

AN ABSTRACT OF THE THESIS OF

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Title: THE BEHAVIOR OF THE PEA CRAB FABIA SUBQUADRATA  
IN RELATION TO ITS MUSSEL HOST, MYTILUS  
CALIFORNIANUS

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Abstract approved: \_\_\_\_\_

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The pea crab Fabia subquadrata is frequently found as a symbiont of mussels, living within the mantle cavity. This study examined the nature of this symbiotic relationship by recording the pattern of distribution of individuals in a mussel bed, testing responsiveness to host secretions, and observing the feeding mechanics and behavior of Fabia.

Individual pea crabs were unevenly distributed in an intertidal bed of Mytilus californianus at Yaquina Head, near Newport, Oregon. The greatest degree of infestation (25%) was in the largest mussels which were subjected to the most nearly continuous water cover. This pattern of distribution was attributed to a combination of the feeding behavior of the crab and the effects of tidal level.

The responsiveness of Fabia to chemical secretions of the mussels was tested by presenting liberated crabs with a choice

between sea water conditioned by live mussels and water drawn directly from Yaquina Bay. Tests were conducted to determine the role of sex and maturation by dividing the pea crabs into three groups: immature females, adult females, and adult males. The effects of light, darkness, and deprivation of its habitat (the host) were also tested. Under these various test conditions, Fabia showed no measurable response to any host factor from Mytilus.

When the crab was inside the mussel it faced the posterior and fed by intercepting the major mucus strand in the food groove of a ctenida. This behavior took full advantage of the feeding tracts of the mussel. When outside the host in undisturbed aquaria, crabs fed on feces and mucus ejected by mussels. This feeding behavior may play a role in the selection and invasion of a host. Quantitative measurements indicated that the feeding on Mytilus by adult female crabs had no significant effects on five parameters used to determine the condition of infested mussels.

The life span of adult female crabs was estimated to be more than two years and less than eight years. The adult male's life span was two years at best with most surviving only a year. Female crabs were capable of producing live zoea from stored sperm for at least two years and possibly more.

The Behavior of the Pea Crab Fabia subquadrata in  
Relation to Its Mussel Host, Mytilus californianus

by

Joseph Stanley Lidrich

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THE BEHAVIOR OF THE PEA CRAB FABIA SUBQUADRATA  
IN RELATION TO ITS MUSSEL HOST,  
MYTILUS CALIFORNIANUS

INTRODUCTION

Two approaches are frequently used to understand the significance of an animal's behavior. One is to study the advantages gained by an animal through its behavior in completing its life cycle, essentially stressing an individual species and its ecology. The other is through the comparative study of several species or groups of animals in an attempt to explain the origin and evolution of their behavior patterns. Von Frish's (1927) study of the life cycle of the honey bee is probably the most renowned classic of the former type. Von Frish brought his behavioral studies into perspective by constant reference to the problems of survival faced by the honey bee. If he had not done this, his results would not have achieved the acclaim they have today. Only by careful study of the ecology and physiology of the honey bee was he able to conceive and design his experiments. Unfortunately, few attempt such depth and breadth of study, especially among invertebrates other than the insects. Many of the decopod crustacea would be fruitful subjects for study in this respect.

Rathbun (1918) considered the family Pinnotheridae, commonly known as pea crabs, exceptionally well suited for productive study. He found them particularly interesting because in many cases male

crabs had not been described and the females were obviously modified for a symbiotic existence. These traits are atypical for decapod crustaceans because most are free living. Fabia subquadrata is a pea crab that is common along the West Coast of the United States and is found in several different hosts living in the intertidal area of the protected outer rocky coast (Wells, 1928). Fabia was first described by Dana (1851), but it was not until 1940 that ecological studies were conducted with Fabia and other pea crabs (Wells, 1940). Irvine and Coffin (1960) reared Fabia from egg to the megalops stage noting behavioral changes associated with light. Pearce (1966a) studied the morphology of the post-megalops stages and collected some data on the general biology of the crabs. These studies paralleled earlier works on various species of pea crabs whose hosts were primarily of commercial value (Atkins, 1926, 1954, 1958; Christensen and McDermott, 1958; McDermott, 1962a; Orton, 1921, 1927; Stauber, 1942, 1945; Welsh, 1932; Williams and Needham, 1938). It was demonstrated that pea crabs as a group were essentially similar to one another in their habits and biology.

The life cycle of Fabia is representative of pea crabs in general. An adult Fabia is usually ovigerous in the months of May and June. The zoea hatch and make their way out of the host and are planktonic until moulting into the megalops stage. The zoea in the plankton are photopositive and the megalops photonegative. According to Pearce

(1966a), the sex ratio is approximately 1:1 in the planktonic stages. Copulation takes place precociously in the planktonic stages before the animals have found a permanent host. The megalops stage is of unknown duration but probably lasts several months, ending in a moult to a true crab stage which is found in a host.

The selection and invasion of a host by Fabia is of interest because nothing is known about it. This is vexing in that it is difficult to form concepts about the utility of an animal's behavior if its definitive host is unknown. The problem is analogous to attempting to determine the ecological significance of an animal's activity without being certain of its habitat. Wells (1928) has reported five different hosts for Fabia, including Mytilus. Unfortunately, no thorough study of the degree of infestation by Fabia in each of the hosts has been reported with the exception of the horse mussel Modiolus modiolus. Pearce (1966a) reported an incidence of infestation of over 80% in Modiolus and concluded Fabia was host specific. He considered the occurrence of Fabia in other hosts to be the result of aberrant behavior, and cited Ricketts and Calvin (1962) as reporting only a 3% infestation in Mytilus californianus. On the basis of chance observations in the laboratory I suspected a considerably higher infestation of Mytilus, at least in Oregon.

Host selection by invertebrate symbionts has been extensively studied by Davenport (1950, 1953a, 1953b, 1955; Davenport and

Hickok, 1951). Chemical products of the host's metabolism have been shown to play decisive roles in such selection and have been termed "host factors." Responsiveness to such host factors is known to occur among several species of pea crabs (Johnson, 1952; Davenport, Camougis, and Hickok, 1960; Sastry and Menzel, 1962). Thus, a host factor could potentially influence host selection by Fabia if such selection indeed exists. It is necessary to determine the degree of host specificity and the mode of host selection in order to determine the "life style" of Fabia. Life style is an inclusive term used to describe behavior patterns like those reported by Nicholson (1957). He referred to the feeding behavior of certain flies which "scramble" among themselves for food as contrasted to those which "contest" for exclusive use of food supplies. In this study life style refers to "opportunist" or "specialist." Crabs that are opportunists take advantage of events as they occur and specialists seek a particular event. Those crabs which are host specific seek a particular host and are specialists. Opportunists employ a variety of hosts for the same reasons specialists find one. A life style, of course, confers survival value. One such advantage could easily be exploitation of a food supply. Thus, feeding behavior of the crab is central to any consideration of the nature of its symbiotic relationship and life style.

Pearce (1966a) has described the feeding behavior of Fabia on

Modiolus and has classified Fabia as a parasite, agreeing with other studies on different species of pea crabs. However, the feeding behavior in Mytilus has never been described, nor have the quantitative effects of Fabia on any host been assessed. I believe a parasitic relationship can only be defined in quantitative terms if the concept of a parasite is to have heuristic value.

Such a definition of parasitism has been made by Burkholder (1952). It is based on the fact that a parasite negatively effects the condition of its host along measurable parameters such as body weight, rate of growth, or ability to withstand stress. The parasite is affected inversely by the host and the relationship can be stated qualitatively that the parasite benefited and the host suffered. Practical application of this approach is not wanting but sometimes differs with expectations based on observations. Muller (1965) demonstrated that a number of rodents infected with Spirometra mansonoides or S. ranarum had a significantly greater growth rate, attained a larger size, and appeared in all ways healthier specimens. This result was the general rule among rodents. Nonetheless, Spirometra has been traditionally classified, like all tape worms, as a parasite in the classical sense. Such a study has never been attempted with Fabia, and would aid greatly in understanding its symbiotic relationship with Mytilus.

It was the purpose of this study, therefore, to determine if

Fabia subquadrata responded to a host factor from Mytilus californianus. Concomitant to host factor analysis is the nature of the Mytilus/Fabia relationship and how Mytilus is affected by it.

These data along with observations of the feeding behavior of the crab would serve as a basis for establishing the life style of the crab. Such data are also necessary to evaluate the observed behavior of the crab in a proper context. In addition, it provides a basis for determining the symbiotic relationship in order to place it into one of the traditional categories used to describe symbiosis.

## PROCEDURE

### Collection, Inspection, and Maintenance of Mussels

The mussels which provided the pea crabs for laboratory tests were collected at Yaquina Head and Boiler Bay in Lincoln County, Oregon (respectively 5 and 15 miles north of Newport). Mussels were removed from the lower levels of the intertidal mussel beds on the most seaward rocks. Only mussels of 100 to 150 mm in length were collected. The animals were transported within an hour to the Marine Science Center in Newport. Animals to be stored for an extended time were inspected for the presence of pea crabs. Infected mussels were then placed in plastic and wooden cages covered with nylon mesh and stored in indoor tanks with continually running sea water from Yaquina Bay. Mussels for more immediate use were stored in small tanks of running water for no longer than two weeks.

Mussels to be examined for the presence of pea crabs were kept in moist burlap bags 24 hours after collection. They were then placed in a tank of sea water until they opened their valves. When the valves were sufficiently parted, a peg was placed between them. The gills were inspected with a probe for a pea crab, to observe the feeding behavior of the crab, or to introduce another crab into the mussel.

### Field Sampling

In late September and early October, 1968, the vertical distribution of pea crabs in a mussel bed was examined at Yaquina Head. The mussel bed selected for analysis was located on the largest and most exposed promontory (Butte Rock) and had the most accessible vertical surface, sloping approximately  $60^\circ$ . Four transects of the mussel bed were made, from the most seaward point toward shore at intervals of 15, 5, and 5 yards. At each point a straight vertical line was sprayed on the bed with orange paint. A twine line, graduated in one foot marks, was affixed on top of the painted line and all of the mussels intercepted by the twine line were collected, labeled by transect number and vertical interval, and taken to the Oregon State University Marine Science Center at Newport where they were examined for pea crabs and measured.

### Construction and Use of the Test Device

A device used for testing the response of the crabs to water conditioned by mussels was a variation of the ordinary T-maze commonly used by psychologists and ethologists. Davenport (1955) attempted to use a similar device to demonstrate a response to a host attractant in pea crabs, but was unsuccessful because the crabs could not locomote in his device. However, with modification in

construction, the same principle was successfully employed without losing the advantages of simplicity.

The apparatus was made from a 14 mm diameter glass tube by blowing a bulb in its center. An opening was then made in the center of the bulb (Figure 1). Transparent centimeter rules were attached along the bottom of the glass arms that extended from each side of the bulb. A 3 x 100 cm length of nylon mesh was passed through the length of the tube and the free ends of the mesh were sewn together.

The purpose of the bulb was to allow the water from the side arms to mix. It also gave a newly introduced animal a small area in which to become accustomed to the change and an opportunity to perceive its new environment. The opening in the bulb was for the introduction of the animal. The nylon mesh provided a substrate which enabled the crab to locomote. Also, at the end of an experiment the animal could be removed from the test device by sliding the mesh to one end of the tube.

In using the device, normal sea water and conditioned sea water were introduced separately into each of the side arms of the test device from reservoirs. The pressure head was maintained by gravity and the rate of delivery was monitored. The rate of flow from each line was set approximately equal to the other by inserting a 5 cc syringe, with the needle but without the plunger, into each rubber tube leading into a side arm. The overflow from the bulb of the device was

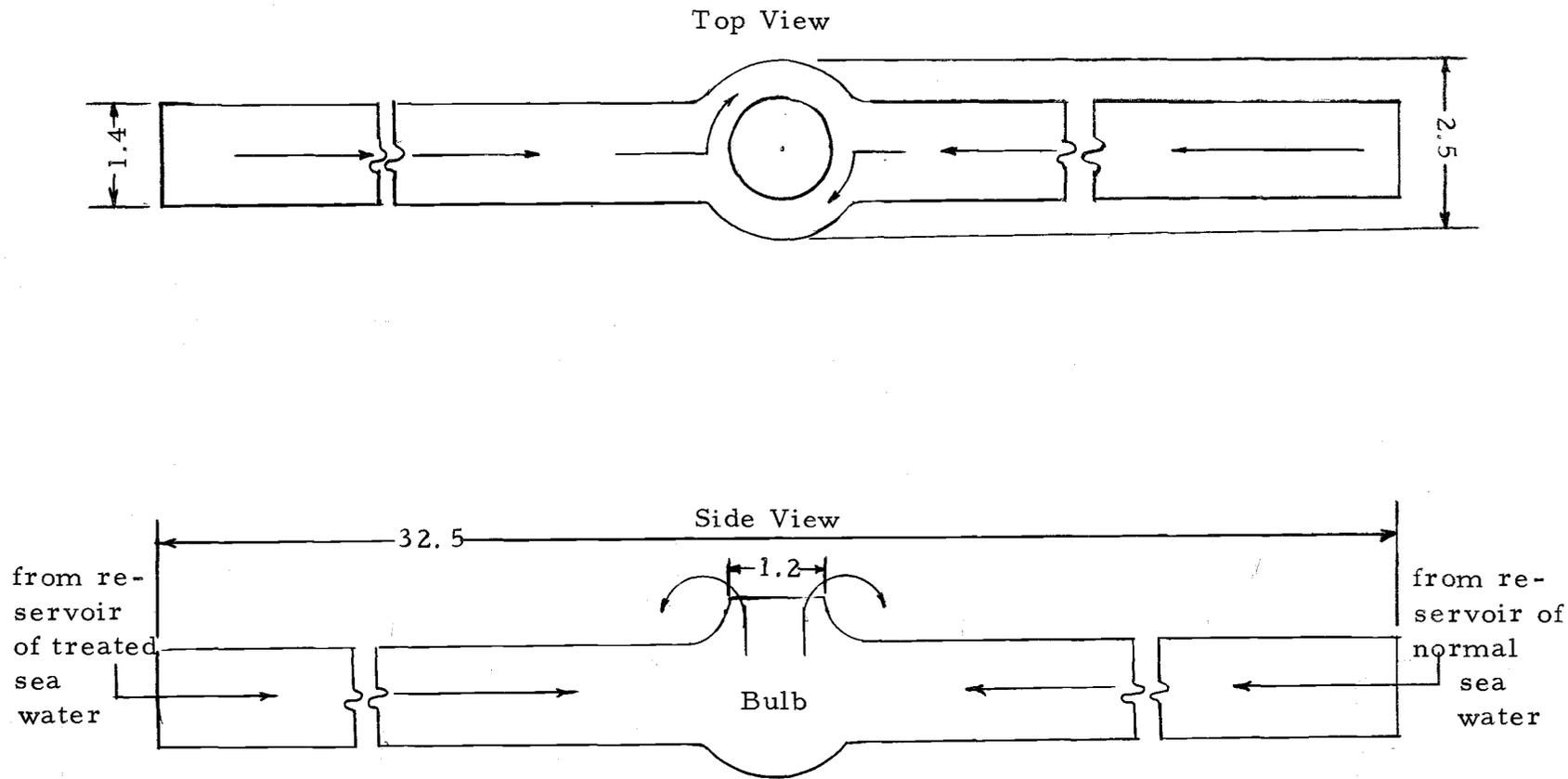


Figure 1. The device used for testing pea crab responses to host factors. Dimensions are in centimeters. Arrows show the direction and flow of water through the device when in operation. See text for further information.

collected in a graduate cylinder to determine the volume of flow. The total rate of flow from both lines was approximately 6 ml/min.

The test device was held in position by the use of a clamp and a support stand. Normal and conditioned sea water were introduced simultaneously and when water overflowed from the opening in the bulb the device was ready for use. Trial runs with suspended particulate matter showed that ordinary and treated sea water mixed well in the bulb of the device. A crab was introduced into the device through the hole in the bulb. After the animal regained a normal upright position inside the bulb the experiment was started. The distance traveled in the device by a crab was measured at five minute intervals, and was recorded as positive if the animal moved toward treated sea water and negative if toward ordinary sea water. The results can be analyzed qualitatively or quantitatively. In this experiment only qualitative analysis made sense. The distances traveled by the crabs were evaluated as choices for normal sea water, conditioned sea water or a nil choice. Such choices have a probability of occurrence which can be calculated.

### Statistical Methods

To determine if the pattern of responses of pea crabs in the test device was random, a modification in the use of the binomial theorem was made because the data were in trinomial form. A binomial

experiment is based on there being two kinds of choices, in this case, conditioned sea water or normal sea water. In this experiment there are actually three kinds of choices: conditioned sea water, normal sea water, and a nil choice. However, we can take advantage of the fact that the probability of a binomial pattern occurring is the sum of the probability for the number of observed choices for conditioned sea water and the probability of the number of the observed choices for normal sea water. Likewise, with a trinomial distribution the probability of the observed pattern occurring is the sum of the probability of the observed number of choices for conditioned sea water, plus the probability of the observed number of choices for normal sea water, and the probability of the number of nil choices occurring.

If responses of pea crabs were random, the theoretical probability of any one of the three possible kinds of choices occurring would be 0.333. This can be made to fit into a binomial distribution by setting the theoretical probability of a choice  $p$ , whose probability is wanted, as 0.333, and combining the theoretical probabilities of the two remaining kinds of choices into one probability  $q$ , which is 0.666. The probability of any of the three kinds of choices occurring can now be calculated by use of the binomial theorem, and the sum of these three probabilities would be the probability of the observed pattern of choices being random.

The equation used in determining the probability of the observed

pattern of choices in an experiment was:

$$p(x)_1 + p(x)_2 + p(x)_3 = p(x)_4$$

where  $p(x)_4$  is the probability of the observed pattern of the three possible kinds of choices in an experiment.

$$p(x)_1 = C_{x_1}^n (p)^{x_1} (q)^{n-x_1}$$

$$p(x)_2 = C_{x_2}^n (p)^{x_2} (q)^{n-x_2}$$

$$p(x)_3 = C_{x_3}^n (p)^{x_3} (q)^{n-x_3}$$

where

$p(x)_1$  = the probability of the observed number of choices for host factor,

$p(x)_2$  = the probability of choices for normal sea water, and

$p(x)_3$  = the probability of nil choices.

$$C_{x_1}^n = \frac{n!}{x_1! (n-x_1)!}$$

$$C_{x_2}^n = \frac{n!}{x_2! (n-x_2)!}$$

$$C_{x_3}^n = \frac{n!}{x_3! (n-x_3)!}$$

where

$n$  = the total number of choices in the experiment,

$x_1$  = the observed number of choices for host factors,

$x_2$  = the number of choices for normal sea water, and

$x_3$  = the number of nil choices.

### Effects of Pea Crabs on Mussels

To examine the effects of pea crabs on mussels, a series of mussels collected at Yaquina Head was segregated into two groups on the basis of the presence or absence of pea crabs. The fleshy parts of the mussel were removed from the shell, placed in pre-weighed pans, and dried at 38° C. The shells were similarly dried and any remaining flesh was scraped into the appropriate pans. The dry flesh weight was determined to the nearest milligram. The shells were scraped free of any marine growth and degenerate shell, and weighed to the nearest hundredth of a gram. The greatest width and length were determined.

The internal volume of the mantle cavity of the mussel was determined by displacement of water in a graduate cylinder. First the volume of both shells was determined, and then the entire volume of the animal was determined by fitting the valves together and filling the resulting space with a plastic glazing compound. The difference between these two values was considered to be the volume of the mantle cavity. In cases where the valves did not fit well, the glazing compound did not extend past the exterior of the shell.

## RESULTS

### Field Samples

The distribution of pea crabs in the mussel bed sampled at Yaquina Head was distinctly non-random, and was related to the size of mussels and their position in the mussel bed (Figure 2). The lower the mussel was in the bed the larger it tended to be, and the more likely it was to be infested by a pea crab. Unfortunately, the data do not indicate whether the apparent choice of pea crabs was a response to elevation, mussel size, or a combination of these factors. A knowledge of what stimulates a crab to enter a mussel may give insight into the problem.

### Responses to Metabolites of Mussels

Of all the possible ways for a crab to perceive a mussel, the most promising would seem to be through a chemical messenger or host factor. In testing the response of pea crabs to a host factor, I assumed that the orientation of crabs in a test device could be influenced by secretions and/or excretions produced by mussels. Since the response of the crabs to such a chemical stimulant may be dependent upon the maturation, deprivation of a host, or some other factor, tests were repeated with various combinations of factors.

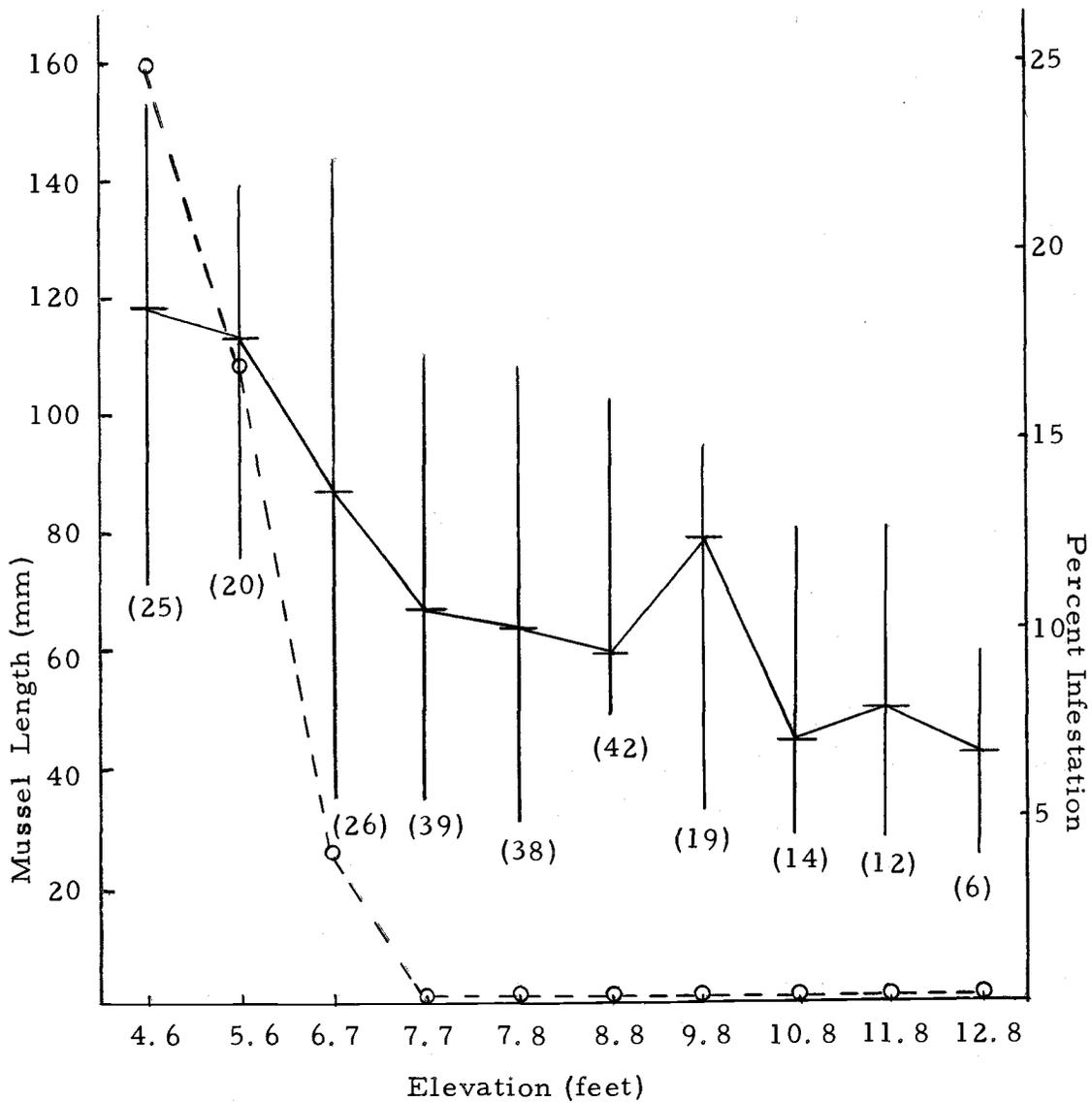


Figure 2. Distribution of pea crabs in a mussel bed on Butte Rock at Yaquina Head, Oregon. Horizontal bars represent mean length of mussels, and solid vertical lines the range. Circles represent the percent of infestation of mussels by pea crabs. Elevation is with reference to mean lower low tide which has the value of zero. Sample sizes are given in parentheses.

While these tests were not exhaustive, I felt that the factors potentially most influential were considered. Crabs were placed into three groups for testing: adult male, adult female and immature female.

Table 1 summarizes the responses of adult female pea crabs to unconditioned sea water. In ten trials there was one choice for the right side arm of the test device, five for the left, and four crabs made no selection. As expected, the distribution of choices is random ( $P = 0.46$ ). When a similar group of pea crabs was given a choice between normal sea water and a solution of liquified mussel (Table 2), they showed a clear preference for normal sea water ( $P < 0.10$ ). The mussel solution was chosen only once. These data demonstrate the ability of the test device to register the crab's response. The test solution was artificial and presumably noxious.

A third test presented adult female crabs with a choice between normal sea water and water conditioned by live mussels. The crabs showed no discrimination between these choices ( $P = 0.56$ , Table 3). Of ten possible choices three were for treated sea water, two preferred normal sea water, and five had no preference. Pea crabs were present in three out of five mussels used to treat the sea water and this may have influenced the results. When mussels without pea crabs were used to condition the sea water no significant change occurred in the distribution of choices ( $P = 0.67$ ). The results of the

Table 1. Responses of female pea crabs to normal (unconditioned) sea water in the dark.

Animal Number	Distance Travelled in cm Per 5 Minute Interval				Net Distance Travelled	Choice
	1st	2nd	3rd	4th		
1	-1.0	0.5	0.0	0.0	-0.5	-
	0.0	0.0	0.0	0.0	0.0	0
2	6.0	0.0	0.0	0.0	6.0	+
	-1.0	-1.3	-3.7	-2.0	-7.0	-
3	-1.0	0.0	0.0	0.0	-1.0	-
	-1.0	0.0	1.0	0.0	0.0	0
4	0.0	0.0	0.0	0.0	0.0	0
	-9.0	8.5	0.0	0.0	-0.5	-
5	0.0	0.0	0.0	0.0	0.0	0
	-1.0	0.0	0.0	0.0	-1.0	-

Positive numbers are the distances an animal moved to the right, negative values the distance travelled to the left, and zero indicates no movement. A choice is represented by the symbols +, -, 0, and is the sign of the integers representing the summation of the intervals.  $P = 0.46$ .

Table 2. Responses of female pea crabs to normal sea water and liquified mussel in the dark.

Animal Number	Distance Travelled in cm Per 5 Minute Interval				Net Distance Travelled	Choice
	Interval					
	1st	2nd	3rd	4th		
1	0.0	-5.0	-2.0	2.0	-5.0	-
	15.0	0.0	-14.0	-13.5	-12.5	-
2	-4.0	-0.5	0.0	0.0	-4.5	-
	-6.5	3.5	-7.5	-3.5	-14.0	-
3	-2.0	-1.0	0.0	0.5	-2.5	-
	-2.5	0.0	0.5	0.0	-2.0	-
4	-6.0	0.0	0.0	0.0	-6.0	-
	-2.0	-1.0	-3.0	0.0	-6.0	-
5	1.0	9.0	-1.0	0.5	9.5	+
	-2.0	0.0	1.0	-1.0	-2.0	-

Positive numbers are the distances an animal travelled toward treated sea water, negative numbers the distance toward normal sea water, and zero indicates no movement. The symbols +, -, 0 represent the choices of the animals.  $P < 0.1$

Table 3. The responses of female pea crabs in darkness, to normal sea water, and sea water treated with live mussels.

Animal Number	Distance Travelled in cm Per 5 Minute Interval				Net Distance Travelled	Choice
	Interval					
	1st	2nd	3rd	4th		
1	0.0	1.5	0.0	0.0	1.5	+
	0.0	0.0	-0.5	0.0	-0.5	-
2	0.0	0.0	-0.3	0.0	-0.3	-
	6.5	0.0	0.5	0.0	7.0	+
3	0.0	0.0	0.0	0.0	0.0	0
	0.0	0.0	-0.5	0.5	0.0	0
4	0.0	0.0	0.0	0.0	0.0	0
	0.0	0.0	0.0	0.0	0.0	0
5	0.0	0.0	0.0	0.0	0.0	0
	0.0	0.5	0.0	0.0	0.5	+

Symbols are the same as Table 2. The same crabs and mussels used for Table 3 were first used in the experiments described by Table 4.  $P = 0.56$ .

15 choices (Table 4) were seven choices for treated sea water, four for normal sea water, and four crabs made no choices.

All of the above tests were conducted in darkness. The data presented in Table 5 suggest that at least under some conditions crabs responded no differently in light ( $P = 0.62$ ). Of 20 possible choices, four were for sea water treated with live mussels, ten for normal sea water, and six made no choice.

Isolation of pea crabs from their hosts for 21 days without food did not influence the distribution of their choices ( $P = 0.63$ , Table 6). Of eight trials, two crabs chose treated sea water, four normal sea water, and two made no choice. Isolation from the host, however, did affect the activity of the crabs, as indicated by the greater distances travelled per interval in Table 6. This will be covered more extensively in a later section.

Thus, adult female pea crabs were not influenced by chemical secretion/excretions from living mussels in the environments in which the tests were conducted. Adult male pea crabs (Table 7) did not differ from the females tested in their reactions to treated sea water. Ten crabs tested in the dark with sea water treated with live mussels without pea crabs responded randomly ( $P = 0.58$ ). Five crabs chose treated sea water, two normal sea water, and three made no choice.

Since pea crabs apparently do not respond to a host factor they

Table 4. The responses of female pea crabs in darkness to sea water conditioned with mussels without pea crabs.

Animal Number	Distance Travelled in cm Per 5 Minute Interval				Net Distance Travelled	Choice
	1st	2nd	3rd	4th		
1	-11.5	-0.5	4.0	-4.0	-12.0	-
2	0.0	0.0	0.0	0.0	0.0	0
3	-0.5	0.0	0.0	0.0	-0.5	-
4	12.0	0.0	0.0	0.0	12.0	+
5	1.0	1.0	0.0	0.0	2.0	+
6	0.0	0.5	0.5	1.0	2.0	+
7	0.0	0.5	0.5	0.0	1.0	+
8	-11.0	1.0	0.5	0.5	-9.0	-
9	-0.5	-0.5	0.0	0.0	-1.0	-
10	-0.5	4.5	3.0	4.0	11.0	+
11	0.0	0.0	0.0	0.0	0.0	0
12	0.0	0.0	0.0	0.0	0.0	0
13	1.0	0.0	0.0	0.0	1.0	+
14	0.0	0.0	0.5	0.0	0.5	+
15	0.0	0.0	0.0	0.0	0.0	0

Symbols are the same as Table 2. The experiment was conducted in the dark with new crabs which were later used in the experiments described by Table 3.  $P = 0.67$ .

Table 5. The responses of female pea crabs to normal and treated sea water in light.

Animal Number	Distance Travelled in cm Per 5 Minute Interval				Net Distance Travelled	Choice
	1st	2nd	3rd	4th		
1	3.0	0.5	-1.3	0.0	2.2	+
	0.0	0.0	0.0	0.0	0.0	0
	1.5	0.0	0.0	0.0	1.5	+
	-2.0	-2.3	0.3	0.0	-4.0	-
2	-2.0	-13.0	0.0	0.0	-15.0	-
	-7.0	-8.0	0.0	0.0	-15.0	-
	15.0	-4.0	-11.0	-1.5	-1.5	-
	-2.3	0.0	-0.3	-12.0	-14.6	-
3	0.0	0.0	0.0	0.0	0.0	0
	-15.0	0.0	0.0	0.0	-15.0	-
	0.0	0.5	-1.0	0.0	-0.5	-
	0.0	0.0	0.0	0.0	0.0	0
4	2.0	0.0	0.0	0.0	2.0	+
	0.0	0.0	0.0	0.0	0.0	0
	0.5	-4.5	-3.0	0.0	-7.0	-
	0.0	0.0	0.0	0.0	0.0	0
5	1.7	-10.2	13.0	-3.3	1.2	+
	0.0	0.0	-2.0	0.0	-2.0	-
	-2.5	0.0	-3.0	-3.5	-9.0	-
	0.0	0.0	0.0	0.0	0.0	0

Symbols are as in Table 2.  $P = 0.62$ .

Table 6. Responses of female pea crabs to treated sea water 21 days after removal from their hosts.

Animal Number	Distance Travelled in cm Per 5 Minute Interval				Net Distance Travelled	Choice
	Interval					
	1st	2nd	3rd	4th		
1	0.0	0.0	0.0	0.0	0.0	0
	1.5	-1.5	0.0	0.0	0.0	0
2	-4.0	-4.0	-5.0	14.5	1.5	+
	13.0	-1.5	1.5	-5.0	8.0	+
3	-15.0	0.0	0.0	0.0	-15.0	-
	-11.5	-1.5	0.5	0.0	-12.5	-
4	-2.0	-11.0	2.0	-2.0	-13.0	-
	9.0	-13.5	-6.5	-1.0	-12.0	-

Symbols the same as Table 2 except crabs tested in the dark.

P = 0.63.

Table 7. The responses of male pea crabs to treated sea water in the dark.

Animal Number	Distance Travelled in cm Per 5 Minute Interval				Net Distance Travelled	Choice
	1st	2nd	3rd	4th		
1	0.0	0.5	0.5	1.0	2.0	+
	0.0	0.5	0.5	0.0	1.0	+
2	-11.0	1.0	0.5	0.5	-9.0	-
	-0.5	-0.5	0.0	0.0	-1.0	-
3	-0.5	4.5	3.0	4.0	11.0	+
	0.0	0.0	0.0	0.0	0.0	0
4	0.0	0.0	0.0	0.0	0.0	0
	1.0	0.0	0.0	0.0	1.0	+
5	0.0	0.0	0.5	0.0	0.5	+
	0.0	0.0	0.0	0.0	0.0	0

Symbols are the same as Table 2 except crabs tested in the dark.  
 $P = 0.58$ .

must use some other stimuli in responding to their mussel hosts. Observations of liberated crabs when isolated or in aquaria with mussels may be useful in identifying these stimuli. Such studies could also clarify the role maturation and gender play in the response of crabs to mussels.

### Observations and Related Experiments

Upon liberation from their mussel host, adult female crabs were initially quite active. Their movements seemed ineffective and they appeared panicked and confused. The crabs remained upright supported by their abdomens, but their walking legs flayed about laterally and not downward to the substrate. They did not locomote well. After about 20 minutes, they calmed considerably and locomoted on the bottom of the dish, but their movements were still awkward.

The immediate fate of such freshly removed pea crabs in nature is obvious. They could not survive long under the harsh conditions of rocky intertidal shelves. However, there was a drastic alteration of this behavior with time. After several days the crabs behaved like free living shore crabs which have been acclimated to the laboratory. So remarkable was the change in behavior that I suspected that there might be a corresponding change in the shape of the crabs.

Table 8 indicates that no such change occurred. The weight and

Table 8. Changes in the mean dimensions and rate of attaining an upright position as a function of time in five "liberated" adult female pea crabs. Numbers are means plus or minus standard errors.

Hours of Exposure	Weight (gm)	Width (mm)	Height (mm)	Reaction Time (sec)
0	0.95±0.19	12.4±0.96	8.5±0.57	2.7 ±1.5
48	0.88±0.19	13.0±0.6	8.6±0.84	1.35±1.0
144	0.94±0.17	12.8±1.0	8.4±0.55	1.25±0.1

shape of adult female pea crabs were not significantly altered after being "freed" from their host ( $P > 0.10$ ). However, their ability to right themselves from an inverted position improved significantly with time ( $P < 0.05$ ). For this shortening of "reaction time" to be important in a natural situation it must be demonstrable in a far shorter period of time. Figure 3 provides evidence that crabs can alter their reaction time significantly with just 15 minutes of practice ( $P < 0.01$ ). None of these reaction times approach those of crabs, freed for 144 hours, which were not trained to a specific stimulus (Table 8). Unfortunately, these tests were made in a laboratory environment, and give little indication of what may occur in a more natural situation.

In an attempt to approach natural conditions, five adult female crabs were released in an aquarium (45 x 15 cm) containing ten uninfected mussels. The crabs were observed almost daily over a two

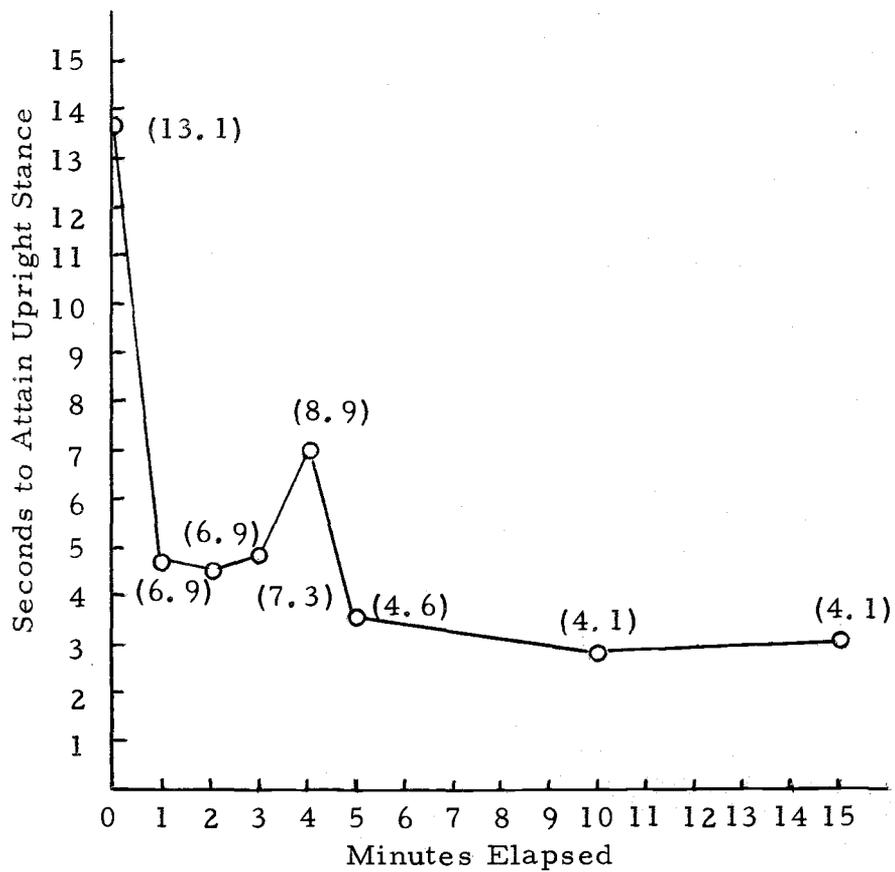


Figure 3. Effect of practice on the mean time required by adult female pea crabs to attain an upright position. Standard errors are given in parentheses.

month period. Initially, they generally sought out shaded areas. They would rest in places shaded by rocks, empty shells or mussels and feed upon detritus, mussel feces, and strands of mucus secreted by the mussels. These pea crabs never re-entered the mussels nor did they appear to respond to them any differently than to the inanimate objects present. The crabs were always aggressive toward other crabs they encountered. This aggression took place when crabs came in contact with one another while "exploring" their environment. If one of the crabs did not escape, they battled until they lost most of their appendages. If more than two centimeters separated the crabs there was usually no reaction. After two or three days the crabs had less aversion to light, had no encounters with other crabs, but continued to respond indifferently to the mussels.

Under similar circumstances the behavior of male and immature female pea crabs was different. These crabs readily re-entered mussels. In addition, male crabs would enter, leave, and sometimes re-enter mussels in time periods ranging from hours to weeks. Immature female crabs were never observed to leave a mussel once they had entered it. However, observations were limited to only two immature female crabs, and this same result occurred for a few males. I never observed crabs in the act of entering a mussel. The crabs did not appear to be aware of the presence of the mussels, but only to the small pile of feces and occasional mucus strands that

collected in front of the excurrent siphon.

Male and immature female crabs never displayed the initial disorientation or aggression shown by adult females upon being freed from a mussel. Both males and young females had good locomotion, and displayed an ability to swim which was quite good for a crab. Such enhanced ability of movement was not without hazards, at least for males. Of the five male crabs used in this test, three died. One of these deaths was observed in its entirety: a male crab, settling down after a short swim, inadvertently placed several walking legs between the valves on the ventral side of a mussel. As soon as the edge of the girdle of the mantle was touched the valves closed. The crab struggled until he tired. The valves relaxed when the crab ceased to move, but clamped shut at the first movement of the crab. The crab eventually died. Before the experiment was terminated, other males on occasion were found trapped with the same result.

Mussels were very sensitive to touch on their fleshy parts except around the siphons. The immediate response of a mussel when touched was to close its valves. However, if just the siphons were stimulated the animal tolerated mild contact with a sharp probe for some time without responding. The siphons would thus be the only good portal of entry or exit for a crab.

Once inside the mussel the crabs' movements and position were most effective in feeding. The feeding behavior of the crabs was

observed by watching them feed on half a mussel, and observing them between the parted valves held open by a wooden peg. Feeding patterns of males and females were basically identical, but that of the adult female is described here because it is the most stereotyped.

The female almost without exception fed in the posterior half of the mussel, positioned with its abdomen against the mussel's gills. It was customary for it to face the posterior less often than the ventral portion of the mussel. Crabs fed by breaking the mucus strand containing the entrapped food going to the labial palps of the mussel. This broken strand was then stuffed into the crab's mouth with its appendages. The dactyls of the walking legs were used to anchor the crabs within the mussel. At least the last pair of walking legs were, without exception, held above the head and fastened to the gill filaments, mantel, or both. The crab usually fastened itself in tissue from each half of the valves of the mussel. This would seem to be the most efficient means of feeding for the crab, taking full advantage of the feeding tracts and mucus flow which the mussel uses to feed itself. Males and juvenile females did not employ the last pair of walking legs in the manner of the adult female, but used them to hold to gill tissue under them. Otherwise, feeding was basically the same. It is evident that the employment of the last pair of walking legs by the female while feeding was a major cause of its ineffective locomotion when first removed from a mussel. After being liberated

from its host the crab attempted to grasp the mantle which had always been over its head. The rest of the walking legs were thrust laterally for the missing gill tissue. The pattern of feeding appeared to be almost identical for a number of individuals, as well as for the same species feeding on different hosts (Orton, 1921; Stauber, 1945; Pearce, 1966a).

Mussels appeared to tolerate the presence of pea crabs, but not without visible effect. The demibranch which the crab used became eroded and sometimes developed a notch where the crab had continually cut the major mucus strand. Occasional swelling developed in mantle tissue where the crab had placed the dactyls of the walking legs. The mussel did not appear able to expel the crab.

Table 9 presents data on the effect of pea crabs upon the condition of their mussel hosts. The length, width and weight of infested mussels were not significantly different when compared to mussels without pea crabs ( $P > 0.10$ ). The lack of significant difference between the dry weights of tissues from mussels with and without pea crabs is of interest when the observable physical changes in gill and mantle tissue of infested mussels are considered. It is possible that the lack of a measurable effect stems from the observation that, without exception, only one pea crab was found in a mussel.

The already mentioned aggressive behavior of the adult female crab favors the situation of only one pea crab to a host. Ten mussels

Table 9. The effects of the infestation of pea crabs on the weight and size of mussels.

	Weight (gm)				Size (mm)				Internal Volume (mm <sup>3</sup> )	
	Dry Flesh		Shell		Shell Width		Shell Length		With Crabs	Without Crabs
	With Crabs	Without Crabs	With Crabs	Without Crabs	With Crabs	Without Crabs	With Crabs	Without Crabs		
$\bar{X}$	6.288	6.682	91.80	85.51	45.44	45.66	127.19	126.35	101.04	88.2
S. E.	1.490	1.590	26.44	30.95	3.28	38.64	11.57	14.71	85.53	86.10
N	36	25	36	25	25	36	25	36	25	36
p	>0.10		>0.10		>0.10		>0.10		>0.10	

$\bar{X}$  = mean

S. E. = standard error

N = sample size

P = probability of difference determined by the t-test.

found containing an adult female were artificially infected with an additional female crab. At the end of a week several dead pea crabs were found in the aquaria. Upon opening the mussels they were all found to have at least one crab feeding as usual. If two crabs were present one was invariably badly damaged and found in any recess within the mussel that offered protection. About half the dominant survivors were the original inhabitants; the other half were the introduced crabs.

When males were used in the same experiment the results differed. One and sometimes both males would leave, usually in less than a day. There were not sufficient numbers of immature females to test these animals.

Adult female crabs were most abundant in population samples. Immature crabs, and to a lesser extent male crabs, were difficult to obtain (Table 10). Extrapolation of the data in Table 10 would give more knowledge of the length of the life cycle of the crabs and the origin of the disproportionate adult sex ratio. Following Figure 1, mussels were collected in a manner to insure a high proportion of infestation. In a 12 month period 450 mussels were collected, of which 119 (26.4%) contained pea crabs. Only during the months of May, June and July were immature or invasive female crabs found. These three individuals represented only 0.7% of the mussel population sampled. Given the present percentage of infestation (26.4%), and a rate of

Table 10. Tabulation of adult female, adult male, and immature female pea crabs from 450 mussels. Collected from July 20, 1967 to July 25, 1968.

	Adult Females	Immature*	Adult Males	Total
Number of crabs	104	3	12	119
Percent of crab population	88	2	10	100
Percent of infested mussels	23.0	0.7	2.7	26.4

\*Immature females were found only in the months of May, June and July.

infestation of 3.4%, or 15 per month, it would take approximately eight years without mortality to realize the present degree of infestation. This is assuming that invasive female crabs occur only three months out of a year. Of the same 450 mussels, only 12 (2.7%) contained adult male crabs, and of these 50% were recovered in the winter. Only about 10% of the adult population was composed of male crabs.

Such a low percentage of male crabs would make annual fertilization of females difficult unless a compensating mechanism was present. Storage of sperm by females over a period of years would be one way of compensating for the unbalanced sex ratio. Mussels containing ovigerous female crabs were placed in long term storage (March, 1968-March, 1969). Ten of the mussels were periodically observed until the crabs they contained produced zoea. I assumed

that the pea crabs in the remaining 30 mussels had also produced zoea. The mussels were then isolated from male crabs, and after a year, ten mussels were taken and the crabs they contained examined. All crabs were ovigerous, but only nine produced live zoea. Fertilization must have occurred from sperm stored from a mating which took place before capture.

## DISCUSSION

The distribution of Fabis subquadrata in a bed of Mytilus appears to be primarily a function of tidal level and the feeding behavior of the pea crabs (Figure 1). Pearce (1966a) found an uneven distribution for Fabia by dredging beds of Modiolus modiolus. His data showed the greatest infestation of adult female crabs (30%) occurred in mussels whose length fell between 61-70 mm. The length of mussels varied from less than 10 to 100 mm. There was a marked drop in the degree of infestation in mussels that deviated from the 61-70 mm size range. Modiolus, however, was not recorded at depths of less than 20 meters. This would make them accessible at all times if water cover was a necessary factor for crab invasion, as it was in the Pinnotheres/Mytilus edulis relationship (Houghton, 1963). Mytilus californianus in the present study was usually completely exposed only at minus tides. At high tide, however, the smaller mussels were covered only by surf. Only the submerged mussels would be accessible if water cover was necessary for invasion, and these individuals would tend to be larger due to a better food supply (Wright, 1917). Water cover, however, would not explain the distribution of Fabia in Modiolus beds, and probably not completely explain the distribution in Mytilus beds as well. Pearce (1966a) believes that the observed correlations between pea

crab distribution and mussel size may possibly be explained by an unsubstantiated host factor, crab food preference, or the differences in  $O_2$  consumption by the different sizes of mussels.

There have been several attempts to establish that a host factor influences the choice of a host by pea crabs. Sufficient work to establish the details of this communication between the crab and its host has not been done. Davenport (Davenport, Camougis, and Hickok, 1960) developed a device which enabled him to analyze the behavior of a pea crab under the influence of host factor. He concluded that the obligate commensal crab Pinnixa chaetopteros found its host by a chemokinesis. Johnson (1952) believed there was a pattern in the responses of various species of pea crabs to host factor. Pea crabs that responded to a host factor were host specific and had difficulty in maintaining a symbiotic relationship because of the physical environment. Heavy surf and shifting sand caused by bad weather were the major barriers to such a relationship. Johnson demonstrated that pea crabs that were protected from the environment by the host were not host specific and did not respond to a host factor. Where surf or shifting sand disrupted the symbiotic relationship easily, a host factor was demonstrated. Of the four different crab species Johnson tested, only Dissodactylus mellita, which lives on the surface of the sand dollar Mellita quinquesperforata, was host specific. It was influenced by a host factor which enabled the crab to

find its host again in periods of calm if knocked off during periods of heavy surf. The other species, which did not respond to a host factor, lived sheltered in the tubes of the worm Chaetopterus variopedatus. The findings of Sastry and Menzel (1962), however, are contradictory. They demonstrated a host factor from scallops and penshells which directed the crab Pinnotheres maculatus to them.

I have been unable to demonstrate any host factor from Mytilus that influenced Fabia and have concluded that it is absent. Pearce (1966a) was not able to demonstrate that Fabia responded to a host factor from the mussel Modiolus, but felt strongly that the crab must have selected its host on the basis of the host's metabolic rate. He believed the crabs were able to perceive the different rates of O<sub>2</sub> consumption of different sized mussels. However, I do not accept Pearce's hypothesis. The possibility exists, of course, that I overlooked a host factor for Fabia because of improper experimental conditions, or the crabs may have been receptive only during a critical period of their maturation which was missed in testing. Other workers, however, have demonstrated that pea crabs respond to a host factor under a wide variety of experimental conditions in simple testing devices, during all stages of maturation. This would be expected, since a host factor must not only lead the symbiont to the host but also play a role in maintaining the relationship (Johnson, 1952). If a complicated framework of environmental stimuli was

necessary for a crab to invade a host then the crab would be at a disadvantage once the relationship was broken, having to arrest re-invasion until the proper conditions occurred again. Crabs that were responsive to host factor only during a critical stage of maturation would have to find their hosts before they became refractive to the host factor, and once refractive could not be separated from their hosts.

There are not sufficient data to indicate precisely the role of food preference in effecting the distribution of pea crabs in a mussel bed. Coe and Fox (1947) have substantiated that Mytilus californianus is preferential in the food it consumes and that water cover favors the execution of this choice. No data exist that correlate the different kinds of food selected with the size or age of mussels. These would be most valuable data. However, it is abundantly clear that the longer a mussel has water cover, the better the supply of all types of food, the greater the selection of only dinoflagellates as food, and correspondingly the greater the rate of growth (Coe and Fox, 1947). Fabia may possess a mechanism for identifying mussels having a greater capacity to filter food or it may select larger mussels because feces and mucus strands have their greatest concentration around such mussels. Wave action would also tend to concentrate excretia from all mussels at the bottom of the mussel bed, and the high concentration may serve to attract the pea crabs. Also such concentrations would

be of longer duration and less disturbed by the surf. These concentrations of excreted material would not affect the results of tests for host factor because of the size of the excreta. Most of it accumulated at the bottom of the reservoir of conditioned sea water and did not enter the test device.

Fabia has the opportunity to be selective in the mussel it chooses for a host because of feeding habits. In laboratory aquaria crabs fed on feces and mucus strands deposited by mussels, and followed such "food trails" to their source. A food preference could possibly be displayed at this time. If the crab selected feces of a particular composition for consumption, as it exhausted this food supply, searching would lead it to the mussel concentrating this type of food. The crab would then be in the region of the greatest supply of this particular food. The mechanism of entry into the mussel is not known, but the search for more food may lead the crab up the ex-current siphon of the mussel, or the crab may respond to the water currents generated by the mussel (Thigmotaxis) and gain entrance. Once inside, the crab could then take advantage of the mussel's ability to concentrate food. However, my data do not exclusively support active food selection on the part of the crab. The concentration of any suitable food supply, and not the concentration of particular types of food may be the cause of the distribution of the crabs. Bivalves are discriminate in the food they finally digest, and reject

copious amounts of detritus and particulate matter which they initially filter from the environment. This material is often rejected in the form of pseudofeces which are nothing more than the concentration of everything filtered by the mussel minus that which it selects for digestion. Pseudofeces are well endowed with mucus. The process of forming pseudofeces may render undesirable material filtered by the mussel more favorable for consumption by pea crabs.

Crabs of the family Galatheididae are basically filter feeders and use modified appendages as filters (Orton, 1927; Nicol, 1932). It appears that pea crabs are similar in that they too are filter feeders but do not have an efficient filtration mechanism of their own. Since Mytilus has the efficient filtration mechanism characteristic of most bivalves, it may be exploited for this purpose by Fabia. For an association to take place, the host then need only meet the physical specifications of the crab.

Fabia is similar to Opisthopus transversus in this regard. Hopkins and Scanland (1964) believed that the host choice of Opisthopus depended upon the crab's maturation, which limited its ability to compete for available food. Opisthopus occupies a wide range of hosts and was found in different sites in different hosts because the crab sought any host that had a cavity of sufficient size to harbor it. In addition, only after invasion were physiological and morphological changes noted in the crab, and these depended on the

host selected. If Fabia used the same criteria as Opisthopus in seeking a host, it would account for its distribution in a mussel bed without involving a host factor or host specificity. Pearce (1966a) believes Fabia is host specific for Modiolus modiolus, but my samples in those areas of a mussel bed where the concentration of crabs was highest show 25% infestation of Mytilus. In addition, Wells (1928) lists three species of mollusks and two species of ascidians as hosts for Fabia, and Pearce (1966a) listed four mollusks as new hosts for Fabia.

The hypothesis that the physical properties of an animal at least partially determine its desirability as a host is further supported by the occurrence of two species of clams that could be differentiated by the presence or absence of pea crabs (Pearce, 1966b). Tresus capax served as the host for the pea crabs Pinnixia fabia and P. littoralis because of a minor variation in its internal structure. T. nuttalli does not have this internal variation and is not a host for pea crabs. This variation favored the feeding and possibly prevented the expulsion of the crab. Once the crab was inside the host, its manner of feeding was remarkably similar to other species of pea crabs in other hosts and very closely approximated the method described for Fabia in Mytilus (Orton, 1921; Stauber, 1945; McDermott, 1962; Pearce, 1966a, 1966b).

Because of its manner of feeding and the concomitant damage

caused to the mussel host, pea crabs are regarded as parasites in the classical sense. Data supporting this position are not wanting (Stauber, 1945; Sandoz and Hopkins, 1945; Christensen and McDermott, 1948; Haven, 1958; McDermott, 1962; Pearce, 1966a), but are equivocal. Stauber (1945) ascribed an unusually heavy mortality in oysters to a large increase in the pea crab Pinnotheres ostreum. No mention was given of how the correlation was made other than the description of damage caused by the feeding of the crab. It is possible that the two events were not related and the death of the oysters was by some other cause. There is no other reported case of pea crabs being lethal to their hosts.

It is commonly reported that pea crabs reduce the fleshy parts of oysters (Stauber, 1945; Sandoz and Hopkins, 1947; Haven, 1958). In these works a ratio was used to demonstrate this reduction in flesh. The mass of the flesh was divided by the volume of the oyster. The resulting number, however, was a misrepresentation because the volume of the oyster was increased by the presence of the pea crabs (Stauber, 1945). This may occur without affecting the mass of the flesh. The Fabia/Mytilus relationship was different in that the crab had no significant effect on any of the five parameters tested (Table 9). The general health or condition of the mussel was not measurably affected by the crab, rendering the exact nature of the symbiotic association more difficult to catalog. Perhaps this is the

"efficient parasite" of Swellengiebel (1939), which does its host no demonstrable harm while it lives in comfort.

Even the aggression of adult female pea crabs toward each other benefits both the host and Fabia. Once inside Mytilus the crab does not allow the presence of another crab. If this were not true, multiple infestations could possibly lead to eventual degeneration or death of the host. With the death of the host, the crabs living upon it would have to invade a new host (which observations have shown was not possible) or survive as free living crabs in the intertidal area (for which they are poorly adapted). If Mytilus is considered the territory of the crab, a comparison can be made with the aggressive behavior of other animals. For example, certain tropical fish inhabiting coral reefs maintain a territory for their exclusive use. This results in more efficient exploitation of limited food supplies in their habitat. The aggressive behavior of the conspecifics was necessary in maintaining such territory. If these fishes were placed in aquaria they battled to a lone survivor, or one dominant fish and several harried survivors (Lorenz, 1966). This approximates my observations of Fabia in laboratory aquaria. This aggressive behavior on the part of Fabia coupled with a precocious mating and storage of sperm, gives the crab an advantage by maintaining a high reproductive rate in relative protection with ample food supplies throughout its adult life.

While Mytilus was not demonstrably affected by the crab, Fabia

was affected by Mytilus. The marked sexual dimorphism may well be selected for because the males tend to leave mussels frequently, and females remain. There is a most cogent advantage for females to remain within their hosts. Since females are most vulnerable while ovigerous, those which had a tendency to remain within a mussel would produce more offspring and thus be selected for this trait. The poor locomotion of the adult female crab after removal from its host can be attributed to the adaptations necessary for the extended life within the mussel. Locomotion within Mytilus can be considered a learned response by the definition of Pantin (1964), and interestingly, this behavior was reversible with time if the crab was removed from the mussel. This ability to change patterns of locomotion to conform to new situations may enable Fabia to take advantage of more than one taxon of hosts. If patterns of locomotion were the result of permanently fixed responses, the number of available hosts would be reduced to those suitable for such fixed patterns. There is a strong suggestion that Fabia may use more than one host to complete its life cycle. The elasticity of responses gained by learning new patterns of locomotion would be of advantage in switching hosts.

In comparison, adult male crabs were found in small numbers presumably because of hazards of life outside the mussel. Adult males have no essential biological role in maintaining the species because the crabs mate precociously (Pearce, 1966a) and females

produce offspring for at least two years after mating and possibly longer. There appears to be no way that natural selection would influence the life of adult male crabs. Christensen and McDermott (1958) believed male Pinnotheres ostreum left their hosts to copulate with females. This was based on the report of Orton (1921) who found a male trapped between the valves of an oyster. Male Fabia were likewise observed in the laboratory where they left their hosts for no apparent reason. Orton supported the same conclusion with the work of Atkins (1926), who found sperm in the spermatheca of older adult females. Considering that females can store sperm longer than a year, this evidence carries little weight. Stauber (1945) believed mating between adults was impossible because of the difference in size between the sexes.

The mean life span of female Fabia subquadrata was calculated to be long (eight years). This was determined by extrapolation from the rate and degree of infestation. Such a procedure has its pitfalls (Weaver, 1965). It is possible that the number of invasive crabs was unusually low or some other unknown factor influenced the result. However, with a knowledge of the longevity of other crabs it seems reasonable to assume ten years represents the maximum longevity of Fabia and two years the minimum (Churchill, 1918). The minimum is based on the fact that Fabia has been maintained for over a year after producing offspring. Pearce (1966a) feels that Fabia survives

for at most two years but presents little data to justify the short life span for the female. His data appeared to be based on the life span of male crabs with the assumption that females had an equal life span.

A most interesting but unsubstantiated explanation for the long calculated life span of Fabia is suggested by the data of Pearce (1966a). Although the actual percentage is not stated by Pearce it appears that immature female pea crabs make up a large proportion of the total population of crabs infesting Modiolus modiolus. These females may be capable of an alternation of hosts, and later invade Mytilus when approaching adulthood. The explanation is worthy of further study considering the phenomena is common with certain helminth parasites. Hopkins and Scanland (1964) believed the choice of a host by the pea crab Opisthopus transversus depended upon maturation. Unfortunately, no mention was made if crabs changed hosts, but if it is true the low incidence of immature female crabs in Mytilus beds would be normal. It was probably the high proportion of immature female crabs that led Pearce to believe the relatively short life span of males applied to females also.

Therefore, it appears that Fabia departs from the typical concept of a decopod crab in maintaining itself and the species. Fabia employs a number of hosts to gain shelter and food. It may even alternate hosts while still immature in order to be more effective in exploiting its environment. Incomplete studies suggest that Fabia is not host specific and does not

maintain a symbiotic relationship using a host factor. The large number of hosts reported for Fabia suggests it takes advantage of situations providing food and shelter as they are encountered rather than specifically seeking out a particular host. These habits make Fabia well suited for being an "opportunist." The advantages in this are clear in that the crab is not limited to finding a particular species of host for survival.

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