

Patterns of Distribution of Two Barnacle Species on the Mangrove Crab, *Scylla serrata*

HAROLD K. VORIS^{1,*}, WILLIAM B. JEFFRIES², AND SOMBAT POOVACHIRANON³

¹*Department of Zoology, Field Museum of Natural History, Chicago, Illinois 60605;*

²*Department of Biology, Dickinson College, Carlisle, Pennsylvania; and*

³*Phuket Marine Biological Center, Phuket, Thailand*

Abstract. Two lepadomorph barnacle species, *Octolasmis angulata* and *O. cor*, were commonly found living together in the branchial chambers of the mangrove crab, *Scylla serrata*. Patterns of distribution are a reflection of cyprid choice at crab ecdysis. Among the 6648 barnacles observed, there were roughly twice as many *O. cor* as *O. angulata* (3670 to 1758). The remaining barnacles were indistinguishable as to species and included 1014 immatures, 168 cyprids, and 38 peduncles. The spatial distributions of both *O. angulata* and *O. cor* on the gills of *Scylla serrata* are nonrandom, uneven, and do not reflect available surface area. Both species are distributed differently on the hypobranchial (inside) and epibranchial (outside) surfaces of the gills. Both species are distributed differently on the gills of immature (<70 mm carapace width) and mature (>70 mm) crabs. Our data also show that the distribution patterns vary with different densities. Support is presented for the hypothesis that current flow through the gill chamber may be an important factor influencing site selection by cyprids.

Introduction

The goose barnacles of the genus *Octolasmis* that are under study here are members of the Lepadomorpha (Zevina, 1982), and they differ from other barnacles in several important ways. Most of the species in the genus *Octolasmis* are symbiotic on decapod Crustacea, particularly crabs and lobsters (Darwin, 1851; Walker, 1974; Jeffries *et al.*, 1992). The integument of these hosts is an ephemeral substrate for attached symbionts because at ecdysis they are shed with the discarded exoskeleton

(Coker, 1902; Humes, 1941; Jeffries *et al.*, 1985). Colonization of newly molted crabs by octolasmid cyprids is highly pulsed because cyprids gather on the premolt crab and transfer from the old exuviae to the newly molted crab at the time of ecdysis (Jeffries *et al.*, 1989). Thus, cyprids colonizing crabs in this way may interact with other cyprids, but there is no chance of their encountering attached adult octolasmids on the recently molted crab.

Octolasmis cor (Aurivillius, 1892) and *Octolasmis angulata* (Aurivillius, 1894) are inhabitants of the gill chambers of numerous decapods found in the seas of South East Asia (Jeffries, *et al.*, 1982), and they are commonly found together in the gill chambers of the mangrove crab, *Scylla serrata* (Forskål, 1755). The two species are distinguishable on the basis of differences in labrum tooth counts; outline and size of the capitulum; size, shape, and arrangement of the calcareous plates; and fecundity (Jeffries *et al.*, 1991). The nauplius and cypris larvae of the two species are now being compared, and the initial results support the two-taxa hypothesis: *e.g.*, the cypris larvae of one species are larger than the other. To these observations we now add new information concerning their relative positions within the gill chambers.

Although the presence of diverse species within the gill chambers of crabs has been documented (Coker, 1902; Pearse, 1932, 1947; De Turk, 1940; Humes, 1941, 1942; Walker, 1974; Lang, 1976; Overstreet, 1983; Shields, 1992), this is the first precise comparison of the distribution of two related *Octolasmis* barnacle species in the gill chambers of a single host crab species, *S. serrata*. As a model system, it provides an excellent descriptive foundation for future experimental study of such aspects of symbiosis as site selection and competition for resources.

The purpose of this report is to describe and consider the spatial distributions of octolasmid barnacles in the gill

Table 1

The distribution of 1758 *O. angulata* over the inside (hypobranchial) and outside (epibranchial) surfaces of the gills in 225 gill chambers of 143 *S. serrata* (top), and the distribution of 3670 *O. cor* over the inside and outside surfaces of the gills in 346 gill chambers of 200 *S. serrata* (bottom)

<i>Octolasmis angulata</i>										
Gill Number	Inside of gills				Outside of gills				In + Out Totals	
	Proximal	Medial	Distal	Totals	Proximal	Medial	Distal	Totals		
1	2	1	0	3	0	1	14	15	18	
2	0	0	2	2	6	6	4	16	18	
3	8	47	17	72	15	6	2	23	95	
4	19	54	11	84	64	28	0	92	176	
5	82	48	10	140	151	68	9	228	368	
6	130	116	19	265	41	45	2	88	353	
7	152	324	38	514	7	13	1	21	535	
8	88	94	5	187	0	3	0	3	190	
TOTALS	481	684	102	1267	284	170	32	486	1753	
ON RAKERS	5	0	0	5	0	0	0	0	5	
				1272				486	1758	

<i>Octolasmis cor</i>										
Gill Number	Inside of gills				Outside of gills				In + Out Totals	
	Proximal	Medial	Distal	Totals	Proximal	Medial	Distal	Totals		
1	30	27	3	60	0	0	0	0	60	
2	2	2	4	8	6	6	2	14	22	
3	133	289	20	442	0	1	0	1	443	
4	540	575	14	1129	4	1	0	5	1134	
5	292	441	18	751	16	7	0	23	774	
6	375	393	21	789	0	3	0	3	792	
7	133	218	17	368	0	0	1	1	369	
8	22	42	6	70	0	1	0	1	71	
TOTALS	1527	1987	103	3617	26	19	3	48	3665	
ON RAKERS	5	0	0	5	0	0	0	0	5	
				3622				48	3670	

chambers of a natural population of the mangrove crab, *Scylla serrata*. In addition, both abiotic and biotic factors that influence the settlement patterns of two barnacle species, *Octolasmis angulata* and *O. cor*, are discussed.

Materials and Methods

We recently reported on the age of the mangrove crab, *Scylla serrata*, at colonization by *Octolasmis* spp. (Jeffries *et al.*, 1992), and the same specimens used in that study form the foundation for the current report. The sample of mangrove crabs, including 403 males and 453 females, and ranging in size from 10.9 to 132.3 mm carapace width (instars 5–18), was collected by hand and trap from a natural population in southern Thailand in 1990 and 1991. The crabs were examined for *Octolasmis* cyprids, juveniles, and adults. Adult barnacles were identified to species, whereas immatures could not be classified. The exact location of barnacle attachment [left or right gill

chamber, gill number, inside (hypobranchial) or outside (epibranchial) gill surface, proximal, medial, or distal region of gill], and the length of the capitulum of each preserved barnacle were recorded by the methods previously employed (Jeffries *et al.*, 1982).

In this study we collected a sample of 856 crabs, among which 260 hosted a total of 6648 octolasmids. The barnacle population included 1758 *O. angulata*, 3670 *O. cor*, 1014 unknowns (all subadults), 38 peduncles only, and 168 cyprids.

Results

Analysis of O. angulata distribution

A total of 1758 *O. angulata* were observed on 143 *Scylla serrata*; 63 of these were female crabs, and 80 were males. All but 13 of the infested *S. serrata* also harbored one or more *O. cor* individuals. Each crab has two gill chambers, and not all of the 286 gill chambers of the 143 infested

crabs held barnacles. In fact, 61 of the 143 crabs had one chamber that hosted no *O. angulata*. Thus, in this analysis the *O. angulata* distributed in 225 gill chambers of 143 crabs are being considered (Table I).

The distribution of *O. angulata* on the inside (hypobranchial) surface of gills 1 through 8 was compared to distributions that reflect gill length and gill surface area (Jeffries and Voris, 1983). The areas of the gills were estimated with the formula for the area of a right cone ($a = \pi rh$). The observed distribution is significantly different (Chi-square test, Mosteller and Rourke, 1973) from an expected distribution based on the length of the gills ($\chi^2 = 976.8$, $df = 7$, $P < .001$) and the area of the gill surface ($\chi^2 = 649.3$, $df = 7$, $P < .001$). For example, gills 4, 5, and 6 are of similar length, and yet gill 6 harbors more *O. angulata* than gills 4 and 5 combined.

By far, more of the *O. angulata* were attached to the inside (hypobranchial) surface of the gills (1267, 72%) than were attached to the outside (epibranchial) surface (486, 28%).

The distribution of *O. angulata* on the inside of gills 1 through 8 (gill totals, Table I) differs significantly from the distribution on the outside of gills 1 through 8 ($\chi^2 = 547.5$, $df = 14$, $P < .001$). For example, the inside surface of gill 7 has 40 percent (514) of all of the *O. angulata* found on the inside surface of the gills, whereas the outside surface of gill 7 has only 4.9% (21) of the *O. angulata* found on the outside (Fig. 1). Thus, the distribution of *O. angulata* on the inside gill surfaces is distinct from its distribution over the outside gill surfaces.

The distributions of *O. angulata* on the proximal, medial, and distal surfaces of the inside of gills 1 through 8 differ from one another for all three comparisons (proximal by medial, $\chi^2 = 84.0$, $df = 14$, $P < .001$; proximal by distal, $\chi^2 = 72.4$, $df = 14$, $P < .01$). Thus, the distribution of *O. angulata* over the inside surface of the proximal, medial, and distal regions of individual gills differs from gill to gill. This is also true for the distribution over the outside surfaces, although the numbers of barnacles are smaller (Table I).

The totals of *O. angulata* on the inside surfaces of the proximal (481), medial (684), and distal (102) regions of gills 1 through 8 (Table I) differ from the totals for the outside ($\chi^2 = 60.8$, $df = 4$, $P < .001$). For example, *O. angulata* are most common on the medial segments of the inside surfaces of gills (684, 54%), whereas they are most common on the proximal portion of the outside surface of gills (284, 58%).

Analysis of *O. cor* distribution

A total of 3670 *O. cor* were observed on 200 *Scylla serrata*, 93 females and 107 males. Of these, 127 harbored one or more *O. angulata*. Of the 200 crabs with *O. cor*,

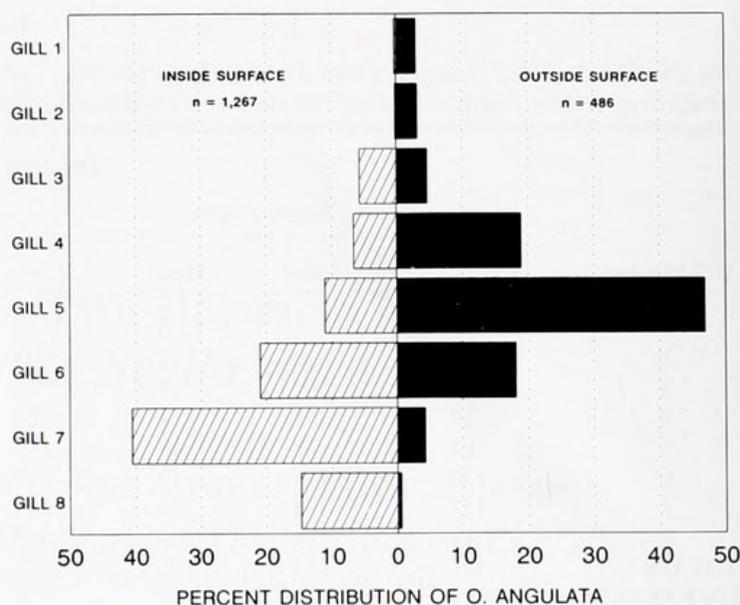


Figure 1. The percent distribution of 1267 *Octolasmis angulata* on the inside (hypobranchial) surfaces and 486 on the outside (epibranchial) surfaces of gills 1 through 8 in 225 gill chambers of 143 *Scylla serrata* is presented.

54 crabs had one chamber that did not host any *O. cor*. In this analysis, therefore, the *O. cor* distributed in 346 gill chambers of 200 crabs are considered (Table I).

The spatial distribution results for *O. cor* are similar but not identical to those for *O. angulata*.

The distribution of *O. cor* on the inside surface of gills 1 through 8 (gill totals of *O. cor*) was compared to distributions that reflect gill length and gill surface area. In each case the observed distribution (Table I) was significantly different from an expected distribution based on gill length ($\chi^2 = 1888.9$, $df = 7$, $P < .001$) and area ($\chi^2 = 1643$, $df = 7$, $P < .001$). For example, gills 4, 5, and 6 are of similar lengths and yet gill 4 harbors roughly 30% more *O. cor* than either gill 5 or gill 6.

The vast majority (3617, or 98.6%) of the *O. cor* were attached to the inside surface of the gills rather than the outside surface (48, 1.3%).

The distribution of *O. cor* on the inside of gills 1 through 8 (gill totals) differs from that on the outside of gills 1 through 8 ($\chi^2 = 682.9$, $df = 14$, $P < .001$). For example, the inside surface of gill 4 has 31% (1129) of all the *O. cor* on the inside surface (Table I), whereas the outside surface of gill 4 has only 10% (5) of all the *O. cor* on the outside. *O. cor*, like *O. angulata*, colonizes the inside surfaces of the gills in a way distinct from its colonization of the outside gill surfaces.

The distributions of *O. cor* on the proximal, medial, and distal surfaces of the inside of gills 1 through 8 differ from one another for all three comparisons (proximal by medial, $\chi^2 = 57.2$, $df = 14$, $P < .001$; proximal by distal, $\chi^2 = 80.6$, $df = 14$, $P < .001$; distal by medial, $\chi^2 = 69.8$,

df = 14, $P < .001$). Thus, the distribution of *O. cor* over the inside surfaces of the proximal, medial, and distal regions of individual gills differs from gill to gill. The number of *O. cor* on the outside surfaces is very small, so the distribution on these surfaces remains unclear (Table I).

The distribution of the totals for gills 1–8 of *O. cor* on the proximal (1527), medial (1987), and distal (103) surfaces of the inside of the gills (Table I) does not differ from the totals for the proximal, medial, and distal surfaces of the outside ($\chi^2 = 5.5$, df = 4, $P < .05$). This lack of difference is unlike our findings with *O. angulata* and may be due to small numbers of *O. cor* on the outside (Table I).

Comparison of *O. angulata* and *O. cor* distributions

The distributions of *O. angulata* and *O. cor* on the inside surfaces of gills 1 through 8 (gill totals) are significantly different from each other ($\chi^2 = 1103.4$, df = 14, $P < .001$). For example, gill 7 has the highest number (514) of *O. angulata* on the inside, whereas gill 4 has the highest number (1129) of *O. cor* on the inside (Table I). Figure 2 illustrates how differently *O. angulata* and *O. cor* are distributed on the inside surfaces of the gills.

Less than 2% of the *O. cor* were found on the outside gill surfaces, whereas 28% of the *O. angulata* were attached to the outside surfaces (Table I). Although these distributions were significantly different ($\chi^2 = 59.0$, df = 14, $P < .001$), the very low numbers of *O. cor* found on the outside make this comparison of questionable biological importance.

The distributions of *O. angulata* and *O. cor* on the proximal, medial, and distal segments of the inside surfaces of gills 1 through 8 (Table I) are different from one another ($\chi^2 = 64.8$, df = 4, $P < .001$). Both species have about 55% on the medial gill region but differ on the proximal and distal regions. A similar comparison for the barnacles distributed over the outside surfaces shows no significant difference ($\chi^2 = .41$, df = 4, $P < .05$).

Distribution of barnacles on crabs of different sizes

In an earlier study (Jeffries *et al.*, 1992), we divided the sample of crabs into two size categories: those with carapace widths below 70 mm ($n=87$), and those above 70 mm ($n = 173$). This size criterion was chosen because crabs larger than 70 mm are much more likely to be infested and have heavier infestations, and because the crab's sexual maturity probably begins at 70 mm (instar 14) (Jeffries *et al.*, 1992). This same carapace size (70 mm), was used to divide the crabs into two groups—larger and smaller—for the following comparisons of distributions.

For both species of barnacles, distribution on the inside of gills 1 through 8 (gill totals) of smaller crabs differs

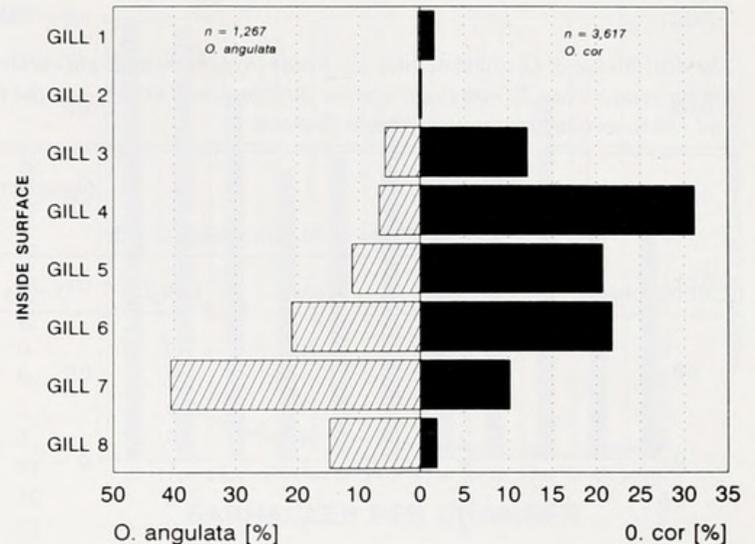


Figure 2. The percent distribution of 1267 *Octolasmis angulata* is compared with the percent distribution of 3617 *Octolasmis cor* on the inside (hypobranchial) surfaces of gills 1 through 8.

from the distribution on larger crabs (*O. angulata*: $\chi^2 = 26.2$, df = 14, $P < .02$; *O. cor*: $\chi^2 = 25.3$, df = 14, $P < .05$). For example, gill 7 bears 17% (11) of the *O. angulata* on the smaller crabs, whereas gill 7 bears 42% (503) of the *O. angulata* on the larger crabs (Table II). The distribution of *O. cor* on the inside of gills 1 through 8 (gill totals) on crabs of less than 70 mm carapace width also differs from the distribution on crabs larger than 70 mm.

The distributions of *O. angulata* on the proximal, medial, and distal segments of the inside surfaces of gills 1 through 8 of smaller crabs were not significantly different from the distribution observed on larger crabs ($\chi^2 = .34$, df = 4, $P > .05$). This was also true for *O. cor* ($\chi^2 = 1.6$, df = 4, $P > .05$).

Table II also shows that smaller crabs (<70 mm) have fewer individual barnacles in their gill chambers than do the larger (>70 mm) crabs. Only two of the smaller crabs had more than 10 barnacles. Thus, crab size and barnacle density go hand-in-hand.

Effects of crowding on barnacle distributions

In analyzing barnacle numbers and barnacle distribution as a function of density, two points must be considered.

First, the "host unit" should be the gill chamber and not the individual crab. We think this because, as cyprids explore a given gill chamber, they can monitor directly only those conditions (whether biotic, *e.g.*, other cyprids or metamorphosed barnacles, or abiotic, *e.g.*, currents and oxygen concentrations) in that chamber. Of course, the two chambers of a crab are not wholly independent; for example, they have in common a crab of the same size,

Table II

The distribution of *O. angulata* over the inside (hypobranchial) gill surfaces of 23 *S. serrata* with carapace widths less than 70 mm and 120 *S. serrata* greater than 70 mm (top), and the distribution of *O. cor* over the inside gill surfaces of 44 *S. serrata* with carapace widths less than 70 mm and 156 *S. serrata* greater than 70 mm (bottom)

<i>Octolasmis angulata</i>										
Gill Number	Crabs < 70 mm; Inside of gills				Crabs > 70 mm; Inside of gills				In + Out Totals	
	Proximal	Medial	Distal	Totals	Proximal	Medial	Distal	Totals		
1	0	0	0	0	2	1	0	3	3	
2	0	0	0	0	0	0	2	2	2	
3	0	3	0	3	8	44	17	69	72	
4	2	4	0	6	17	50	11	78	84	
5	8	5	1	14	74	43	9	126	140	
6	8	13	3	24	122	103	16	241	265	
7	4	7	0	11	148	317	38	503	514	
8	3	4	0	7	85	90	5	180	187	
TOTALS	25	36	4	65	456	648	98	1202	1267	
ON RAKERS	0	0	0	0	5	0	0	5	5	
				65				1207	1272	

<i>Octolasmis cor</i>										
Gill Number	Crabs < 70 mm; Inside of gills				Crabs > 70 mm; Inside of gills				In + Out Totals	
	Proximal	Medial	Distal	Totals	Proximal	Medial	Distal	Totals		
1	1	0	0	1	29	27	3	59	60	
2	0	0	0	0	2	2	4	8	8	
3	5	14	0	19	128	275	20	423	442	
4	15	9	0	24	525	564	14	1103	1127	
5	10	16	0	26	282	425	18	725	751	
6	7	17	2	26	368	376	19	763	789	
7	8	18	1	27	125	200	16	341	368	
8	0	1	0	1	22	41	6	69	70	
TOTALS	46	75	3	124	1481	1910	100	3491	3615	
ON RAKERS	1	0	0	1	4	0	0	4	5	
				125				3495	3620	

general condition, health, and molt cycle stage, and a history of habitats visited.

Second, the density of barnacles in a chamber should be based on the sum of all barnacles found there. Thus, *O. angulata*, *O. cor*, unidentified specimens (mostly subadults), peduncles, and cyprids were all counted. The numbers of each of these categories for the 6648 barnacles observed are provided in the Materials and Methods section.

The first three columns of Table III present barnacle densities per chamber in increments of 10, the total number of chambers, and the total number of all barnacles per chamber. These data demonstrate that most chambers (292) had only 1 to 10 barnacles.

The remaining columns in Table III present the number of chambers and the number of barnacles, both *O. cor* and *O. angulata*, on the inside and outside gill surfaces. Both species are usually found exclusively on the inside gill surfaces when the barnacle density within the chamber

is less than 20. This pattern continues to hold for *O. cor* at densities of 100 or more, but at densities above 20, *O. angulata* occurs on both the inside and outside gill surfaces (Fig. 3).

The above results are of limited significance because they do not allow discrimination between the two mitigating factors, crab size and barnacle density. Small crabs have fewer barnacles.

In an attempt to separate these two factors, a subset of crabs with similar carapace widths, between 70 and 90 mm, was considered; they were small- to medium-sized adults representing instars 14 to 16 (Ong, 1966). These crabs were separated into two groups: one group with from 1 to 20 barnacles per chamber (low density), and one group with from 21 to 98 barnacles (high density). All species and stages were counted.

The distributions of *O. angulata* over the inside surfaces of gills 1 through 8 (gill totals) of the low and high density

groups were not significantly different from each other ($\chi^2 = 6.6$, $df = 14$, $P > .05$). Moreover, the distributions of the totals of *O. angulata* on the proximal, medial, and distal segments of the inside surfaces of gills 1 through 8 of both groups were also not significantly different ($\chi^2 = 2.1$, $df = 4$, $P > .05$).

The distributions of *O. cor* over the inside surfaces of gills 1 through 8 (gill totals) for the low density group and for the high density group (Table IV) are also not significantly different from each other ($\chi^2 = 21.2$, $df = 14$, $P > .05$). But the distributions of the totals of *O. cor* on the proximal, medial, and distal segments of the inside surfaces of gills 1 through 8 of the low density group and the high density group are significantly different ($\chi^2 = 13.8$, $df = 4$, $P < .01$). Thus, at higher densities there are more *O. cor* on the proximal portion of the gills and fewer (less than 1%) on the distal portion in comparison with the distribution observed in the low density chambers (Table IV).

Discussion and Conclusions

The ability of barnacle cyprids to locate highly specific substrates (microhabitats) for colonization is well documented in the literature (Foster, 1987). Hui and Moyses (1987) have suggested that the cyprids of "parasitic or obligate commensal species . . . must be [attracted] to the host animal." Moyses (1971) reported that *Megatrema anglicum* is secondarily attracted to conspecifics after the host coral has been located.

Most species within the genus *Octolasmis* colonize a limited number of host species (usually decapods) and are typically very selective as to the site of attachment on the body of the host. Moreover, a symbiont may exploit only

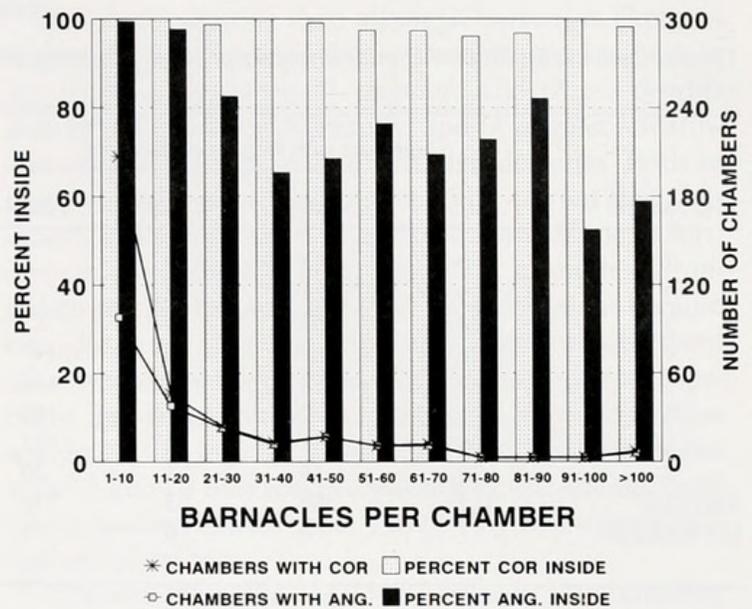


Figure 3. The percentages of *Octolasmis angulata* and *Octolasmis cor* on the inside (hypobranchial) surfaces of gills 1 through 8 are shown for chambers with barnacle densities that increase by 10. On the second Y axis the number of chambers with *Octolasmis angulata* and *Octolasmis cor* is shown with connected symbols.

a subset of a host population, partitioning the population by factors such as age, sex, and environment. For example, cyprids of *O. angulata* and *O. cor* prefer adult hosts, and small juvenile crabs are rarely colonized (Jeffries *et al.*, 1992). *Callinectes sapidus* harbors *O. mülleri* in the Chesapeake Bay, from the mouth of the Rappahannock River south, but not to the north (van Engel, pers. comm.).

Our results demonstrate that the spatial distribution of *O. angulata* and *O. cor* on the gills of *Scylla serrata* is nonrandom and does not reflect available surface area as

Table III

The total numbers of *O. cor* and *O. angulata* over the inside (hypobranchial) and outside (epibranchial) of *S. serrata* gill surfaces is given for gill chambers according to the range in density of all barnacles per chamber

Range of density	Total number of chambers	Total number of barnacles	Number of chambers with <i>cor</i>	Total <i>cor</i> inside	Total <i>cor</i> outside	Number of chambers with <i>ang.</i>	Total <i>angulata</i> inside	Total <i>angulata</i> outside
1-10	292	985	207	522	0	98	157	1
11-20	49	739	46	478	0	38	123	3
21-30	24	594	24	378	5	23	94	20
31-40	14	506	13	240	0	12	96	51
41-50	17	765	17	418	4	17	180	83
51-60	11	602	11	298	8	11	145	45
61-70	12	791	12	427	12	11	113	50
71-80	3	225	3	120	5	3	48	18
81-90	3	259	3	148	5	3	50	11
91-100	3	285	3	138	0	3	77	70
>100	7	897	7	456	8	6	190	133
	435	6648	346	3623	47	225	1273	485

Table IV

The distribution of *O. cor* on the inside (hypobranchial) surfaces of the gills 1 to 8 in 169 gill chambers of 99 *S. serrata* with carapace widths of 70 to 90 mm

Gill Number	Chambers with 1 to 20 ootolasmids				Chambers with 21 to 98 ootolasmids				In + out totals
	Proximal	Medial	Distal	Totals	Proximal	Medial	Distal	Totals	
1	0	1	0	1	0	3	0	3	4
2	0	1	2	3	0	1	0	1	4
3	24	52	6	82	9	32	2	43	125
4	95	97	5	197	68	62	0	130	327
5	46	112	2	160	38	57	0	95	255
6	61	112	7	180	36	34	0	70	250
7	39	78	10	127	12	31	0	43	170
8	3	16	1	20	7	8	2	17	37
TOTALS	268	469	33	770	170	228	4	402	1172
ON RAKERS	1	0	0	1	0	0	0	0	1
									1173

measured by gill length or gill area. These findings, although more detailed, are consistent with what has been reported for *O. mülleri* on *Callinectes sapidus* (Walker, 1974; Jeffries and Voris, 1983; Gannon, 1990) and for *O. angulata* and *O. cor* on *Scylla serrata* (Bullock, 1964; Arudpragasam, 1967; Venkateswaran and Fernando, 1982; Jeffries *et al.*, 1982, 1992).

In this study, we found that the distributions of *O. angulata* and *O. cor* on the inside and outside surfaces of the gills are distinct. The distributions over the proximal, medial, and distal surfaces (inside and outside gill surfaces) of individual gills also vary from gill to gill. Although Bullock (1964), Arudpragasam (1967), and Venkateswaran and Fernando (1982) all presented some numerical data on distributions, they did not make comparisons, and their categories are not directly comparable to ours.

If adult barnacle distributions mirror cyprid settlement patterns, then our results suggest that the cyprids of *O. angulata* and *O. cor* distribute themselves differently. Bullock (1964) did not address this point, but he did present tabular data on the distribution of four variants of *O. cor* removed from an unspecified number of *S. serrata*. For each variant he gave the distribution of the barnacles over gills 2 through 8 and over each of four gill regions. Using his sketches, we pooled his data and assumed that his variant "a" was *O. angulata* and his variants "b," "c," and "d" were *O. cor* (Jeffries *et al.*, 1991). The distributions of these two species over gills 2 through 8 are significantly different ($\chi^2 = 141.6$, $df = 12$, $P < .001$), thus corroborating our findings.

Both *O. angulata* and *O. cor* are distributed on the gills of smaller crabs (<70 mm carapace width) in a pattern that is distinct from that over the gill surfaces of larger crabs. Our data also reveal different patterns of distribution under different densities. Both *O. angulata* and *O.*

cor are nearly always found on the inside gill surfaces when the density of all barnacles is less than 20 per chamber; this continues to hold for *O. cor* as densities increase to 100 or more per chamber. At densities above 20 per chamber, however, *O. angulata* appears on both the inside and outside gill surfaces.

The above conclusions are not independent, because they do not separate crab size from barnacle density. Recall that smaller crabs (<70 mm) have fewer individual barnacles in their gill chambers (see Fig. 3 on page 190 in Jeffries *et al.*, 1992).

A comparison of distributions on crabs of similar sizes, but containing different densities of barnacles, leads to different conclusions. The distributions of *O. angulata* on the inside gill surfaces of crabs of high and low densities do not differ. Thus, density did not affect how the cyprid of this species settled on the inside of the gills. But even among similar sized crabs, when barnacle densities were less than 20 per chamber, there were no *O. angulata* on the outside surface of the gills. Thus, density does seem to be a crucial factor in determining when *O. angulata* selects the outside surface of gills.

The distributions of *O. cor* on the inside gill surfaces of crabs of high and low densities do not differ over gills 1 through 8, but do differ over the proximal, medial, and distal portions. Thus, density does appear to have some effect on how the cyprids of *O. cor* are distributed on the inside surfaces of gills.

Determination of settlement sites

Adults of *O. angulata* and *O. cor* are permanently fixed to the substrate (gill lamellae) at the sites where their cyprids settled. Thus it is the cyprid larva that makes the key decision about where the adult barnacle will live.

Having established that the congeneric species *O. angulata* and *O. cor* live together in the gill chambers of the same host, *S. serrata*, the intriguing question is what factors direct the cyprids to select different settlement sites within the gill chambers. Site selection by *O. mülleri* cyprids on *Callinectes sapidus* (Jeffries and Voris, 1983) and the otolasmids on *Scylla* under study here is not random. Nor is site selection by cyprids governed by available space alone, whether the measurement is made by gill length or gill area. The high degree of similarity among the gills argues against the idea that substrate is an important factor for site selection within the gill chamber.

Several lines of reasoning support the hypothesis that current flow through the gill chamber (see Wolvekamp and Waterman, 1960; McMahon and Wilkens, 1983) is the single most important factor influencing site selection by otolasmid cyprids. First, the direction, path, and intensity of current flow govern the distribution of both food and oxygen within the gill chamber. Flow through the chamber also influences the disposal of respiratory and metabolic waste products and, by affecting sedimentation rates, influences fouling.

Water enters the crab hypobranchial chamber through openings at the bases of the thoracic appendages, and this occurs as a result of negative pressure created in the branchial chamber by the pumping action of the scaphognathites (Arudpragasam and Naylor, 1964a, b; Hughes *et al.*, 1969; McDonald, 1977; Taylor, 1982). Thus we assume that otolasmid cyprids entering *S. serrata* first encounter the inner sides and the proximal regions of the gills. This is likely the case as the cyprids converge on intermolt crabs. But at the molt of host mangrove crabs, when the major infestation by otolasmid cyprids takes place (Jeffries *et al.*, 1989), the scaphognathites are inactive for a time. With complete cessation of pumping, pressure in the branchial spaces immediately falls to zero (Hughes *et al.*, 1969), so factors other than current may be governing cyprid behavior during this period of quiescence. As the crab exoskeleton splits on the outer surface of each gill, proximal to distal along the afferent branchial blood vessel, the otolasmid cyprids would have access to the newly exposed gill.

Among symbiotic otolasmid barnacles, cyprid orientation is correlated with the direction of current on the gill surface of lobsters (Dinamani, 1964) and on sea snakes (Jeffries and Voris, 1979).

The orientation of the barnacle capitulum on the gills of lobsters has been studied by Dinamani (1964), and on the gills of *Scylla* by Bullock (1964). Although neither of these studies focused on cyprids or incorporated current flow measurements, both reported that the anterior-posterior orientation of the capitulum tends to parallel the major flow patterns in the chambers (Wolvekamp and Waterman, 1960; McMahon and Wilkens, 1983).

Our study suggests that, although current is likely an important factor influencing settlement patterns, it may not be the only factor. *O. angulata* and *O. cor* cyprids distribute themselves differently, and *O. angulata* distributes itself differently at low and high densities. Both of these behaviors might be explained by current flow, but other explanations, including historical and biotic factors, deserve consideration and testing. For example, *O. angulata* and *O. cor* may have different distributions because one species is a generalist, "averaging" optimal settlement sites over many host species, whereas the other is a specialist and is optimizing its distribution for a single host species, *Scylla serrata*. *O. angulata* may be the generalist with 17 known host species, whereas *O. cor*, known from 6 host species (Jeffries *et al.*, 1982), may be the more specialized of the two.

Although the density of adult barnacles may influence current flow within the gill chamber, the density of cyprids within the chamber just after molt would have negligible effect on current. Thus, *O. angulata* cyprids may assess overall cyprid densities (encounters) on the post-molt crab and distribute on the inside versus the outside accordingly.

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