the carapace (Fig. 3), but this was not quantitatively examined. On a crowded substrate, available space imposed by previously settled larvae also obviously constrains barnacle orientation (Knight-Jones, 1953). The lack of barnacle orientation documented in this study may be due to these competing controls or to barnacle reorientation which is possible with later growth (Crisp, 1953; Anderson, 1994).

The barnacles were also analyzed for their spatial distribution on the crabs. Barnacles from the appendages were excluded from this

analysis as mentioned above. There were significantly more barnacles on the dorsal surfaces of the crabs (mean = 2.9 ± 4.6) than on the ventral surfaces (mean = 0.6 ± 1.3) (*t*-test, *P* < 0.001). This reflects the fact that the entire thoracic sternum (Fig. 3) was devoid of barnacles on all 168 crabs.

Why would the dorsal surface of the crabs be more fouled? (1) The dorsal surface is more available to the settling larvae. (2) The settling barnacle larvae may prefer the dorsal surface because it is exposed to more light or because it has a more attractive biofilm (Crisp, 1974). (3) The prevalence of barnacle settlement may be lower on the ventral surface because of the presence of dense aggregations of setae on the subbranchial sector of the ventral surface (Fig. 4). (4) The ventral surface may experience more abrasion and siltation when the crabs walk along the substrate (Van Engel, 1979). (5) Host copulation may also abrade epizoans. During copulation, the male holds the dorsal surface of the female close to his ventral surface for 5–12 h (Churchill, 1919; Truitt, 1939; Van Engel, 1958; Williams, 1965). The risk of abrading epizoans during copulation is a greater problem for male crabs, since female crabs copulate only immediately after molting, when they would be soft and likely devoid of epizoans. Compared to other turtle barnacles, *C. patula* has a highly conical profile, lacking internal, buttressed plates that strengthen other turtle barnacles (Frazier and Margaritoulis, 1990). As a result, *C. patula* is unlikely to survive physical abrasion with other organisms or the substrate (Frazier and Margaritoulis, 1990).

The second set of analyses involved comparing the relative prevalence of barnacle fouling on the various sectors of the dorsal surfaces of the crabs. Barnacles from the ventral surface (15% of total number of barnacles) were excluded from this analysis because of the different relative surface areas of the ventral sectors (e.g., abdomen) between male and female crabs. The percentage of barnacles on each sector of the carapace was compared to the relative surface area of each sector (Fig. 3). The results indicate no significant difference in the number of barnacles settling on any one particular region of the carapace (χ^2 test, *P* > 0.05).

There was a distinctive pattern of more barnacles than expected on the lateral (i.e., hepatic, epibranchial, branchial, mesobranchial, and metabranchial) sectors and fewer than expected on the medial (i.e., orbital, protogastric, mesogastric, metagastric, cardiac, and intestinal) sectors (e.g., Fig. 5). The only exceptions to this pattern were the urogastric and frontal, both medial, with slightly more barnacles than expected. To test the significance of this pattern, the barnacle data were grouped into the medial and lateral sectors and standardized for the relative surface areas. The results indicate that there are significantly more barnacles per unit area (mm^2) in the lateral sectors (mean = 0.00023 ± 0.00039) than in the medial sectors (mean = 0.00007 ± 0.00015) (*t*-test, *P* < 0.001).

The relative lack of barnacles on the medial sectors may reflect relatively more abrasion during burrowing. 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 barnacles more on the medial sectors, since the medial sectors are topographically higher than the lateral sectors (Fig. 4b).

Another analysis grouped the number of barnacles into anterior (i.e., frontal, mesogastric, protogastric, orbital, hepatic, and epibranchial) sectors and posterior (i.e., metagastric, urogastric, cardiac, intestinal, branchial, mesobranchial, and metabranchial) sectors. The data were standardized for the relative surface areas of these two groups of sectors. The results indicate that there is no significant difference in the number of barnacles per unit area (mm^2) between the anterior (mean = 0.00012 ± 0.00024) and posterior sectors (mean = 0.00017 ± 0.00030) (*t*-test, *P* > 0.05).

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/barnacle relationships addressed in the present study.

There are potential costs for the host blue crabs that are fouled by this barnacle. Several studies have argued that *C. patula* 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 after spawning gradually become debilitated under epizoic attack (Williams, 1984).

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 a problem for the blue crab, which is an omnivorous predator, scavenger, and 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 barnacles.

The only potential benefit to the host blue crabs is if *C. patula* 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, since the barnacles are sloughed off after each molt, unless the hosts are anecdysial.

The potential costs of epibiosis to the barnacles are few. The motile host blue crabs may expose the barnacles to environments where the temperature, salinity, and/or dissolved oxygen are suitable for the crab, but harmful to the barnacle. As mentioned above, the ecological range of the blue crab is much greater than that of the barnacle. The ectosymbiotic barnacles may also be abraded by a variety of host activities such as burrowing and copulation. 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 barnacles is obviously the molting of the host crab, which removes the barnacles from their living host. This may lead to their demise if the molted shell is eaten or buried.

There is 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 barnacles in the present study obviously depend on whether or not the barnacles are able to sexually reproduce before the host blue crabs molt. (1) Since most marine communities experience intense competition for substrate space (Paine, 1974; Jackson, 1977; Connell and Keough, 1985), colonization of living substrates may be beneficial to epizoans. Intertidal barnacles in particular experience intense substrate competition and predation pressure (Connell, 1961a, b). The epibiosis of some species of barnacles on crabs may have evolved in response to this substrate competition and predation pressure on the barnacles (Foster, 1987). (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 barnacle/crab relationships have repeatedly evolved suggests that there is a real benefit to the barnacles (Foster, 1987). 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.

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