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Age of the Mangrove Crab *Scylla serrata* at Colonization by Stalked Barnacles of the Genus *Octolasmis*

WILLIAM B. JEFFRIES[1], HAROLD K. VORIS[2], AND SOMBAT POOVACHIRANON[3]

[1]*Department of Biology, Dickinson College, Carlisle, Pennsylvania 17013;* [2]*Department of Zoology, Field Museum of Natural History, Chicago, Illinois 60605; and* [3]*Phuket Marine Biological Center, Phuket 83000, Thailand*

Abstract. Cyprid larvae of the lepadomorph *Octolasmis* colonize the gill chambers of the edible mangrove crab, *Scylla serrata* (Forskål, 1755), sometimes in debilitating numbers. We set out to determine when, in the life cycle of the host, barnacle infestation begins. A total of 856 mangrove crabs, ranging in size from 10.9 to 132.3 mm carapace width (instars 5 to 18), were collected from natural populations in Phuket, Thailand, and examined for these barnacles. Almost a third harbored one or more barnacles. The smallest crab to host a barnacle was 34.3 mm (instar 10); 233 smaller crabs, representing instars 5–9, had none. Infestations by more than one barnacle were uncommon among crabs of less than 70 mm carapace width (instar 13). The percentage of crabs hosting barnacles increased as the crabs approached sexual maturity, and the magnitude of infestation on individual crabs increased with their size. The distribution of octolasmids on the gills of immature crabs differed from that on mature crabs. In the former, all barnacles were on the inside of the gill surfaces and none were on the outside, whereas in the latter, 11% were on the outside of the gills. The numbers of barnacles on the inside and the outside of the gills is a function of the number of barnacles in the gill chamber. The major inhalant aperture size, and gill chamber size were eliminated as possible factors limiting infestation. Instars 10 and 11 may be suboptimal for infestation by octolasmids because the intermolt time between instars does not allow sufficient time for production of barnacle nauplii. Current data do not permit us to distinguish the relative influences of microhabitat use, host hormonal changes, and behavioral changes on infestation.

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Introduction

Many interesting and diverse symbiotic relationships (*sensu lato,* de Bary, 1879) exist between decapods and metazoans of different phyla. The growth of some rhizocephalans, *e.g., Sacculina* spp., results in parasitic castration of hosts so that male crabs develop some of the secondary sexual and behavioral characteristics of female crabs (Bang, 1983; Cressey, 1983; Overstreet, 1983). Infestation of crab branchial lamellae and subsequently crab egg masses by nemertean worms, *e.g., Carcinomemertes* spp., likely impedes the free flow of water over the gills and results in the predation of host eggs (Humes, 1942). Colonization of crab respiratory surfaces by *Octolasmis* spp. may result in heavy infestations that overwhelm the cleaning capacity of grooming appendages and make respiration difficult (Overstreet, 1983).

As is the case with many edible crab species, the respiratory chambers of the mangrove crab, *Scylla serrata* (Forskål, 1755), are inhabited by stalked barnacles, which occupy space on the gills normally available for respiratory exchange of oxygen and carbon dioxide. To colonize the crabs, octolasmid cyprid larvae collect on the host just prior to molt and transfer from the old exoskeleton to the newly molted crab at the time of ecdysis (Jeffries *et al.,* 1989). Following attachment, the cyprid metamorphoses to the adult barnacle body form and is sessile thereafter. Because they are sessile, these barnacles cannot recolonize crabs that have molted. Thus for a barnacle to achieve reproductive success, there must be a sufficient interval between crab molts for the cyprid to attach, metamorphose to the adult form, reach sexual maturity, copulate, oviposit, and release nauplii.

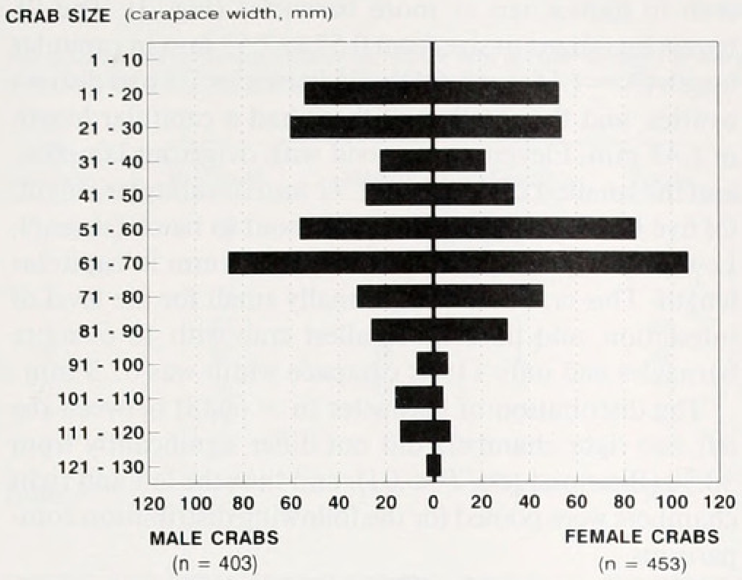

Figure 1. The size distributions for 403 male and 453 female mangrove crabs (*Scylla serrata*) collected from mangrove areas in the immediate vicinity of Phuket, Thailand.

Some small crabs also harbor octolasmids, *e.g., Uca minax,* with a carapace width of 38 mm (Williams, 1965) was reported to bear *Octolasmis mülleri* (Coker, 1902), (Pearse, 1936). In a survey of the decapods of Sabah, Malaysia (unpublished), we noted that three different crab species, all small, harbored *Octolasmis angulata* in their branchial chambers: 2 male *Pilumnus scabriusculus* (Adams & White), 32.1 and 36.3 mm, respectively; 1 male *Pilumnus vespertilio* (Fabricius, 1793), 23.2 mm; and 1 male *Actaeodes* sp., 26.9 mm. These observations, together with the observation that smaller *S. serrata* had few or no octolasmids, prompted us to ask whether host size might be a consideration in the mangrove crab-octolasmid symbiosis.

The purpose of this research was to determine the stage and time in the life cycle of the mangrove crab when *Octolasmis* spp. colonize its gill chambers. Specifically, we sought to identify the youngest crab instars that harbor *Octolasmis,* and to compare the number and distribution of barnacles on their gills with those on mature crabs.

Materials and Methods

During 1990 and 1991, *S. serrata* were collected from shallow seas adjacent to mangroves, mostly within 2 km of the town of Phuket, Thailand, for study at the Phuket Marine Biological Center. The very small instars were caught by hand, whereas larger crabs were caught in baited traps. The crabs were sexed, weighed, and their carapace lengths and widths measured (Heasman, 1980). They were preserved in formalin and stored in 70% ethanol for later examination. The crabs were examined for *Octolasmis* cyprids, juveniles, adults with distinct ovaries, and gravid adults. The exact location (left or right gill chamber, gill number, inside or outside gill surface, proximal, medial, or distal region of gill), and the length of the capitulum of each barnacle were recorded using the methods previously employed (Jeffries *et al.*, 1982). A dissecting microscope was used to determine the reproductive status of the barnacles.

Results

A total of 856 *S. serrata* were examined; 403 were males and 453 females. The carapace width of the male and female crabs ranged from 10.9 to 125.5 mm and from 11.2 to 132.3 mm, respectively. The size distributions of the male and female crabs examined were very similar (Fig. 1).

Of the 6648 barnacles observed, 168 were cyprids, 3670 were *Octolasmis cor,* 1758 were *Octolasmis angulata,* and the remainder were too small to identify. Except where noted, all stages and both species were pooled in the analysis because the focus of this paper is on barnacle colonization relative to crab age. In a subsequent paper about the ecology of barnacles resident on mangrove crabs, we will address the differences between the two species. That subject deserves individual treatment because opinion is divided on whether *S. serrata* branchial chambers bear several varieties of *Octolasmis cor* (Monod, 1922; Newman, 1960) or two species, *O. cor* and *O. angulata,* as we assert.

The percentage of crabs that harbored barnacles was very low (<5%) for crabs of less than 50 mm carapace width, whereas the incidence of infestation rose sharply as crab size increased above 50 mm (Fig. 2).

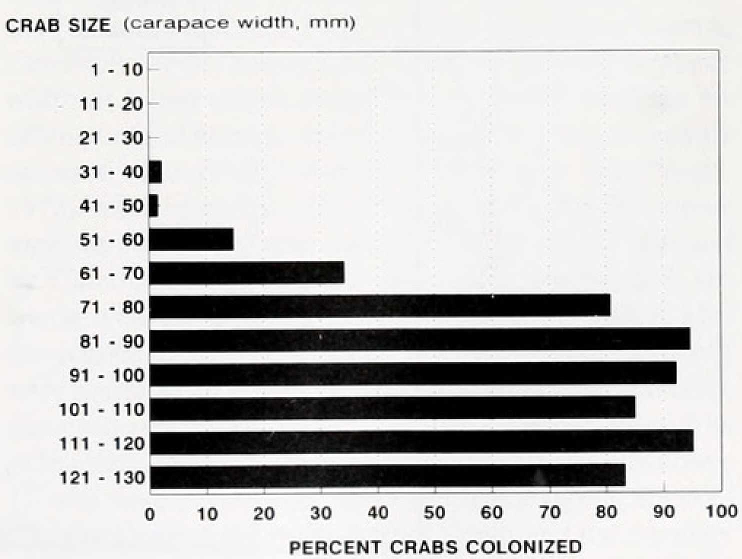

Figure 2. The percentage of mangrove crabs (*Scylla serrata*) of different sizes with one or more octolasmid barnacles present in a gill chamber. The 856 crabs range in size from 10.9 to 132.3 mm in carapace width.

Of the 856 crabs examined for barnacles, 260 (30.4%) had one or more barnacles in their gill chambers. Of these, 134 crabs were males and 126 were females. The percentage of male crabs harboring barnacles (33.3%) was only slightly greater than for female crabs (27.8%), and both males and females showed increased numbers of barnacles with increased carapace width (Fig. 3).

The smallest crab in the sample bearing a barnacle in its gill chamber was a male with a carapace width of only 34.3 mm (instar number 10; Ong, 1966). The solitary octolasmid (*O.* sp.) was found on the inside of the seventh gill; it was reproductively immature and had a capitular length of 0.86 mm. The next smallest crab to have a barnacle in its gill chamber was a female with a carapace width of 43.1 mm (instar 11; Ong, 1966). This crab had a single cyprid on the inside of the sixth gill. The carapace widths of all other barnacle-bearing crabs were more than 50.0 mm, corresponding to instar 12 or greater.

Two male crabs with carapace widths of 51.3 mm were the next smallest crabs to harbor single barnacles. One crab had a cyprid, whereas the other was the smallest crab to possess a sexually mature *Octolasmis cor,* measuring 1.72 mm in capitular length, with a distinct ovary indicating that it was potentially reproductively active.

The smallest crab with multiple barnacles, a female, had a carapace width of 54.5 mm; it harbored two *O. cor* with distinct ovaries and capitular lengths of 1.86 and 2.43 mm. Figure 2 shows that the incidence of barnacles increased on crabs between 60 and 70 mm, but most crabs below 70 mm had no more than 5 barnacles. One notable exception was a female crab with a carapace width of 60.4 mm and 95 barnacles. This crab was also the smallest crab to harbor ten or more barnacles (Fig. 3). The 95 barnacles ranged in size from 0.57 to 2.57 mm in capitular length ($\bar{X}$ = 1.66 mm). Of the 95 barnacles, 38 had distinct ovaries, and the smallest of these had a capitular length of 1.43 mm. Eleven were gravid with ovigerous lamellae, and the smallest of these was 1.72 mm in capitular length. Of five bearing nauplius I larvae about to hatch (stage N; Lewis, 1975), the smallest was also 1.72 mm in capitular length. This crab was exceptionally small for the level of infestation, and the next smallest crab with 10 or more barnacles had only 11; its carapace width was 67.3 mm.

The distribution of barnacles (n = 6648) between the left and right chambers did not differ significantly from 50:50 (Binomial test, $P < .01$), and thus the left and right chambers were pooled for the following distribution comparisons.

To explore possible differences in patterns of colonization among crabs of different sizes, the 260 infected crabs were divided into two groups: those with carapace widths below 70 mm (n = 87) and those above 70 mm (n = 173). This division point was selected on the basis of observed infestation levels (Fig. 3) and the knowledge that 70 mm (instar 14) likely corresponds to the beginning of crab sexual maturity. Among female mangrove crabs of instar 14, the ovaries are considerably developed and easy to see grossly as was reported for female *Callinectes sapidus* (Rathbun, 1896) following the penultimate molt (Johnson, 1980).

All 303 barnacles found on the 87 crabs with carapace widths of less than 70 mm were located on the inside surface of the gills (Table I). This distribution is significantly different (df = 1, χ^2 = 38.8, $P < .001$) from that

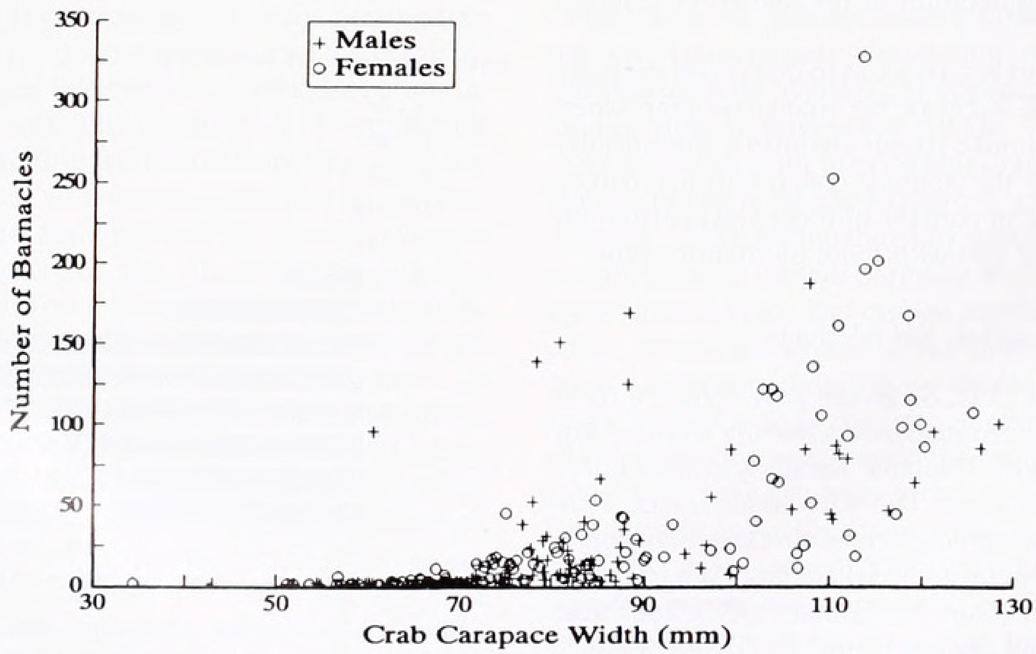

Figure 3. The relationship between the crab carapace width and the number of octolasmid barnacles present in the gill chambers for 134 male and 126 female mangrove crabs (*Scylla serrata*).

Table I

The distribution of barnacles over the inside and outside surfaces of the gills of the 87 crabs with carapace widths less than 70 mm

Gill number	Inside of gills				Outside of gills				In + Out totals
	Proximal	Medial	Distal	Totals	Proximal	Medial	Distal	Totals	
1	1	4	0	5	0	0	0	0	5
2	0	0	0	0	0	0	0	0	0
3	9	22	0	31	0	0	0	0	31
4	33	32	1	66	0	0	0	0	66
5	27	38	1	66	0	0	0	0	66
6	26	42	5	73	0	0	0	0	73
7	16	31	2	49	0	0	0	0	49
8	5	8	0	13	0	0	0	0	13
Totals =	117	177	9	303	0	0	0	0	303
								On Rakers	1
								Total =	304

observed for the 173 crabs with carapace widths of greater than 70 mm, where 5609 barnacles were found on the inside surface of the gills and 723 (11%) were found on the outside (Table II). The smallest crab having a barnacle attached to the outside surface of its gills had a carapace width of 76.8 mm, and the inside surface of the gills in that chamber had a total of 20 barnacles. The smallest crab having multiple barnacles attached to the outside surface of its gills had a carapace width of 78.2 mm, and the numbers of barnacles on the inside and outside surfaces of the gills were 64 and 2 in the left chamber, and 61 and 3 in the right chamber.

For the 87 crabs less than 70 mm, and the 173 above 70 mm in carapace width, the distribution of barnacles on the inside of gills 1 through 8 (Tables I, II) did not differ significantly (df = 7, $\chi^2 = 6.1$, $P > .05$). Nor did the distribution of barnacles along the length of the gills (proximal, medial, and distal) on the inside surface differ significantly (df = 2, $\chi^2 = 2.4$, $P > .05$) between the crabs above and below 70 mm.

The distribution of barnacles on the inside *versus* the outside of the gills among all 260 crabs with barnacles (data from Tables I and II combined) showed significant differences. The distribution of barnacles on the inside *versus* the outside, and over gills 1 through 8, differed significantly (df = 7, $\chi^2 = 525.9$, $P < .001$). In addition, the distribution of barnacles along the length of the gills (proximal, medial, and distal) on the inside *versus* the outside surface differed significantly (df = 2, $\chi^2 = 87.3$, $P > .001$). Whether on the inside or outside surface of the gills, barnacles in this sample were least common on the distal third of the gills. On the inside surface, the medial section of the gill was the most densely populated, whereas on the outside surface, the proximal portion of the gills was the most populated.

Discussion

These data support four major conclusions about colonization of mangrove crabs by barnacles: (1) juvenile crabs are virtually free of octolasmids; (2) as crabs approach sexual maturity, the percentage of crabs hosting octolasmids increases; (3) the level of barnacle infestation of individual crabs increases with crab size; and (4) the distribution of octolasmids on the gills of immature crabs is different from that on mature crabs. Our discussion will focus on possible explanations for these findings.

In this study we found that 233 crabs, representing instars 5 through 9 (Ong, 1966), did not host a single barnacle. Several previous studies of decapods and their symbionts also have suggested size thresholds for infestation. Although the intertidal shore crab, *Hemigrapsus oregonensis* (Dana, 1851), of either sex, mature or not, may become infested with juvenile nemertean worms, *Carcinonemertes epialti* Coe, 1902, a threshold carapace width of 8 mm exists; above that threshold, both the incidence of infestation and the average burden of worms increase dramatically with increasing host size (Kuris, 1978). Also, juveniles of the edible dungeness crab, *Cancer magister*, below 20 mm carapace width are not infested by *Carcinonemertes errans*, whereas worm burdens increase with crabs above 20 mm (Wickham, 1980). Metacercariae of the trematode, *Spelotrema excellens* Nicoll, were found in 103 of 115 specimens of the portunid crab, *Carcinus maenas* (L.). Twelve crabs with carapace widths of less than 15 mm were not parasitized, whereas all above 15 mm were parasitized, and there was a significant correlation between the crab carapace width and the intensity of infection (Threlfall, 1968).

These studies suggest that size thresholds do exist among the host decapods in such symbiotic relationships. However, there has been very little critical examination of the

Table II

The distribution of barnacles over the inside and outside surfaces of the gills of the 173 crabs with carapace widths greater than 70 mm

Gill number	Inside of gills				Outside of gills				In + Out totals
	Proximal	Medial	Distal	Totals	Proximal	Medial	Distal	Totals	
1	37	36	4	77	1	1	23	25	102
2	5	4	6	15	14	13	9	36	51
3	162	398	45	605	16	18	2	36	641
4	607	691	33	1331	87	41	0	128	1459
5	431	564	39	1034	209	95	10	314	1348
6	579	577	43	1199	72	73	2	147	1346
7	322	633	66	1021	11	18	2	31	1052
8	144	171	12	327	0	6	0	6	333
Totals =	2287	3074	248	5609	410	265	48	723	6332
								On Rakers	12
								Total =	6344

possible effects of host ontogenetic changes on symbiosis involving Crustacea. This is important because the way that symbionts interact with different host ontogenetic stages can contribute to our understanding of the mechanisms underlying the symbiotic relationships.

For the relationship between *S. serrata* and *Octolasmis* spp., we have considered the following possible influences on the observed non-random distributions: ontogenetic differences in physical barriers such as the size of the major incurrent respiratory apertures, and gill chamber size; duration of intermolt period; crab macrohabitat distribution; crab microhabitat distribution; and crab behavior.

In order to be a limiting factor, the incurrent respiratory apertures of the crab would have to be small enough to exclude cyprid larvae. The average length and diameter of 10 preserved *Octolasmis* cyprids was 0.82 × 0.35 mm. By comparison, the average width and height of the major apertures of five of the smallest crabs (carapace width 10–19 mm) examined in this study was 1.9 × 1.0 mm. Clearly, crab intake aperture size is not a limiting factor to cyprid larvae trying to enter the branchial chambers of *S. serrata.*

If space in the gill chamber were a major factor in limiting the occurrence of barnacles on immature crabs, we would expect the numbers of barnacles on crabs to increase steadily with increased crab size. This does not seem to be the case. For example, two crabs with carapace widths of 60.4 and 61.4 mm had large populations of barnacles, although their sizes are at the threshold where colonization is just beginning (Fig. 3).

For the length of the crab intermolt period to strictly limit the effective colonization by barnacles, the crab intermolt period must be shorter than the total time necessary for the cyprid to attach, metamorphose, reach sexual maturity, become gravid, and release nauplius I larvae. This is the case because post-metamorphic barnacles are sessile, and when a crab molts, individual barnacles remain attached to the crab exuviae and are unable to recolonize a host. Thus there is the potential for a fine-tuned host/symbiont relationship predicated on the intermolt time period of the host and the time the symbiont requires to complete its life cycle.

Earlier work provided an estimate of 24 h for *Octolasmis* cyprid attachment to metamorphosis, an estimated daily growth rate of 0.336 mm in capitular length (Jeffries *et al.*, 1985), and demonstrated that the major colonization of crabs by cyprids occurs immediately after ecdysis (Jeffries *et al.*, 1989). In this study, the capitular length of the smallest *Octolasmis cor* (1.72 mm) observed with ovigerous lamellae compares favorably with the 1.6 mm specimen reported with mature eggs by Matheswari and Fernando (1989), and exceeds the 1.14 mm gravid specimen of *O. mülleri* reported by Jeffries and Voris (1983). On average, the capitular length of the newly metamorphosed barnacle is 0.57 mm, and thus it takes about 3.4 days to reach 1.72 mm at the daily growth rate of 0.336 mm. Hence, the time from cyprid attachment to a gravid barnacle at oviposition with ovigerous lamellae is about 4.4 days.

The development time from oviposition to the release of nauplius I larvae is unpublished for octolasmids, but it has been reported for other lepadomorphs. For *Ibla quadrivalvis* Cuv., it was 16 to 17 days at 23°C (Anderson, 1964), and for *Pollicipes polymerus,* it averaged 25.4 days at 12 to 16°C (Lewis, 1975). Because seawater temperatures at the *S. serrata* collection sites near Phuket, Thailand, range from 27 to 31°C, it is very likely that for *O. cor* the required time from oviposition to release of nauplius I larvae is no more than 14 days, and may be as little as one week. Thus, the time required for *O. cor* to attach and reproduce is likely no more than 18.4 days (4.4 plus 14) and may be as little as 11.4 days (4.4 plus 7).

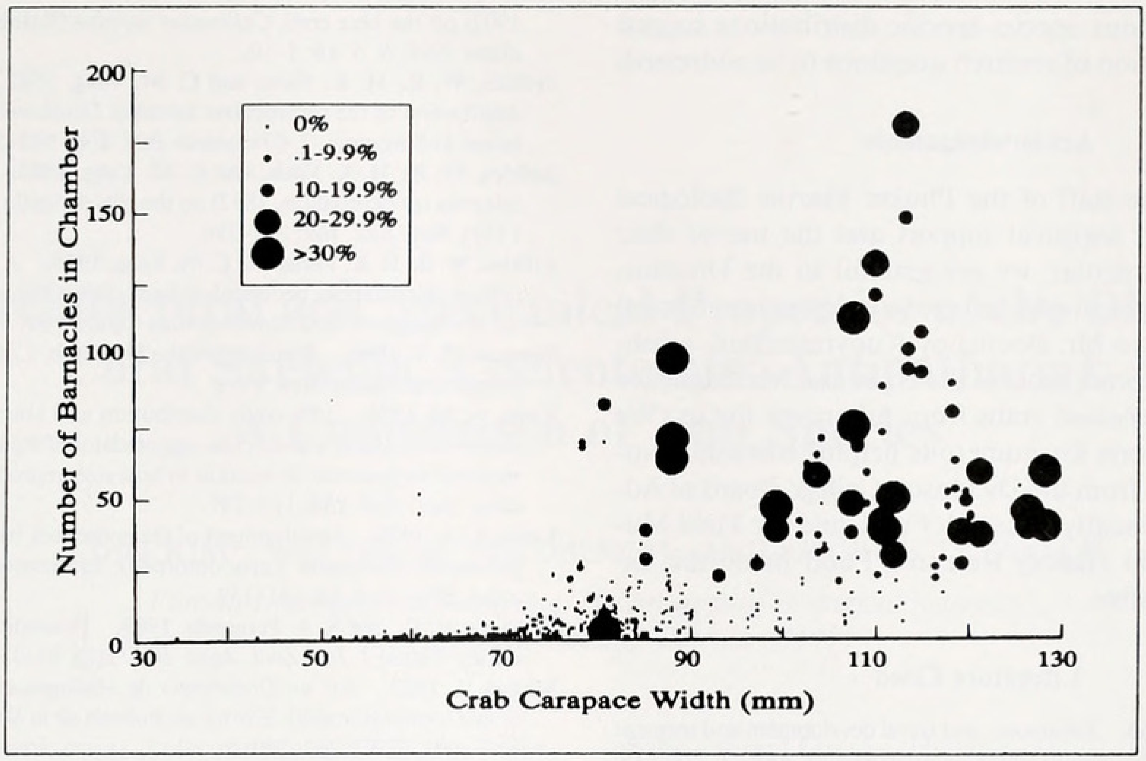

Figure 4. Of the 260 crabs with barnacles, 435 of the 520 gill chambers contained one or more barnacles. For each chamber, the size of the crab is plotted against the number of barnacles present in the chamber. The symbol size indicates the percentage of the barnacles present on the outside surface of the gills in increments of 10%.

S. serrata instar 9 crabs range in size from 26 to 33 mm in carapace width and have an intermolt period of at least 15 days (Ong, 1966). The absence of any barnacles on the 233 crabs of instars 5 to 9 in this study may be attributable to barnacle avoidance because the intermolt period is too short to allow for barnacle reproduction.

Crab instars 10 to 11 range from 33 to 48 mm in carapace width and have minimum intermolt periods of 16 and 22 days, respectively. According to our earlier calculations, these are minimum time periods that octolasmids require to produce offspring and they would not allow individuals to produce multiple broods, thus limiting fecundity (Jeffries *et al.,* 1985). In this study, the fact that only a small fraction of instars 10 and 11 harbored barnacles (Fig. 2) and none had heavy infestations (Fig. 3) is consistent with the idea that these crab instars represent suboptimal substrata.

Instars 12 and above have carapace widths greater than 45 mm and intermolt periods of 30 days or more. Such intermolt periods are sufficient to allow for the production of multiple broods. This is consistent with our observations that the incidence of infestation increases among crabs above 50 mm carapace width (Fig. 2) and is further supported by the observation that one crab of 60.4 mm carapace width (instar 13) had 95 barnacles (Fig. 3), many of which harbored nauplius I larvae.

In this study, mangrove crabs of different sizes—juveniles and adults—were collected at the same time in the same shallow water mangrove macrohabitat, thus diminishing the possibility of a difference in availability of cyprids to potential hosts at the macrohabitat level.

Differences in infestation rates among successive instars of *S. serrata* might be the result of ontogenetic changes in microhabitat use, shifts in host hormone levels (chemotaxis), or behavioral changes. However, we cannot discriminate among these factors on the basis of current information. For example, it was reported that juvenile mangrove crabs use shelter under existing bottom debris in open areas (Heasman, 1980), whereas older crabs use burrows. But we do not know whether this difference has an impact on mangrove crab colonization by *Octolasmis* cyprid larvae.

The differences observed in the distribution of barnacles on the inside and outside of the gills in crabs less than and those greater than 70 mm carapace width (Tables I, II) could be due to a density-dependent response to crowding on the inside surface of the gills, or it could be due to a lack of space in the chamber on the outside surface of the gills. The former explanation is better supported by our data. If space on the outside of the gills controlled colonization, we would expect larger crabs with modest numbers of barnacles (*e.g.,* 5 to 20) to have barnacles on both the inside and outside surface of their gills. This is not the case. Barnacles are only found on the outside gill surfaces in significant numbers when the inside surface has 20 or more barnacles, regardless of crab size (Fig. 4).

These non-random, species-specific distributions suggest the next generation of research questions to be addressed.

Acknowledgments

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