

The Biology of the Mussel Crab, *Fabia subquadrata*, from the Waters of the San Juan Archipelago, Washington

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THE MUSSEL CRAB, *Fabia subquadrata*, described by Dana in 1851 from material collected in Puget Sound, is placed in the subfamily Pinnotherinae Milne-Edwards, one of the two subfamilies of the Pinnotheridae indigenous to the Americas.

Most species of pinnotherids live in association with a host organism. The relationships have been variously described as parasitism, commensalism, or mutualism. Although the mussel crab is usually found in association with the horse mussel, *Modiolus modiolus*, several other pelecypod hosts as well as a tunicate have been reported (Wells, 1928:289). The present research has revealed additional bivalve host species. It is frequently reported from both species of *Mytilus* in waters south of Puget Sound, although in the latter waters it does not appear to frequent these hosts.

The life cycle of *F. subquadrata* is complex and, as with many pinnotherids, includes several developmental forms subsequent to the typical decapod larval stages (i.e., the zoea and megalops) and before the definitive adult stage is reached. As in most marine decapods, the early pinnotherid zoea and megalops are planktonic. Upon moulting from the megalops into the first true crab stage the animal, it is thought, leaves the plankton and becomes associated with its host.

Postplanktonic developmental stages of a pinnotherid were first described by Atkins (1926:475) for *Pinnotheres pisum*, which is common to the coast of the British Isles. Later Stauber (1945:269) found that the developmental cycle of the North American east coast pinnotherid, *Pinnotheres ostreum*, was very much the same as that previously described for *P. pisum*. The re-

sults of the present study indicate that *F. subquadrata* passes through stages comparable to those reported for *P. pisum* by Atkins and *P. ostreum* by Stauber and by Christensen and McDermott (1958:150). There are, however, important differences in the developmental cycle of *P. subquadrata*.

The present known range of the mussel crab is from the coast of Alaska to southern California. Rathbun (1918:102) noted it in waters 250 m deep and Wells (1940:47) found it in mussels dredged at a depth of 220 m. Hart (personal communication) has found it in *M. modiolus* taken intertidally near Victoria, Vancouver Island, British Columbia.

While it is true that pinnotherid crabs have been known from ancient times, only recently have there been any comprehensive studies of any member of this family. Atkin's early observations (1926) on the moulting stages of *P. pisum* laid the groundwork for future studies. This was followed by Hart's investigations (1935) in which she reported success in hatching the eggs of *Pinnotheres taylora* and rearing them through the first true crab stage. Sandoz and Hopkins (1947:250) were able to rear *P. ostreum* to this same stage. These investigations extended the earlier work of Atkins, in which the hard and posthard stages subsequent to the first crab stage had been described. Atkins (1955) later raised two species of British pinnotherids, *P. pisum* and *P. pinnotheres*, through the megalops stage.

Most of the workers cited above were concerned largely with the early development of the crabs rather than with their ecology or association with the hosts. Wells' studies (1928, 1940) were among the first published papers concerned with the biology of American species of pinnotherids. Later Stauber (1945) investigated the postlarval development and habits of the oyster crab, *P. ostreum*. This work was followed by that of Christensen and McDermott (1958) which

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represents the most comprehensive study of this or any other species of the Pinnotheridae.

Except for purely taxonomic studies, these papers are the main reports concerning the pinnotherids despite Rathbun's (1918:10) early admonishment concerning the lack of knowledge of this family and the inherent rewards to be found in its study.

Other than Wells' data (1928, 1940) there have been no extensive reports concerning the biology of *F. subquadrata*. It is, therefore, one of the least studied species of the Pinnotheridae. Until Wells' work of 1928 the male of the species had not been recognized and was, in fact, described as a separate species in a different genus, *Pinnotheres concharum*.

The present paper is concerned with the biology of this neglected species. The principal study was conducted over a period of one and one-half years, from June, 1958 to January, 1960, but many observations made subsequent to the main investigation have been incorporated in this paper. Information on the developmental cycle, reproductive biology, relationship to the host organism, distribution and size in relation to water depth, and ecdysis is reported here.

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MATERIALS AND METHODS

All field work involved in this study was carried out at the Marine Laboratory of the Uni-

versity of Washington, Friday Harbor, San Juan Island, Washington. Observations were made on the contents of host mussels collected at least once but frequently twice per month throughout the period of study. In addition, materials were collected once a week during the summer of June, July, and August of 1958 and 1959. A total of 3,480 host mussels were examined during this period.

The mussels were collected by dredging in localities where they are known to occur. The dredging gear included either a standard rock dredge or beam trawl, depending upon the type of bottom from which the mussels were to be removed.

Several areas within the San Juan Archipelago, selected as dredging sites, were chosen as being representative of a variety of depths and bottom types. The deepest stations were located in President Channel northwest of Orcas Island ($48^{\circ}39'45''\text{N}$, $123^{\circ}1'\text{W}$), where the water is 195 m in depth. The shallowest station is off Point Lawrence, Orcas Island ($48^{\circ}39'30''\text{N}$, $122^{\circ}44'45''\text{W}$), where the water is 22–30 m in depth. Other stations were located near Point Caution, San Juan Island ($48^{\circ}34'\text{N}$, $123^{\circ}0'48''\text{W}$) in water 130 m in depth; off Mineral Point, San Juan Island ($48^{\circ}35'10''\text{N}$, $123^{\circ}3'35''\text{W}$) in waters 55 and 130 m deep; and in East Pea Vine Pass ($48^{\circ}35'30''\text{N}$, $122^{\circ}47'30''\text{W}$) in 48 m of water.

Upon being brought to the surface the mussels were immediately placed in live boxes with circulating sea water. The drains of these boxes are covered with screening of a gauge sufficient to insure that any swimming stage crabs would be retained should they leave their hosts. The mussels were then brought into the laboratory where they were opened and examined alive for the presence of crabs. In those mussels that were infested, any damage which may have occurred as a result of a crab's presence was noted. A dissecting microscope was always used in these examinations. Each mussel was measured, the larger ones (greater than 10 mm in length) with a vernier caliper, the smaller with a dial caliper. The larger mussels were measured to the nearest 0.5 mm, the smaller (less than 10 mm) to 0.1 mm. All crabs collected after July 15, 1958 were measured with an ocular microm-

eter to the nearest 0.01 mm. The greatest width of both carapace and abdomen were noted.

The crabs were then placed in standard household polyethylene ice cube trays. Each tray consists of 14 cubicles and 1 crab was held in each of these. A "vaporite" pen was used to number each cubicle with the crab's respective catalog number. In this manner several hundred crabs could be retained, facilitating observations on their behavior, ecdysis, and subsequent changes. The crabs were kept at temperatures approximating those of their natural environment, and either a flow of water from the sea water system or several daily changes were used to maintain adequate environmental conditions.

DEVELOPMENTAL STAGES IN *F. subquadrata*

As previously noted the life cycle of *F. subquadrata* is similar to that described for *P. pisum* (Atkins, 1926:475) and *P. ostreum* (Stauber, 1945:272; Christensen and McDermott, 1958:150). The typical planktonic zoeal and megalopal stages are followed by a series of true crab instars. The first of these is the invasive crab (Christensen and McDermott, 1958:150). Following the invasion of the host organism several instars occur which are collectively designated as *prehard stages*. These prehard crabs have a soft, membranous exoskeleton. With the exception of the initial invasive stage there is little setal ornamentation on the pereopods, which are cylindrical in shape.

While the prehard instars were thought to occur they were not described for any pinnotherid until the investigation of *P. ostreum* by Christensen and McDermott (1958:147). The total number of prehard instars is still not known for any species, although Hart (personal communication) has found up to five prehard instars in *F. subquadrata*. Since the terminal one of these is smaller than the smallest Stage I crabs of this species it is certain that at least seven prehard instars normally occur between the megalops and the Stage I crab. Because there is a considerable variation in the size of the terminal prehard instar it may be assumed that the total number of prehard instars also varies somewhat.

Subsequent to the series of prehard crab

stages a very anomalous instar appears. First described by Atkins (1926:478) for *P. pisum* as the Stage I crab, this instar is, in its morphology and behavior, entirely different from any of the stages preceding or following it. The exoskeleton is well calcified and very hard. It is, in many species, highly pigmented with definite patterns on the carapace. Above all it is highly modified for a temporary, freeswimming planktonic existence. The setal ornamentation found on the pereopods is extensive and, in addition, these appendages are broad and flattened in contrast to the cylindrical condition noted in the prehard instars. They thus serve as very effective swimming appendages. It has been reported for *P. pisum* (Atkins, 1926:475) and *P. ostreum* (Stauber, 1945:272; Christensen and McDermott, 1958:152) that at this stage of development the males leave their host to seek out females, copulating with them in their host.

To this point of development the male and female crabs have paralleled each other. The external morphology of both sexes is very similar throughout the prehard series and the Stage I instar. Only by the examination of the external genitalia can the two sexes be distinguished.

Following this stage a dichotomy occurs in the developmental cycle of the two sexes. The male is thought to remain in the hard stage, dying after breeding. The female, however, moults soon after copulation and the new posthard instar is soft, with a membranous exoskeleton comparable to that of the earlier prehard stages. The first posthard stage is referred to as the Stage II female. It is followed, both in *P. pisum* and *P. ostreum*, by Stages III, IV, and V. These stages are characterized by an overall increase in size, greater complexity of the pleopods, and an increase in the width of the abdomen relative to the carapace width. The Stage V crab is the terminal adult female. Although subsequent moults may occur, they result largely in an increase in size and there is little morphological change.

The Stage II crab is very similar in appearance to the terminal prehard instar. In *F. subquadrata* there is little increase in carapace or abdomen width during the terminal prehard–Stage I and Stage I–Stage II moults. This stage (II) is very difficult to identify unless the actual Stage I–

Stage II moult is observed. Stages following it can be readily distinguished, however, on the basis of the differential growth of the abdomen and increased complexity of the pleopods.

Since Atkins (1926:475) recognized only the Stage I–Stage V crabs and did not describe the prehard series, the nomenclature originally applied by her to the pinnotherid developmental instars is no longer adequate. However, as all the prehard stages have not been described for any pinnotherid crab it would be difficult to rename or renumber these forms at this time. For this reason her original terminology, with some modifications made by Christensen and McDermott (1958), has been retained in this investigation.

Invasive and Prehard Stages

The carapace of the invasive first crab stage of *F. subquadrata* is more square in outline than are the later prehard stages, which tend to be ovoid in shape. The eyestalks and pereopods of the first crab stage are also proportionately larger in relation to the rest of the body than are those of succeeding prehard instars. The pereopods of this instar are covered with swimming hairs or setae. The distributional pattern of these hairs is different, however, from that of the Stage I or hard crab, which also has similar setae. The pereopods of the first crab stage occur with the hairs distributed over much of the surface, giving the appendage a bottle-brush appearance. The hairs of this stage are also much more sparse and the entire structure does not appear to be as efficient an arrangement for swimming as that of the pereopods of the Stage I crab. Since the first stage crab apparently seeks out or in some manner becomes associated with a host immediately after moulting from the megalops, appendages well adapted to extended swimming activities are not necessary. This instar is able to swim, however, as is demonstrated by its activities in the laboratory.

As an individual crab progresses through the series of prehard moults the swimming hairs found on the pereopods, as well as the swimming abilities and activity, are lost until the Stage I or hard instar is attained. At this point the swimming hairs, as well as the general mor-

phology, become highly modified. The significance of this sudden transformation is discussed in a later portion of this paper.

The pleopods of the first crab stage and the first few prehard instars subsequent to it are merely small knobs protruding from the ventral surface of the abdomen. At this time there is no differentiation into endo- or exopodites. In the later prehard instars immediately preceding the Stage I or hard instar, the pleopods become very conspicuous and show clear differentiation into endo- and exopodite portions.

The smallest *F. subquadrata* found within a mussel measured 0.85 mm in carapace width. This crab is somewhat larger than the first crab stage of this species reared by Hart (personal communication), which had a carapace width of 0.76 mm. This difference in size may be accounted for by assuming that the formerly planktonic first crab stage undergoes a moult very soon after entering the host mussel. Consequently it would be difficult to find a true first stage crab in a host mussel.

However, comparison of the supposed first crab stages removed from mussels with the known first crab stage raised by Hart indicates that morphologically they are very similar or identical.

As earlier noted, Hart has reared *F. subquadrata* through five prehard instars, the largest of these still being somewhat smaller than the smallest Stage I instar yet observed (1.3 mm). For this reason it may be suspected that several instars intervene between the aforementioned forms. Christensen and McDermott (1958:150) found that the smallest *P. ostreum* collected measured 0.59 mm. They suggested that at least four moults occur before a crab would moult into the Stage I instar. The smallest Stage I instar in their collection also measures 1.3 mm. Since, however, the Stage I *F. subquadrata* is normally somewhat larger, it is suspected that at least seven moults occur between the invasive first crab stage and the average Stage I instar. When the method used by Hiatt (1948:165) to extrapolate the number of intermoult periods in *Pachygrapsus crassipes* was applied to *F. subquadrata* it was confirmed that approximately seven to eight moults occurred between the first crab stage and the average size Stage I instar.

The abdomen width of the smallest *F. subquadrata* removed from a mussel was 0.26 mm or approximately one-third the carapace width. This is a ratio that is approximated in all developmental instars through the Stage II posthard. With the exception of a few abnormal females it is true for the hard Stage I form.

Apparently it is rare for a male Stage I *F. subquadrata* to moult into a posthard, soft carapace crab. As will be discussed later, however, such males do occasionally occur and, in fact, may be more common than suspected. In order to obtain an approximation of the size of the terminal prehard instars, both males and females, each individual collected was measured. If, within a week, the crab moulted into a Stage I instar the previous dimensions were recorded as those of a terminal prehard.

The carapace width of 19 male prehard crabs varied from 3.0–5.3 mm, with a mean width of 4.3 mm. The abdomen width ranged from 1.1–2.1 mm and averaged 1.7 mm. It should be kept in mind, however, that males may occasionally moult into a soft instar from the hard Stage I form. Furthermore, as will be discussed later, this soft instar may subsequently revert to the hard form. Such a moulting sequence may thus invalidate these measurements.

Since the female regularly moults from a terminal prehard form into the Stage I instar any dimensions of these forms can be accepted as valid. Thirteen such moults were observed and the individuals involved ranged from 2.7–5.1 mm in carapace width prior to the moult. The average carapace width of these terminal prehard females was 4.1 mm.

The Stage I (Hard) Crabs

This is one of the stages originally described for *P. pisum* by Atkins (1926:478) and subsequently applied to the comparable instar of *P. ostreum* by Stauber (1945:272–276). The latter suggested that it was during this stage that *P. ostreum* invaded its oyster host.

The Stage I instar of *F. subquadrata* is in many ways morphologically similar to the Stage I form in both *P. pisum* and *P. ostreum*. In all three species the exoskeleton is well calcified and very hard. The pereopods are flattened

and well ornamented with functional swimming hairs; in *F. subquadrata* and *P. ostreum* only the second and third pereopods bear the long plumose swimming hairs, whereas they are present on all the walking legs of *P. pisum* (Christensen and McDermott, 1958:152). While Darbishire (1900) is quoted (Christensen and McDermott, 1958:152) as stating that the Stage I *P. pisum* uses the third and fourth pereopods for swimming, in contrast with *P. ostreum* which uses the second and third, recent observations by Christensen (personal communication) confirm that *P. pisum* uses primarily the second and third pereopods, as does *F. subquadrata*.

The carapace of the Stage I *F. subquadrata*, like that of *P. pisum*, is quite convex. The surface of this structure has a distinct pattern of bright orange markings (see Maerz and Paul, 1930, plate 10, E-12). This pattern is very constant and is found in almost all Stage I crabs. The background is a brilliant white. The orange pattern tends to fade to a dull brown (Maerz and Paul, plate 13, G-11) some weeks after being removed from the host mussel. Other stages of this species, both pre- and posthard, do not present any indication of this pigmentation. Macroscopically the exoskeleton in these latter forms appears colorless, although microscopic examination reveals isolated black and red chromatophores. Finally, as reported for the comparable stage of *P. ostreum* by Christensen and McDermott (1958:152), the Stage I *F. subquadrata* was noted to have two cylindrical rods connecting the dorsal and ventral sides of the body. These structures, along with the already discussed exoskeletal rigidity, may be modifications for a freeswimming existence.

Finally, in addition to these differences, the Stage I *F. subquadrata* varies from the other stages in having a heavy pubescence along the antero-lateral margins of the carapace. This pubescence appears somewhat heavier in the male, but such differences are hard to quantitate.

The average carapace width of 54 male Stage I crabs, selected at random from collections made on July 29, 1959, is 4.1 mm, with a range of from 1.3–6.8 mm. The mean of 29 female Stage I crabs collected on the same date is 3.5 mm, with a range of 1.5–6.2 mm. This does not

appear to be as large a size difference between sexes as was found for *P. ostreum* by Christensen and McDermott (1958). In addition to a sexual dimorphism in size the Stage I crabs have other sexual differences. The abdomen of the female is different in shape from that of the male; the lateral margins of the male's abdomen are concave, whereas those of the female are straight. It has also been noted that an occasional Stage I female will have an abdomen which is relatively wider than the 1:3 abdomen-carapace ratio which is characteristic of most of the Stage I crabs, both male and female. Finally, the abdomen of the female bears four well developed pairs of pleopods which contrast markedly with the two pairs of highly modified reproductive appendages borne by the male.

Both the male and female Stage I crabs have much stouter chelipeds than either the pre- or posthard growth forms. The merus and carpus are heavier and both fingers of the chela are swollen.

As observed by Stauber (1945:274) in *P. ostreum*, the Stage I *F. subquadrata* possesses a locking mechanism whereby the abdomen may be secured in the sternal groove. On the fifth thoracic segments of the sternal groove there are pairs of antero-ventrally directed knobs. These knobs hook under shelves found on the opposing ventral surfaces of the abdomen in such a manner as to become securely locked when any attempt is made to lift forcibly the abdomen of the living crab. Consequently, whereas it is easy to displace the abdomen of the pre- and posthard instars it is very difficult to free the abdomen from the sternal groove in the Stage I crabs.

The reproductive appendages of the male Stage I mussel crab are very similar to those described for *P. ostreum* by Stauber (1945:276), and quite dissimilar from the reproductive appendages of *P. pisum* as described by Atkins (1926:476). Atkins described the first copulatory appendage of *P. pisum* as blade-like and hairy. Recent examination of preserved *P. pisum* material by the present author verified a considerable difference. While the appendages of *P. pisum* are broad with almost parallel margins, except for the distal one-fourth of its length

where tapering occurs, they are, in *P. ostreum* and *F. subquadrata*, slender and lanceolate.

The Stage II Females

There is no apparent increase in body size of this instar over the Stage I female. The average carapace width of seven Stage II female crabs which were observed to moult from the Stage I instar is 3.4 mm, with a range of 2.9–3.9 mm. The average abdomen width is 1.1 mm, with a range of 0.9–1.3 mm.

The exoskeleton of the Stage II crabs is soft and membranous, as is that of the prehard instars. There are few swimming setae or hairs to be found on the pereopods, nor is there any pubescence along the anterolateral carapace margins.

The appendages are subcylindrical, not flattened as in the Stage I instar. The carapace is ovoid; the angles of the subpentagonal carapace of the Stage I form have become rounded. It is during this stage that the lateral carapace sulci (one of the definitive characters of the genus; Rathbun, 1918:101) become pronounced. They appear faintly in the prehard stages and are hardly present at all in the Stage I instar. Wells (1928:289) notes that these sulci are present in the newly moulted Stage I crab but are lost with subsequent hardening. As previously noted, the typical pigmentation of the Stage I instars is lost in the Stage II forms.

Stauber (1945:275) indicates large differences between the pleopods of Stages I, II, and III in *P. ostreum*. Christensen and McDermott (1958:152) suggest that Stauber's series of Stage II crabs may have included some prehard individuals. At any rate, no such marked differences could be found between the pleopods of terminal prehards and Stages I, II, and III of *F. subquadrata*.

There is little or no widening of the abdomen relative to the carapace in the Stage II crab. The ratio between the two is approximately the same as that of the Stage I forms. The sternal groove remains deep and is only as wide as the abdomen. The locking mechanism which was present and functional in the Stage I crabs no longer operates. As was surmised by Stauber (1945:278) for *P. ostreum*, this may be due to

the diminished rigidity of the exoskeleton in the posthard instars.

The Stage III Females

This is the first stage subsequent to the Stage I instar in which there is an increase in carapace width over that of the preceding instar, the Stage II form. The average width of 41 Stage III females was 5.4 mm, with a range of 4.0–5.9 mm. This instar is also the first in which the abdomen is more than one-third as wide as the carapace. The average abdomen width of the above Stage III crabs was 3.6 mm. The range was 3.2–4.2 mm.

Except for the relatively wider abdomen and larger overall body size the Stage III crab is, externally, morphologically similar to the Stage II form. The carapace is soft and membranous, the pereopods are slender and subcylindrical and devoid of swimming hairs. The sternal groove, however, is shallower and the abdomen no longer lies within the confines of this depression. Rather, it extends both laterally and anteriorly beyond the borders of the groove. The pleopods are almost identical in both structure and setation with those of the Stage II instar.

The Stage IV Females

The average carapace width of 33 Stage IV crabs is 5.8 mm. They range in width from 5.3–6.1 mm. The average abdomen width of these crabs is 5.4 mm with a range of from 4.8–5.9 mm. This stage is not only larger than the Stage III instars but in addition obvious external changes indicate that it is sexually more mature than those stages which precede it. Ovaries containing large numbers of developing eggs were observed in 29% of the Stage IV crabs. Also, while no ovigerous Stage IV crabs have been noted, it is significant that at this time the pleopods undergo the greatest change since their initial appearance. These modifications in the pleopods involve changes in size, proportion, and setal decoration. This is in preparation for the deposition and attachment of eggs. Finally, the abdomen is now nearly as wide as the carapace and is more concave than in previous instars.

The Stage V Females

This is the definitive adult female crab and the stage most commonly found throughout the year. As in previous posthard forms the exoskeleton is membranous and, while the body shape is similar to the Stage IV crabs, the relatively large growth of the abdomen causes this instar to become very awkward in its movements, especially when compared with the earlier stages. The abdomen is as wide or wider than the carapace and normally it protrudes laterally beyond the coxopodites and anteriorly to the mouth parts.

There is a great deal of variability in this stage, especially in the size and width of the abdomen relative to the carapace. From observations made on moulting Stage V crabs it has been found that this stage consists of not just one instar, as is usually true in the previous stages, but rather of a series of growth instars, in which the general morphology remains the same but with each succeeding instar become somewhat larger than the one preceding. This results in a wide range of size within this one, arbitrarily designated stage. The smallest Stage V crab observed measured only 4 mm in carapace width, whereas several Stage V crabs were found to measure 14 mm. The average carapace width of all observed Stage V crabs (831) was 9.5 mm, and the average abdomen width was 10.3 mm.

Christensen and McDermott (1958:162) discuss the effect of the presence of *P. ostreum* in slow-growing spat. They suggest that, while the growth of the crab is retarded in such host oysters, the development is not affected to a similar extent. The data gathered on the *F. subquadrata*-*M. modiolus* relationship would suggest that a similar situation prevails. The very small, below average in size, Stage V *F. subquadrata* are usually found in relatively smaller host mussels. In a more recent study Houghton (1963:254) reports a similar situation for *P. pisum*.

In addition to a positive correlation between crab and host size it has been determined that there is a negative correlation between the size of the Stage V crabs and the depth of the water from which they were removed. Crabs reaching

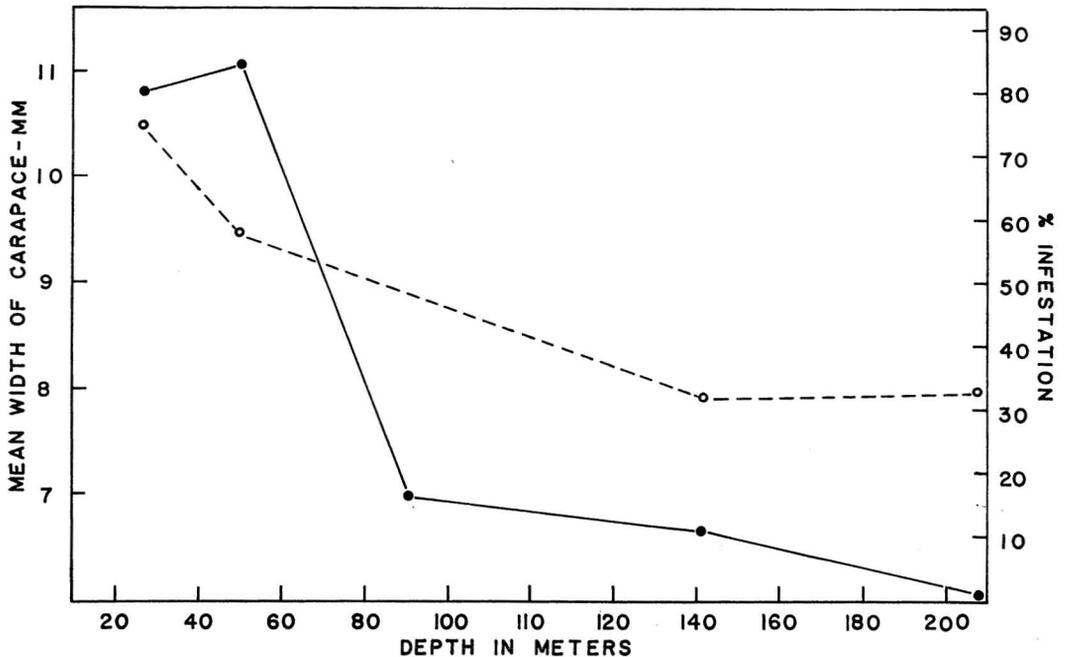


FIG. 1. Curves showing: *dash line*, correlation between mean width of Stage V crabs and depth of water from which their host mussels were collected; *solid line*, correlation between per cent of infestation of host mussels and depth of water from which they were removed.

maturity in relatively shallow waters were, larger on an average, than crabs which have developed and are collected from deeper waters (Fig. 1). This relationship was noted to exist throughout the entire one and one-half years that the crabs were studied. A further discussion of these correlations is deferred to another part of this paper.

The highly colored eggs contained in the gonads show clearly through the thin membranous exoskeleton. The color varies during development; initially appearing chrome yellow, they appear coffee brown immediately prior to their deposition (see Maerz and Paul, plate 9, K-2 and plate 15, A-11). Unless a crab has just become ovigerous, eggs are almost always present in some stage of development. It has been observed that within a week after egg deposition new eggs begin to form and become visible in the gonadal tissues.

While the gonads of Stage IV crabs occasionally contain developing eggs no Stage IV ovigers have been found. It is not until the adult

Stage V instar is reached that egg deposition occurs. The smallest oviger found measured 5 mm in carapace width; the largest was 13.4 mm. The largest crabs collected (i.e., those 14 mm in carapace width), were not ovigerous. However, their gonads did contain large numbers of well developed eggs and it appeared that these were about to be spawned.

The average carapace width of 187 ovigers collected from two depths off Mineral Point (55 and 130 m) was 8.5 mm. These crabs were removed from mussels collected during a period (November, 1959) when the ovigerous females constituted almost 60% of the total population. These ovigers were, on the average, 1 mm less in carapace width than the average of all the Stage V crabs collected during the period of study. This is undoubtedly due to the fact that many of these crabs were still in their first year and had not attained full adult size. In addition, part of this sample was taken, as noted, from relatively deeper waters where the average size of the Stage V is smaller.

Abnormal Instars

Although the sequence of developmental instars, as already described, represents the normal situation, investigations preceding this one have revealed occasional deviations from this general pattern by other pinnotherid species. Orton (1921:533) described a single male *P. pisum* which was morphologically similar to a soft, posthard female. Stauber (1945:280) discussed a second stage, posthard male *P. ostreum* which appeared externally to resemble the Stage II or III females. He notes that they were found in "appreciable" numbers and that their size distribution was somewhat greater than that of the typical Stage I males. He suggested that these atypical males might be "... the result of some sort of parasitism as Mercier and Poisson (1929) have reported for *P. pisum*." Stauber further suggested that these posthard male forms were copulatory partners for the larger posthard females. Christensen and McDermott (1958:152) suggest that the abnormal *P. ostreum* referred to by Stauber were actually prehard and that the greater size range of Stauber's second stage, posthard male over his Stage I series of male crabs was probably due to a sampling error. They do make the reservation that a hard Stage I male may, "now and then," moult to a soft-shelled form. Atkins (1958) presents evidence that, at least in *P. pisum*, the hard or Stage I males do quite frequently undergo a metamorphic moult into a soft posthard form. She has repeatedly observed the same crab change from one form to another with usually two or three soft forms intervening between hard instars. These soft posthard males are usually found during the summer months, June–August inclusive, in southwest England. It is during this period that the males moult and young crabs are found in mussels. Because of this she suggested that the soft posthard males occur during the periods of rapid growth.

A similar situation has been found with regard to *F. subquadrata*. During the summer of 1959 eight Stage I males were observed to moult into soft posthard forms. The latter are similar in body shape to the Stage I instars but are soft and membranous. The pereopods of these soft posthard males are, as those of posthard females,

subcylindrical and with few swimming hairs. Such moults are not accompanied by significant growth. In no case has a posthard male been observed to undergo further moulting, as was observed by Atkins in *P. pisum*.

These posthard male *F. subquadrata* were observed only during the summer months of July and August. This does not necessarily mean that they do not occur at other times, since they could easily have been mistaken for prehard forms had they not been observed moulting from the Stage I instar.

Apparent abnormalities are found not only in the males but also in the morphology of the Stage I females. In these cases Stage I females are noted whose abdomens are precociously widened. This increase in width over that of the normal individuals is quite large, the abdomen-carapace ratio approaching that found in the Stage III females. Other morphological aspects of these individuals tend to be normal, although these forms are invariably larger than the average female Stage I instar. Of 183 Stage I females examined, 5 were of this anomalous type.

Christensen and McDermott (1958:152) report similar anomalies in the Stage I females of *P. ostreum*. In two cases they found individuals considerably larger than the normal Stage I females. Both these crabs had abnormally formed pleopods. However, they do not mention any extraordinary increase in the relative abdomen width of these crabs. It was their opinion that they had been retarded in their development.

ECDYSIS IN *F. subquadrata*

Ecdysis is one of the most significant events in the life history of any crustacean. In a few crustaceans it has evolved to be primarily a mechanism allowing an increase in size to occur. This is true both in the freshwater decapods, the Potamonidae, crabs which hatch from the egg as a replica of the adult (Rathbun, 1918: 11), and in a species of the Oxyrhynca or spider crabs, *Nacioides serpulifera* (Rathbun, 1914: 653). In most marine crustaceans, however, moulting is accompanied not only by increased size but also by considerable morphological change. In no group is this more true than in the family Pinnotheridae. Certainly other

crustacean groups have representatives which undergo extensive changes through ecdysis, but few others, particularly among the brachyuran families, have fitted into the postlarval (post-planktonic) portion of their life cycle such complex morphological changes as accompany ecdysis in the pinnotherids.

While previous investigators have described ecdysis and accompanying phenomena in other brachyurans (Drach, 1939; Hiatt, 1948; Guyselman, 1953; and Knudsen, 1957), little information is available concerning these processes in the Pinnotheridae. For this reason careful notes were made of any moulting activities of *F. subquadrata* during the period of this study. Subsequent studies of ecdysis in *F. subquadrata* as well as other West Coast pinnotherids have been made (Pearce, 1962*b*). These studies involved the use of both light and electron microscopes in determining tissue changes which occur during ecdysis. These data will be included in a separate paper, the present work noting only the macroscopic aspects of ecdysis in *F. subquadrata*.

Two distinct phases of ecdysis can be recognized in all brachyurans. The first is preparatory and, to all outward appearances, is passive in nature although there can be no doubt that physiologically the animal is very active. The second, or active phase, involves the actual exuviation of the cast. This phase is characterized by a great deal of movement by the crab.

Most observations concerning the moulting of *F. subquadrata* were made on animals recently removed from a host mussel. A total of 134 moults were recorded. In 61 of these the dimensions were noted both before and after ecdysis.

Prehard and posthard crabs that are about to moult can be easily detected. One to two days prior to exuviation animals in this state become "creamy" and very opaque in appearance. Unlike other species which have been studied (Hiatt, 1948:155), they do remain quite active. All stages of *Fabia* have moulted under laboratory conditions—some after being held as long as six weeks. Christensen and McDermott (1958:150) found it difficult to obtain moulting *P. ostreum* under the laboratory conditions in which they worked. Unless crabs were "obviously ready to moult on arrival to the laboratory" no moulting occurred in the Petri dishes in which they were

held. These authors, therefore, had to resort to other techniques in order to obtain moulting specimens.

No external change in color or opacity heralds approaching exuviation in the hard Stage I crabs. Only the somewhat more flexible nature of the exoskeleton and the appearance of a crack along the postero-lateral margins of the carapace indicates that ecdysis is under way. The carapace of the Stage I form does not become as soft or decalcified as is indicated for some other brachyuran species (Hiatt, 1948:156); however, a recent paper by Knudsen (1957:134) states that in the California Xanthidae the exoskeleton does not become fragile prior to ecdysis. It may be that, at least in the case of *F. subquadrata*, since the following posthard instars are not heavily calcified the hardening salts remain in the exuviae of the Stage I instar rather than being retained in the crab's tissues to be subsequently redeposited in the new exoskeleton.

About one day after the onset of the opaque appearance in the pre- and posthard crabs a crack appears along the epimeral line, and at this time the active phase begins. The body now expands due to the uptake of water (Drach, 1939; Guyselman, 1953:129). This in effect lifts and frees the posterior portions of the carapace. In the pre- and posthard stages the old integument being shed has the consistency of heavy, wet cellophane. Further, because of its supple nature, it is never lifted to the extent of a 30° angle as was noted in *Pachygrapsus crasipes* by Hiatt (1948:157) or as is found in the Stage I mussel crabs. Rather, the old integument lies free upon the dorsal surface of the new integument of the carapace.

As is noted by Knudsen (1957:136) for the xanthid crabs, it is evident that muscular movements occur during this period since the new integument can be observed to be pulled inward, forming surface depressions.

Following the freeing of the posterior portions of the carapace the last pair of thoracic appendages, the fourth pereopods, and the abdomen are simultaneously freed from the old integument. This is a procedure intermediate between that observed by Knudsen (1957:136), who insists that the abdomen is freed first in

the xanthid crabs which he studied, and Hiatt (1948:157) who reports that in the grapsoid, *P. crassipes*, the legs are first removed, then the abdomen.

As soon as the posterior pair of appendages are free the animal then apparently uses them to exert pressure against the old integument in such a manner as to push the rest of the body free of the exuvia or cast. By this time the crab has moved far enough posteriorly within the cast to allow the more anterior pereopods and mouth parts to be freed. The former can then be pulled into the area vacated by the cephalothorax proper. This description is true of all the pre- and posthard crabs which were observed. In the case of the Stage I crab it is more difficult to determine the manner in which the anterior appendages are freed since the exoskeleton of this stage is completely opaque.

The active phase of exuviation varied between 15 and 45 minutes, with the average time being 20 minutes. The larger crabs (greater than 10 mm in carapace width) took, on an average, somewhat longer. There were exceptions, however. The longest period observed was taken by a Stage III female 5.7 mm in carapace width. There was little difference in the average time required by hard Stage I or pre- and posthard crabs.

In only 2 out of 61 closely observed moultings was *F. subquadrata* seen to moult during the daylight hours. This might seem surprising in view of the fact that mussel crabs are rarely in a photic situation and thus darkness would not be of protective advantage during the crucial period of moulting. However, since most of the freeliving brachyurans do moult at night (Broekhuysen, 1941; McKay, 1942; Hiatt, 1948; and Knudsen, 1957), it can be hypothesized that *F. subquadrata* retains an inherited mechanism involving the inhibition of moulting by light. As noted by these authors such a mechanism would have obvious adaptive advantages to freeliving forms, but it would be of little significance to a symbiotic crab living in a non-photic situation.

The length of time required for the maximum postexuvial expansion to occur was not determined in every observed moult. However, in the cases in which a crab was measured more than

once following ecdysis no measurable expansion was noted after the first postmoult measurement was made. The first postmoult measurement was routinely taken 30 minutes following the completion of exuviation. This implies that the crab expands to its postexuvial dimensions during and immediately following ecdysis, with little or no increase occurring over an extended period following ecdysis. This agrees favorably with the minimum time required for the final expansion of the freeliving xanthid crabs (Knudsen, 1957: 141). The latter required from 30 minutes to 2 hours.

The degree of postexuvial size increment in *F. subquadrata* varies not only with the stage at which the moult occurs but also to some extent between individuals of the same stage. Prehard crabs moulting into new prehard instars had an average increase of 16.5%, with the smaller crabs, i.e., the second or third postplanktonic instars, increasing as much as 20%. Similar increases have been found in the early instars of other brachyuran species (Olmstead and Baumberger, 1923; Broekhuysen, 1941; McKay, 1942; Hiatt, 1948). However, no *F. subquadrata* of any stage ever showed the 400% variation indicated by Hiatt (1948:163) for *P. crassipes*. Generally, during the moulting from the terminal prehard instar into the hard Stage I crab, and from the Stage I into the Stage II instar, there is little or no increase in size.

Only two Stage II females were observed undergoing ecdysis. The first of these crabs showed no increase in carapace width although the abdomen became 20% wider. The other observed Stage II crab increased 10% in carapace width and 40% in abdomen width during the moult into the Stage III form. It is during this moult that a significant change occurs for the first time in the carapace-abdomen width ratio. Needham (1950) has discussed the quantitative aspects of this allometric growth in *P. pisum*.

The moult from the Stage III to the Stage IV instar, in six observed cases, was accompanied by an average 12.2% increase in carapace width and a 65% increase in the width of the abdomen. During this moult occurs the greatest increase in abdomen width relative to the carapace width.

Only a single Stage IV crab was observed undergoing ecdysis. A 10% increase in carapace width occurred during this moult. The abdomen of the new instar (Stage V) increased 34% over that of the original Stage IV crab. Assuming this single observed moult to be typical of all Stage IV crabs, this is a considerable reduction in abdomen increase compared to the Stage III-IV moult. Following this moult (Stage IV-V) the abdomen is, for the first time, either as wide or wider than the carapace, and the definitive adult, Stage V female is attained.

Future ecdysis in the Stage V crabs is largely a matter of increase in size and not an alteration of morphological characters. The average increase in carapace size with each moult of the stage is 9% (in 33 individuals). The abdomen increases an average of 13.1%. It was noted that, as is the case when all stages are considered, the smaller Stage V crabs showed proportionately larger increases than did the larger crabs (greater than 10 mm) of this stage.

The pre- and posthard stages of *F. subquadrata* require only three or four days before an

apparently normal exoskeleton consistency is reached following ecdysis. However, more recent work (Pearce, 1962*b*) on related species indicates that, while external appearances suggest a "normal" intermoult condition, the actual deposition of new endocuticular lamellae continues for several weeks. The exoskeleton of the hard Stage I crabs requires somewhat longer for the integument to become completely hardened. Three weeks were required by one individual before the carapace was completely calcified and rigid. This could be due to the fact that the animal was kept in an artificial environment in which the normal parameters were not present. Hiatt (1948:163) conclusively demonstrated that changes concomitant with the moulting of *P. crassipes* are affected by prolonged laboratory conditions.

In no case was any self- or exuvial mutilation observed, such as was noted in *P. crassipes* by Hiatt (1948:158) and in the xanthid crabs by Knudsen (1957:140).

Moulting was most frequent during the summer months, particularly during early and

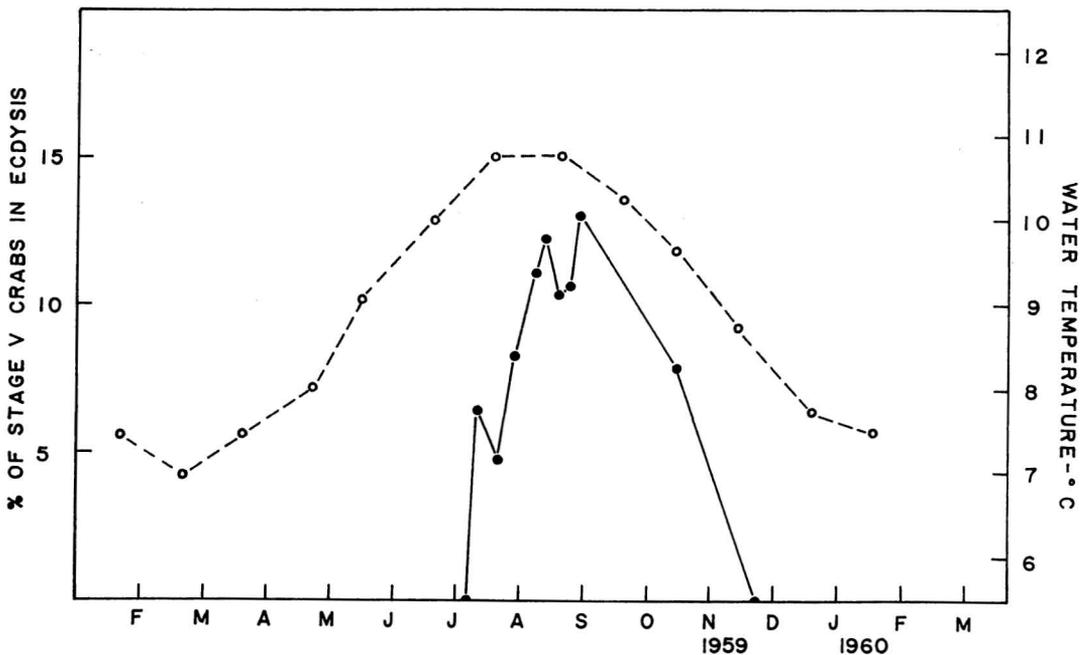


FIG. 2. Curves showing: *dash line*, surface water temperatures taken in the San Juan Archipelago during 1959 and early 1960; *solid line*, per cent of Stage V crabs in ecdysis during the period from February, 1959 to March, 1960.

middle August. During this period as much as 13% of the observed population was undergoing ecdysis. Just as a correlation was noted by Hiatt (1948:161) for *P. crassipes*, so was a correlation noted between monthly temperature means and the percentage of ecdysis for *F. subquadrata* (Fig. 2). The temperatures are surface water recordings made by the U. S. Coast and Geodetic Survey in 1958–59 for the waters of the San Juan Archipelago, and closely approximate the means recorded over a five-year period by Phifer and Thompson (1937). While these temperatures are taken at the surface, it is assumed that they would be valid at the depths from which the mussels were removed since Phifer and Thompson (1937:34) note that the waters of San Juan Channel are very homogeneous to a depth of 100 m.

It was noted that the percentage of Stage V females in ecdysis was greatest during August, regardless of the depth from which they were removed. Figure 2 represents only Stage V crabs and does not include those immature crabs observed undergoing developmental moults throughout the year.

While increased temperature may not in itself be the direct cause for the onset of ecdysis, it may be an indirect factor. Certainly the moulting sequence is correlated in a number of ways with reproduction, the success of which in turn depends upon factors favoring the survival of the zoea. Since it is known that phytoplankton standing crops vary with water temperatures and in turn are important for the development and survival of many zooplankton larval types, including zoea and megalops, so temperature may be correlated with the periodicity of ecdysis.

THE DEVELOPMENTAL CYCLE

Early investigators (Thompson, 1835) assumed that the male pinnotherid sought out his copulatory partner by moving from host to host during the reproductive period. Later Orton (1921:533) tended to substantiate these views by his discovery of individual male *P. pisum* caught between the valves of the host mussel, *Mytilus edulis*. The implication was that the males were trapped while seeking to gain entrance to the host of a female. In addition, Or-

ton found a Stage I female with its spermathecae filled with viable sperm. This latter discovery was repeated by Atkins (1926:478) and was indicative of a precocious copulation in *P. pisum*.

Examination of mid-water plankton trawls made by members of the Department of Oceanography of the University of Washington in the southern waters of Puget Sound during May, 1957 resulted in the finding of 56 Stage I *F. subquadrata* of both sexes. Examination of materials collected in a similar manner prior to and subsequent to this period revealed a paucity of these crabs, only 2 being found. Microscopic examination of the spermathecae of the females taken in the trawls, as well as those removed from host mussels, revealed that *F. subquadrata*, like *P. pisum* and *P. ostreum* (Christensen and McDermott, 1958), copulates precociously.

Since the sample taken from these plankton tows represents the only time that female and male *F. subquadrata* have been found together, it is probable that copulation in this species occurs during a period when both the male and female Stage I crabs leave their host bivalves and assume a temporary freeliving existence.² Of the total of 56 Stage I *F. subquadrata* taken in these tows, 29 were males and 27 females. Conversely, in only 3 out of 2,088 total observed infestations were double infestations of the host mussel ever found. In 2 of these cases 2 male Stage I crabs were found together, and in the remaining example a Stage I female was found together with an unsexable prehard crab.

If copulation occurs while the female is in the Stage I form, as seems likely from present evi-

² It has only recently come to my attention that Sakai (1939:604) has reported a similar swarming in the pinnotherid, *Tritodynamia borvatbi*, which is found in Japanese and Korean waters. He notes that both males and females swarm together in large numbers. The swarming or migrations occur in Japanese waters "... from the middle of autumn to the beginning of winter." In Tinkai Bay, Korea, however, Kamita (1935:36) reports it as occurring in June and July. The crabs are often found in such dense numbers that they are harvested and used for fertilizer. In addition, large schools of fish follow the moving crabs, obviously feeding upon them. No ecological significance was attached to the swarming, and Sakai does not distinguish at what stage of the life cycle the swarming occurs.

dence, and if copulation were consummated in the host mussel, it would be expected that occasional pairs of males and females would be found in the large numbers of mussels examined throughout the year. Such double infestations have not been found, however. Furthermore, the finding that Stage I males and females swarm together in open water gives evidence that the copulatory act takes place outside the host. This is contrary to what other investigators have found to be true in related pinnotherids (Thompson, 1835; Orton, 1921:533; and Christensen and McDermott, 1958:166).

More recent evidence, involving the attraction of swimming Stage I crabs to a "night light" used at the Friday Harbor Laboratories, indicates that the swarming behavior is probably restricted to late May and early July. Of eight crabs taken in this manner during the spring and summer of 1961 only one was obtained later than mid-June and none earlier than the 4th of May.

It is of interest that the average sizes of the swarming Stage I males and females, taken in the mid-water trawl and at the "night light," are approximately the same. The average carapace width of 32 males is 3.51 mm, while the same number of females averaged 3.58 mm.

Collection data show that swarming was not restricted to only one station or limited area. Rather, it was found to occur at several widely separated stations in the San Juan Archipelago and Puget Sound. Since the host mussel is widely distributed in these waters, it would be expected that the crab symbiont is found equally dispersed.

A current investigation of *Pinnotheres maculatus* as part of the benthic community in the Woods Hole area indicates that this species also engages in a copulatory swarming. In 1963 this swarming reached its peak during the last two weeks of October. A more detailed account of this and other aspects of the biology of *P. maculatus* will appear in a later paper.

When all the material collected from the San Juan Archipelago area in 1958-59 is considered, it is clear that the greatest number of ovigerous females appears during the winter months. Large numbers are initially found in early November and form a significant portion of the population

through the middle of February, with a peak at the last of January. As many as 75 (60%) of the total adult population of 126 Stage V females collected off Point Caution on January 28, 1959 were ovigerous. Collections made during the winter of 1959-60 indicate that the ovigers were more numerous earlier in the season during this particular year. A sample of 22 Stage V crabs collected off Mineral Point and examined on November 23, 1959 contained 19 ovigerous crabs (87%). Large percentages of ovigers were found at the other collecting sites during this period.

Since the swarming females copulate in late May, an interval of some 21 to 26 weeks would ensue before the start of egg deposition in November and December. During this period the precociously inseminated female must undergo the series of growth and metamorphic moults which have already been described. Because there is no overwintering of immatures as reported for *P. ostreum* by Christensen and McDermott (1958:158), the number of immatures, both male and female, present in the population is low during the winter months of November, December, and January.

The immature crabs are found in greatest numbers during the early- and mid-summer months. On July 21, 1959 they constituted 56% of a total sample of 119 crabs collected off Point Caution. They formed a comparable percentage of the population at the other stations during the period of June 15-August 1. The Stage I crabs were particularly prevalent in the samples taken during May. The collection taken at Mineral Point on May 4, 1959 included 37 Stage I instars. These 37 crabs constituted 31% of the total population. The remainder were mostly prehard stages which would moult into the Stage I form before the month was over. The early posthard forms (the Stage II and III instars) were more in evidence during June and early July, with the later posthard forms (the Stage IV and V instars) becoming prevalent in August and September.

From the discussion above and Figure 3 it is obvious that the ovigerous females occur predominantly during the months of November, December, and January. During February the eggs begin to hatch and the new larvae spend

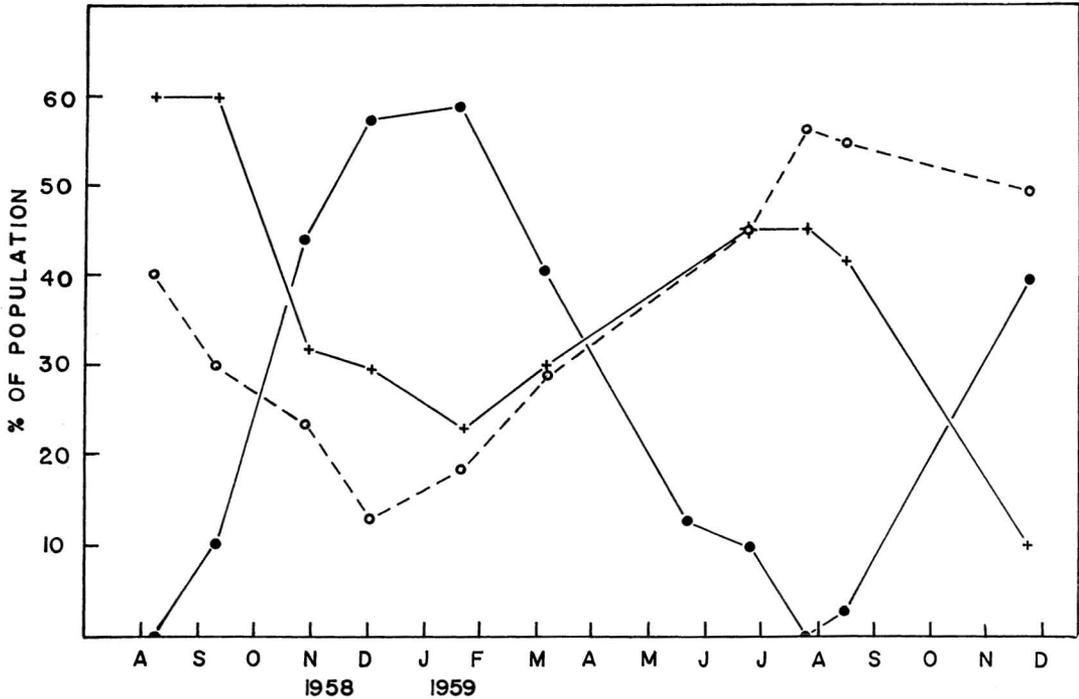


FIG. 3. Curves showing per cent of total crab population constituted by: *solid line broken by circles*, ovigerous Stage V females; *solid line broken by crosses*, nonovigerous Stage V females; *dash line broken by circles*, immature crabs of both sexes. Samples collected from San Juan Channel off Point Caution, San Juan Island, Washington between August 8, 1958 and November 23, 1959.

upwards of eight weeks in attaining the first true crab stage. Hart (personal correspondence) has recently reared *F. subquadrata*. She found that eggs laid on October 27, 1958 hatched on February 6, 1959 and moulted into the first true crab stage on April 6, 1959. As already discussed, it is assumed that the first crab stage enters an initial bivalve host, usually *Modiolus modiolus*, and completes a series of prehard moults which culminate in the hard, Stage I instar. This is true both of the male and of the female. It is suspected that in general the prehard series occupies the interval between early April and late May. At this time the Stage I crabs leave their hosts and engage in the swarming activities which culminate with copulation. Following these activities the Stage I female, and at least some males (since larger Stage I males occur in the collections throughout the remainder of the year), return to a bivalve host, where the female undergoes a series of at least four posthard

moults which terminate in the definitive adult, the Stage V crab.

The immature posthard and Stage V crabs retain the full spermathecae which result from the precocious copulation of the Stage I instar. Nonovigerous Stage V females are present in the greatest numbers during August, September, and October, and this is the period when the numbers of immature crabs are sharply decreasing. During late October and early November the ovigerous females become more numerous and once again, during mid-winter, they constitute the majority of the population.

There is a period of three months between the time the Stage V crabs are first found in increasing numbers and when the ovigerous females are noted to represent a significant portion of the population. Furthermore, since many Stage V crabs are found moulting during this period one may assume that at least one or two moults will occur in this period. This assump-

tion is supported by the fact that the earlier Stage V crabs (found in late summer) are always smaller on an average than are the ovigers taken later in the year at the same station and depth.

The only previous study concerning the complete postplanktonic life cycle of a pinnotherid is that made by Christensen and McDermott (1958). They found that: (1) the number of Stage I *P. ostreum* was at a minimum during the winter and spring months and that in June large numbers of Stage I crabs appear in the oyster hosts; (2) the Stage I crabs represented, during this period, up to 60% of the total population; (3) 45% of the Stage I crabs were males; (4) by the end of July only 5% of the crabs collected were males and by early September not a single male could be found.

In addition to the ultimate disappearance of the males from the *P. ostreum* population they noted that during a period in late June a significant number of double infestations began to appear. They suggested that these could only be due to new invasions by male Stage I crabs seeking copulatory partners within the host oyster. In view of this fact, and of the present observations that *F. subquadrata* engages in swarming and the male survives through the summer, it can only be assumed that *P. ostreum* and *F. subquadrata* have diverged widely in their reproductive habits.

It is believed that some female *F. subquadrata* live for more than one year and also reproduce more than once. Figure 3 shows that there are always residuals of the nondominant stages. For instance, in the summer when the immature instars (of all stages) predominate, there is always a percentage of Stage V crabs and occasionally an ovigerous female. Since these crabs were frequently much larger than average (often greater than 12 mm in carapace width) it is thought that they are remnants of the previous year's adult population and not merely precociously developed individuals of the present year. Christensen and McDermott (1958:159) present evidence that *P. ostreum* may live as long as three years. There can be no doubt, however, that some of the smaller, "residual," Stage V *F. subquadrata* are the result of spawnings occurring somewhat earlier in the year than the majority

It is possible that they are the offspring of second year females.

The immature crabs which are found later in the season and throughout the winter (Fig. 3), when the Stage V crabs are predominant, are almost certainly the result of the egg deposition subsequent to the period when the majority of the crabs spawn. Similarly, Stage I males are found throughout the winter. Since they too are larger than the average Stage I males collected during May, when the swarming occurs, it is believed that they represent a remnant of the male population of the previous summer.

Atkins (1955:689) has shown that it is possible for one implantation of sperm to successfully fertilize a second egg deposition which might be produced by a female *P. pisum*. Christensen and McDermott (1958:167) also present evidence tending to confirm the same thing in *P. ostreum*, as do Wells and Wells (1961:275) in *Pinnaxodes floridensis*, and Pearce (1962*b*) in *Pinnixa faba* and *P. littoralis*.

Whether it is possible for a second copulation to occur in *F. subquadrata* is extremely doubtful. Christensen and McDermott (1958:167) report what might be a copulation between a male, Stage I crab and a female, Stage V instar of *P. ostreum*. They doubt, however, that such a copulation would normally occur in this species. If copulation in *F. subquadrata* is restricted to the period of swarming in open waters it is obvious that, because of its morphology, the Stage V instar can never leave the host and is thus unable to copulate a second time in open water. Since no Stage V female has ever been noted to be accompanied by a hard stage male or, for that matter, a male of any other stage, it can probably be assumed that a second infestation is not tolerated and it is thus doubtful that a second copulation would or could occur. Furthermore, as was pointed out by Stauber (1945:270) for *P. ostreum*, the size difference between the average adult female and the hard stage male probably makes copulation mechanically impossible.

GROWTH AND DEVELOPMENT CORRELATED WITH HOST SIZE

Wells (1940:45) found that a definite positive correlation could be established between the

carapace width of the mussel crabs and the length of their host mussels: by grouping shell lengths and plotting them against the mean carapace width of all the crabs found in each shell length group, he could obtain a curve indicating that the carapace width was, in general, proportional to the shell length of the host. Atkins (1926:482) was able to find a size correlation between 34 *P. pisum* and their bivalve hosts. More recently Christensen and McDermott (1958:160) established a similar relationship between all stages of *P. ostreum*, as well as for only the Stage V instars of that species, and their host, the American oyster, *Crassostrea virginica*. The latter proposed that external factors, with the amount of food probably being the most important, act upon both the bivalve and its symbiont crab so as to regulate the growth of the crab in such a manner that it "fits" the host.

They further note that while smaller crabs may occasionally be found in proportionately larger bivalves, the converse seldom occurs, i.e., large crabs are rarely found in proportionately smaller oysters.

The present work extends that of Wells, who used a relatively small sample of 111 unstaged crabs in his study. During the present investigation examination of 305 crab-mussel associations has resulted in the curve presented as Figure 4. This curve, derived from material collected at one station during the period July 8 to November 11, 1959, is indicative of this correlation.

After examination of the host mussels for the presence of the pinnotherid crabs two rather interesting facts emerge. One was that immature crabs are almost always found in the proportionately smaller host mussels. This is true even

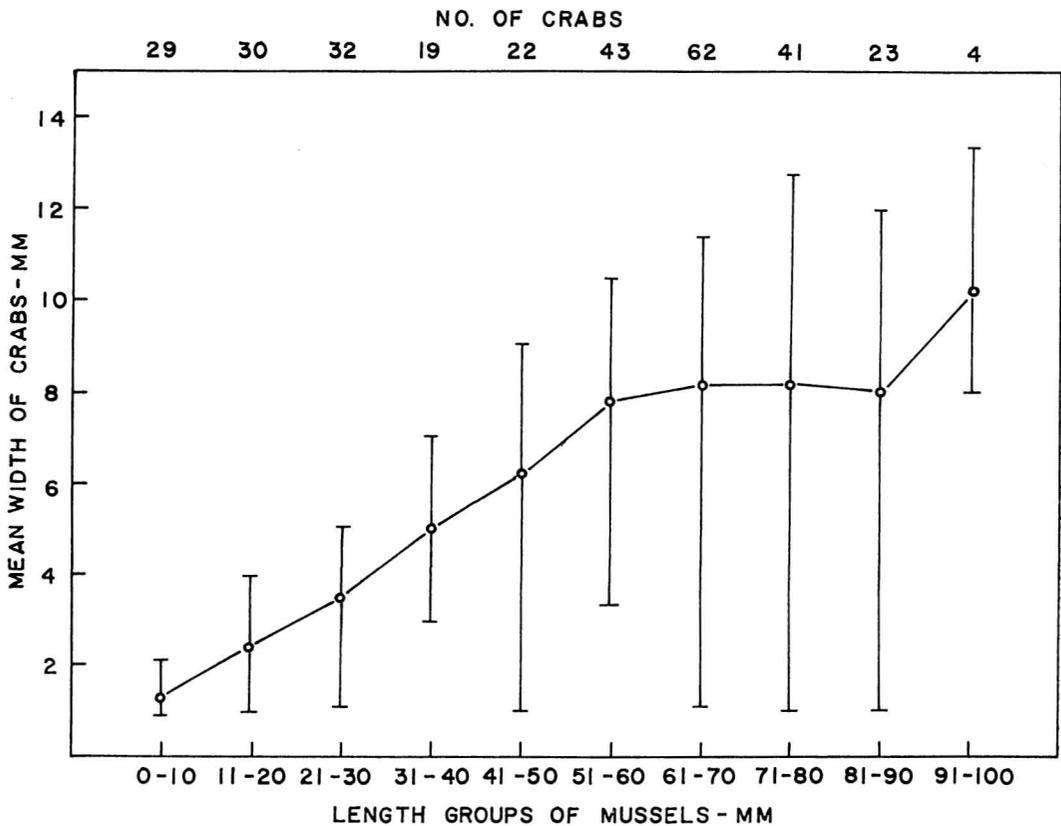


FIG. 4. Curve showing positive correlation between carapace width of all stages of *F. subquadrata* and length of host mussels from which they were removed. Both mean width and size range are given for the crabs.

though the larger mussels could obviously accommodate them. Second, the very large mussels, i.e., over 85 mm in length, seldom contain a crab. It is easy to see, as did Christensen and McDermott (1958:161), why small mussels only rarely contain relatively larger crabs. The reverse, however, is not so easy to explain, i.e., why are smaller crabs seldom found in relatively larger mussels? Also, why is it rare that few crabs, of any size, are found in the very large mussels above 85 mm in length, the latter in spite of the fact that such mussels are relatively abundant?

The occurrence of the early postplanktonic stages has been noted only in the mantle cavity, and not throughout the entire water-conducting system as noted for *P. ostreum* by Christensen and McDermott (1958:173). Therefore, it is not felt that such crabs have been overlooked in the microscopic examination of the larger host bivalves.

Because the very small prehard and invasive stages (1.0 mm or less in carapace width) are most frequently found in the smaller mussels (15 mm or less in shell length), it is thought that the newly moulted true first crab stage, when settling out of the plankton, usually selects a mussel of this size for its host. Figure 5 indicates that 80% of the true first stage crabs are found in mussels ranging from spat to 20 mm in valve length. The mechanism affecting this selection is not definitely known, but at least two possibilities might be suggested.

It is possible that the smaller mussels use qualitatively or quantitatively different food materials than do the larger mussels. Further, it is quite possible that the invasive and other prehard instars require a similar size or type food and are thus obliged to infest initially the smaller, immature mussels. Small crabs which fortuitously find their way into compatible small mussels would survive, while those crabs that infest the larger mussels would not. The fact that occasionally small, invasive stage crabs are found in larger mussels (Fig. 5) could be explained by regarding these crabs as in a transient situation, in which the mussels have only recently become infested by the invasive crab, which would soon be eliminated. The waste which would accompany this elimination is another example of the normal larval or juvenile

"wastage" noted by Thorson (1950:3) in so many marine forms.

The second suggestion involves the hypothesis that the crabs are attracted, selectively, to the smaller mussels by a "host factor." Recent studies by Davenport (1950, 1953a, b), Johnson (1952), Hickok and Davenport (1957), and Sastry and Menzel (1962) indicate that in certain cases of symbiosis the commensal or parasite is indeed attracted to the host by a diffusible factor from the host. The same factor may be used to maintain the relationship once it has been established. Preliminary work recently carried out by Davenport (personal communication) at the Friday Harbor Laboratories did not reveal evidence to support the existence of any such mechanism between *F. subquadrata* and its host, *M. modiolus*. It is important to note, however, that these experiments were conducted only with the Stage I and older instars; and it is quite possible, in fact probable, that such an interaction might be found only between the invasive stage and its host, and perhaps even at a particular time during the instar's existence.

Johnson (1952) reported that a chemotaxis existed between the pinnotherid, *Dissodactylus mellitae*, and the echinoid, *Mellita*. His work with two other pinnotherid species, however, did not reveal the existence of any attractive mechanism between them and their hosts. He suggested that the chemotaxis between *Dissodactylus* and *Mellita* acted to enable the pinnotherid to maintain a continuous relationship with the host in an environment (heavy surf) in which they might readily become separated. In the *Pinnixa chaetoptera*-*Chaetopterus* relationship, as well as the *Pinnotheres*-*Ostrea* relationship, both of which he studied, it was suggested that the negative evidence for the existence of a host factor might be the result of using the experimental devices with a stage of the crab's life cycle which is not attracted to the host. It might well be that other stages do respond.

The recent study by Sastry and Menzel (1962), while indicating that *Pinnotheres maculatus* is attracted both to the bay scallop, *Aequipecten irradians concentricus*, and the penshell, *Atrina rigida*, makes no mention of the stage of the females used in the experiments. They do

distinguish between adult and "early" male stages, although this distinction is not evident in the summary of their experimental results.

The hypothesis that the invasive stage *F. subquadrata* is selectively attracted to the immature spat of the host mussel is made more plausible in the light of recent evidence presented by Blake (1960). He has found that the predator oyster drill, *Urosalpinx*, is attracted selectively to its prey, *Crassostrea virginica* and *Modiolus*

demissus, on the basis of oxygen consumption (used as an index of metabolic activity). One of four factors affecting the metabolic rate was the age of the prey (the others were species, growth rate, and feeding). Both Haskin (1950) and Carriker (1955:49) have shown that there is a predilection by the drills in their choice of younger prey. It is hoped that further investigation of this aspect of the relationship between *F. subquadrata* and *M. modiolus* can be made in

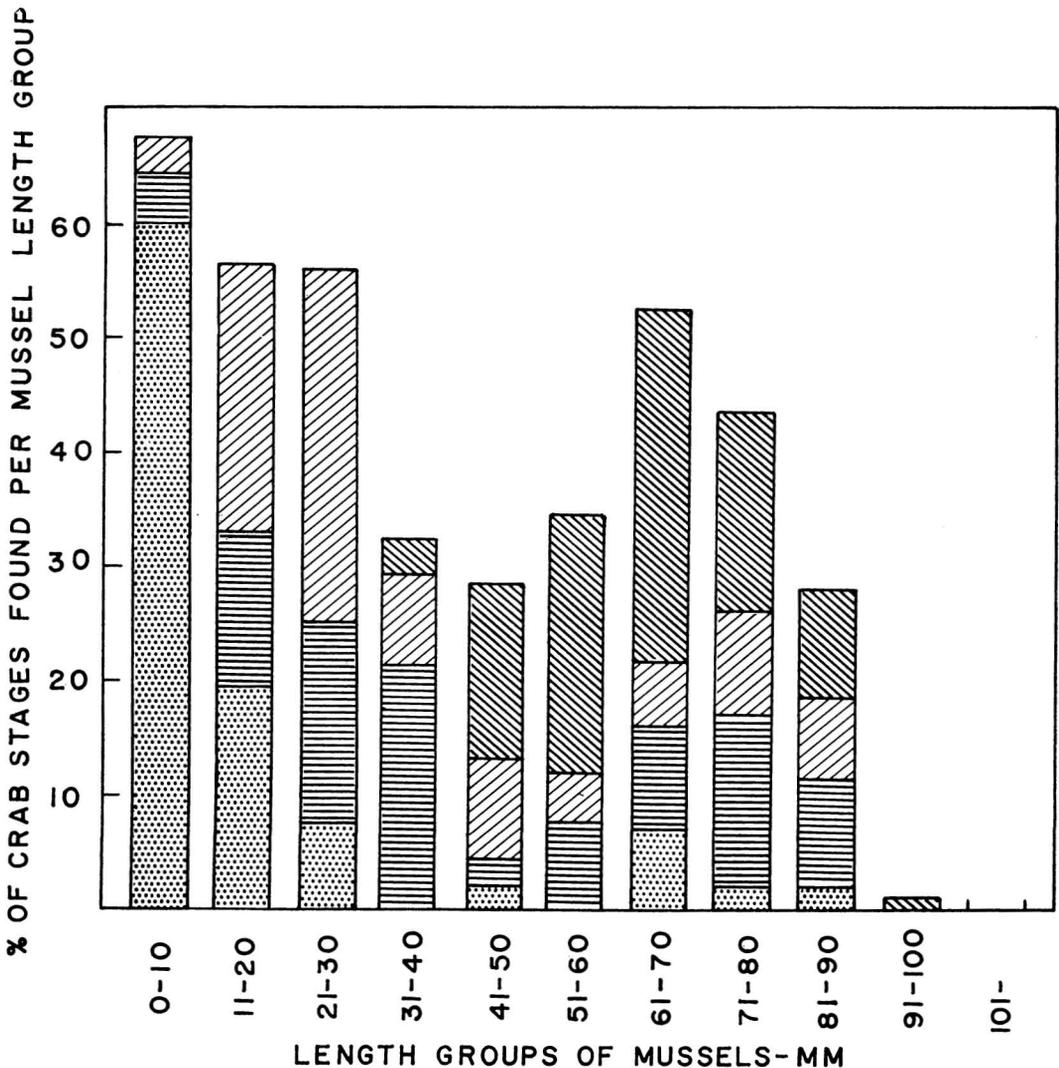


FIG. 5. Histogram showing percent of first true crab stage (stippled fraction of bars), immature females of all stages (horizontal lines), males (fine oblique lines), and Stage V females (heavy oblique lines) found in each length group of the host mussel, *M. modiolus*.

order to attempt to establish the validity of the hypothesis that the invasive stage crab is attracted to the smaller host mussels on the basis of the latter's relatively higher metabolic rate.

An experiment, in which first stage crabs or very early prehardens were placed in small, previously uninfested mussels, indicates that the growth rate of these mussels was sufficient to accommodate the growing crabs. More details regarding this experiment will be presented in a separate paper.

While the foregoing discussion suggests some reasons for the propensity of smaller crabs to associate with the proportionately smaller mussels it does not give any indication regarding the almost general absence of crabs from the

very large mussels over 85 mm in length. It has been reported that *M. modiolus* is an extremely slow grower in its later years and quite long lived (Wiborg, 1946; Coe, 1948). Wiborg reports that off the coast of Norway the horse mussel attains its maximum size of 118 mm at an age of 18 years. It is therefore quite possible that the hosts outlive their original symbiont crabs. Furthermore, since there appears to be a tendency toward the initial infestation of the small, immature bivalves, these larger host mussels might never be reinfested once their original symbiont crab has perished. This would be especially true if the host mussel is selected by the invasive crab on the basis of relative metabolic activity.

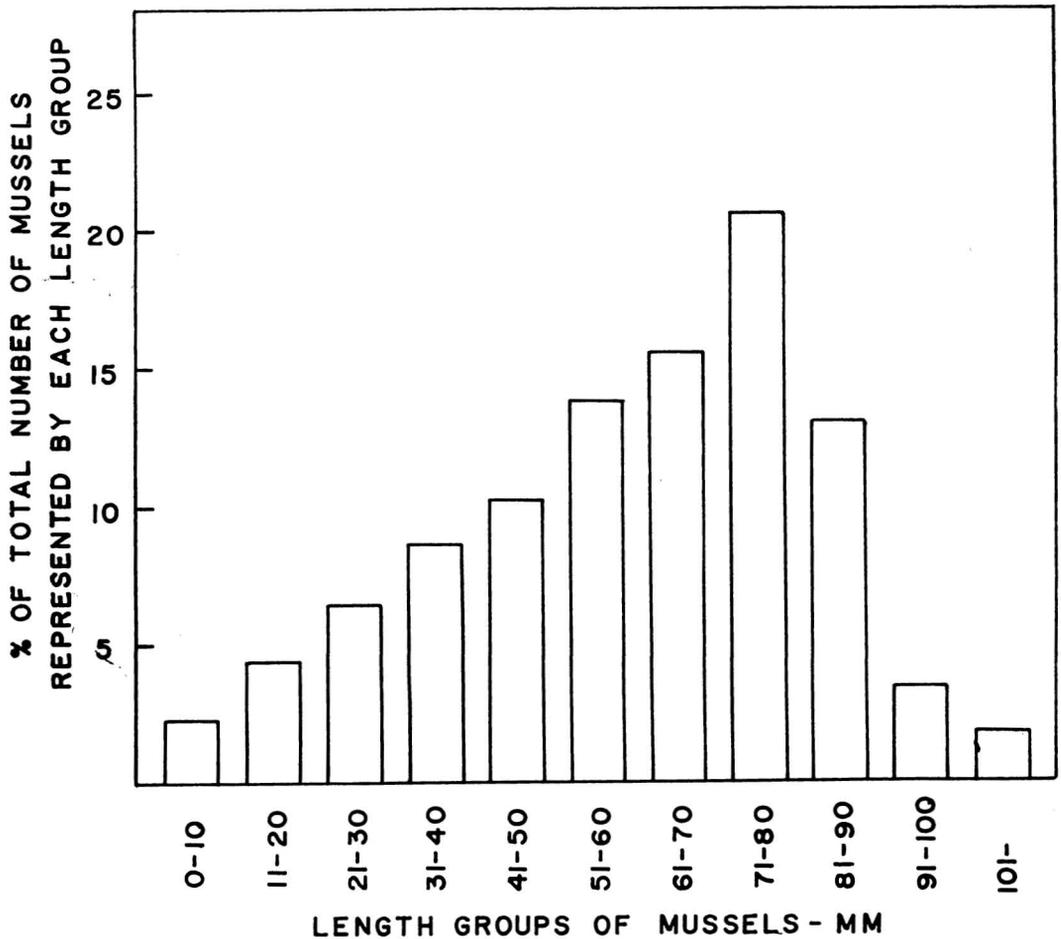


FIG. 6. Histogram showing per cent of total population of *M. modiolus* constituted by each length group.

Observations on the percentage of infestation of the various size groups in the mussel population tend to confirm this speculation. From Figure 4 it may be seen that the average adult size (8 mm) of the crabs on this date is reached in the mussel length group of 51–60 mm. This same average size is also typical of the crabs found in the larger mussel length groups, i.e., larger than 60 mm, although the total number of adult crabs found in each mussel length group decreases above the 61–70 mm range (Fig. 5). This decrease in the number of crabs per group is probably due to the postreproductive mortality following the adult and ovigerous stages. It can also be noted that the greatest number of mussels is found in the 71–80 mm length group (Fig. 6); and furthermore, while there are almost as many mussels to be found in the 81–90 mm group as in the 61–70 mm range, the number of infested mussels in the former group is only one-third that in the latter. Since this is generally true of the mussel populations at all the collecting sites, it seems to indicate that the crabs are outlived by their hosts which, usually, are not subsequently reinfested.

Closely related to the problem of the size relationship existing between *F. subquadrata* and its host is the problem of how permanent is the relationship between the crab and its individual host mussel once this has been established. Does the crab remain within the host after having initially infested it, or is the relationship transitory, with the crab at some period leaving the host?

Rathbun (1918:62), Orton (1921:533), and Berner (1952:345) all suggested that the various hard stage male pinnotherids with which they worked were freeliving. Christensen and McDermott (1958:175) doubt this for *P. ostreum* and *P. pisum*, and they report that the male leaves the host only temporarily during the copulatory period to seek a mate. They state also that this migration is only a phase in the ordinarily commensal or parasitic life of the crab. More recently, Sastry and Menzel (1962:390), in their discussion of the chemotactic responses of the pinnotherid, *Pinnotheres maculatus*, to its bivalve hosts, quote Rathbun (1918:76) to the effect that the early stages of the male are freeliving whereas the later adult males

are commensal in habit. A current investigation of this species in the temperate waters off Cape Cod indicates that, as with *P. ostreum* and *F. subquadrata*, all the stages, with the exception of the invasive first true crab stage and the swarming Stage I instar, are normally symbiotic.

It has been observed that Stage V crabs and posthard forms can and do vacate a host mussel which is moribund. This is, however, the only time that these stages have been found outside a host organism under laboratory conditions.

During August 1959 several immature crabs were found in bivalves not previously recorded as hosts for *F. subquadrata*. The new host species include *Astarte compacta*, *Cardita ventricosa*, *Crenella columbiana*, and *Kellia* sp. All these species are quite small. None, according to Oldroyd (1928), reaches a length greater than 25 mm. One of them, *C. columbiana*, rarely exceeds 16 mm. All the crabs found in these hosts were either prehard or Stage I crabs. Because none of these bivalves normally attains a size sufficient to contain an adult *F. subquadrata* it is thought that the Stage I crabs, after leaving these small initial host species to take part in the copulatory swarming, do not return to the smaller bivalve species but rather secondarily infest a larger host, usually *M. modiolus*. If the smaller initial host species are reinfested by postswarming crabs it is quite likely that the definitive adult crab stage is not attained. Examination of 262 individuals of these small bivalve species has not revealed the presence of a single adult crab.

A comparable host change has been described for *P. pisum* by Christensen (1958:3). He found that on the west coast of Sweden the first crab stage initially infests the lamellibranch *Spisula solida* and that later, upon reaching the Stage I instar, it leaves *S. solida* and secondarily infests *M. modiolus*. The major difference between *F. subquadrata* and *P. pisum*, in this regard, is that in the latter the host change between lamellibranch species seems to be regular or obligate, whereas *F. subquadrata* appears only occasionally to undergo interspecific change, the usual situation being intraspecific. In a more recent report, Christensen (1962:6) notes the occurrence of an ovigerous *P. pisum* in a primary host, *S. solida*, collected at Frederikshavn, Denmark, in the summer of 1960. This indicates

that *P. pisum* is occasionally capable of reaching adulthood in the primary host.

THE RELATIONSHIP BETWEEN *F. subquadrata*
AND ITS HOST, *M. modiolus*

By placing various stages of *F. subquadrata* within mussels which have had a "window" opened in one of the valves, in the manner reported by Orton (1921) and MacGinitie and MacGinitie (1949:313), it has been possible to observe the behavior of the crabs within the host.

Probably the most noticeable feature of the relationship is the comparative inactivity of the Stage V crab within the bivalve host. Most of the movements noted were associated with feeding activities.

The adult female, without exception, is found occupying the anterior half of the mussel's mantle cavity. This is generally the widest part of the mussel. The crab's abdomen is always placed against a pair of demibranchs, with the carapace facing the center of the mantle cavity and the frontal region oriented ventrally with respect to the mussel. Such a position insures that the chela and mouth parts of the crab are in a position which facilitates feeding. The crab maintains this position by inserting the dactyls of the pereopods into the gill filaments and/or mantle tissues.

In general the feeding is, as described by Orton (1921) for *P. pisum*, a matter of picking the mucous food strings from the food grooves of the ctenidium upon which the crab is sitting. The chelae are used initially to catch the strings which are passed to the mouth parts. The anterior pair of pereopods are observed sometimes to play a part in the manipulation of the food strings.

Prolonged feeding in this manner ultimately results in extensive ctenidial erosion, as was reported as occurring in *Crassostrea virginica* (Stauber, 1945:284) and *Mytilus edulis* (McDermott, 1962a:163) due to the presence of *P. ostreum*. Ctenidial or gill erosion caused by adult crabs involves the entire portion of the ctenidium underlying the crab. This portion of the gill is eventually destroyed. Figure 7 reveals this damage and shows the difference between

the eroded and undamaged ctenidia of a mussel. The damage seems to be caused by the constant contact of the chela against the edge of the ctenidium. It is also noted that the crab "nips" at the food string with the chela, and very likely the gill margins will also be pinched and cut as a result of this action. Damage to the palps often accompanies ctenidial erosion, and they may be much reduced in length as well as malformed due to the presence of a pinnotherid crab.

Besides the effects of the chelae during feeding, the dactyls of the pereopods, used to support the crab, also contribute to the gill erosions. By repeatedly inserting the dactyls into the gill lamellae the crab causes progressive erosion dorsally from the point of the initial damage. Once the entire underlying gill has been eroded away the crab maintains its position by inserting the dactyls into the mantle. This results in a pathological condition in which the constant irritation by the dactyls causes a blister or cyst-like formation. This anomaly was found to be present in 55% of the mussels infested with Stage V crabs. A similar condition has also been reported in *Anomia simplex* infested by *Pinnotheres* (McDermott, 1962a:163). As the erosion progresses dorsally toward the suspension of the ctenidium, the food groove is continually reconstituted. Without such a continuous regeneration it is doubtful whether the crab-mussel relationship could long endure, since the food groove is necessary to the feeding process of both organisms. Atkins (1931) has reported a similar regeneration of the food groove following deliberate mechanical damage to the gills of *Mytilus edulis*.

As reported by Stauber (1945:284) for *P. ostreum*, the ctenidial damage inflicted by the immature *F. subquadrata*, especially the Stage I forms, differs markedly from that described for the adult crabs. Because the Stage I crab is considerably smaller, and much flatter dorso-ventrally, than the Stage V crab, it is able to move about more extensively within the confines of the host. As a result of this movement the gill erosion is not restricted to the area beneath and in immediate contact with the crab, but is found along the entire margin of the ctenidium. Moreover, erosion of both ctenidia is common. These erosions quite often cause the

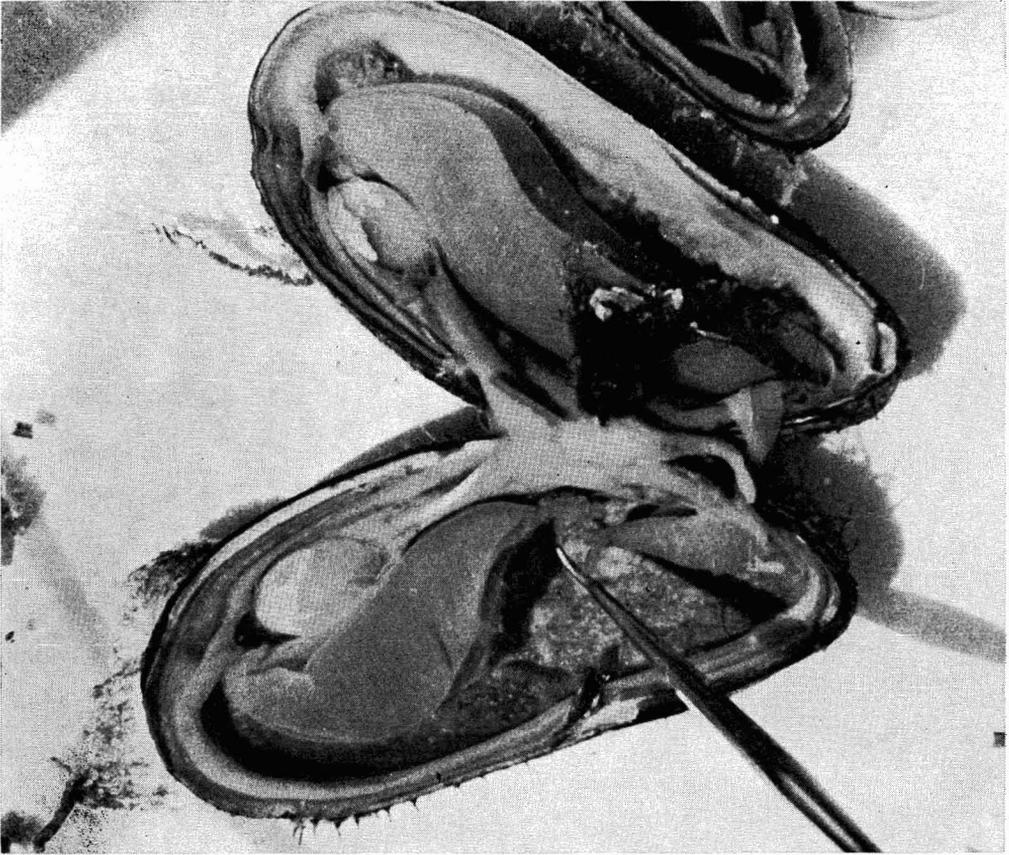


FIG. 7. Photograph showing damage done to ctenidia of *M. modiolus* by a Stage V crab 9.3 mm in carapace width. Note that the ctenidia lying in the left (*lower*) valve are eroded dorsally to the line of suspension. The ctenidia in the right (*upper*) valve are almost entire and serve for comparison. Cystlike anomalies can also be noted on the mantle tissues of the left valve. $\frac{1}{3} \times$.

gill edges to appear serrated. Indentations caused by immature *F. subquadrata* are only one-fourth to one-third the dorso-ventral dimension of the gill, whereas the gill damage caused by the adult crab almost always appears as a single, crescent-shaped erosion, often extending to the base of the ctenidium (Fig. 7).

It appears likely that the erosion of a mussel's ctenidia always starts with the small-crab type and, as the crab matures, the damage becomes that typical of infestations with the adult crabs. Christensen and McDermott (1958:171) note that the erosion caused by *P. ostreum* in the American oyster also progresses from an initial small-crab type damage to the more extensive destruction of tissues connected with the

infestation by a large adult crab.

It is noteworthy that only 58% of the small-crab infestations seen during the months of June and early July are accompanied by extensive erosion, while Stage I infestations prior to and following this period are almost invariably accompanied by extensive, small-crab type erosions. This effect could quite possibly be due to the infestation of previously uninfested mussels following copulatory swarming by the crabs, which thus did not have time to cause extensive erosion.

Both kinds of damage appear to be about equally detrimental to the individual host mussel. Because the smaller Stage I or prehard crabs are usually associated with smaller mussels, the

small-crab type erosion is prevalent in hosts of this size range. Similarly, while the small-crab type of erosion may not appear to be as extensive as the adult-crab type, it may well result in as much, or more, relative surface area being removed from the ctenidia. In addition, the food groove in the former type of erosion may be mutilated over much of its entire length, and it is this structure which is essential to the feeding of the host mussel as well as the symbiont crab. Finally, small-crab damage, unlike adult-type erosions, usually affects both ctenidia.

It is apparent from the foregoing that *F. subquadrata* is not the harmless commensal that it has been considered to be (Wells, 1940:26; MacGinitie and MacGinitie, 1949:312). As does *P. ostreum* this pinnotherid induces an actual physical damage to the mussel host which by its very nature must be harmful to some degree. Under normal conditions, however, the crab is a very effective parasite. Its presence does not seem to affect the growth of or cause the death of the host, nor does it appear to so weaken the host as to render its own position precarious. However, under other than normal conditions the effect of the relationship may be more serious. As Hopkins (1957:414) points out, ". . . an organism which robs its host of nourishment must be harmful in some degree, even if the host shows no apparent effect, but under favorable conditions it is probably not difficult for the host to compensate or even over-compensate for the loss by ingesting more food. Under conditions of food scarcity the same parasite might become harmful."

That such a situation may possibly occur can be shown by studies of the distribution of the crab with regard to water depth. Mussels removed from relatively shallow waters, i.e., 20–60 m, have a much higher percentage of infestation than do mussels taken from waters at a depth of 200 m. Mussels collected from waters of intermediate depths (120–140 m) have a percentage of infestation intermediate between those typical of shallower and of deeper waters. As seen in Figure 1, mussels removed from 30–60 m of water are consistently more than 80% infested. Mussels removed from waters 200 m and greater in depth are rarely more than 2% infested and frequently less than 1%.

Within the waters surrounding the San Juan Archipelago this relationship of the degree of infestation to the water depth appears to hold regardless of the geographic area from which the mussels are removed. Mussels from the shallow waters off Point Caution, San Juan Island, have more than an 80% infestation just as do mussels removed from the shallow waters off Point Lawrence on Orcas Island, and Pea Vine Pass, all relatively separated areas. Mussels removed from any of the deeper waters of President Channel always have a low percentage of infestation.

It was also found that the mussels themselves removed from the deep waters of President Channel were in very poor condition. The gonads usually appeared atrophied, while the visceral masses were, in general, very much reduced. The valves of these mussels, while on the average the same approximate length as those from shallower waters, were thin, brittle, and much more subject to breakage than were those of the shallow water mussels.

Wright (1917) reports that *Pinnotheres* never, or at the most very rarely, occurs in poorly nourished mussels, although it was frequent in those forms from areas where the host mussels were obviously well nourished and making rapid growth.

Thus it can be concluded that when host mussels occur in an environment that is deficient in some factor the infestation by the pinnotherid crabs is reduced, either primarily or secondarily, by the same limiting factor. On the basis of known information it cannot be determined what the limiting factor might be in the present case. Considering the poor physical condition of the mussels found there, it is possible that there may be a deficiency in the amount or kind of available nutrients in the deeper waters.

A number of recent papers (Blake, 1960; Haskin, 1940, 1950; Janowitz, 1956) have indicated that certain gastropod predators are able to locate their prey on the basis of the latter's relative metabolism. Apparently the diffusible end products of the metabolic processes of the host species form gradients up which the predator is able to move. Similarly, Wilson (1948) has recently demonstrated the ability of certain larval forms to "select" appropriate substrates

upon which to settle. Therefore, it does not seem improbable that the settling first stage crabs and the postswarming Stage I crabs might use similar metabolic "targets" in selecting their hosts. This not only would account for the lack of infestation in the poorly nourished, and hence slower metabolizing, mussels found in the deeper waters, but also could explain, as previously discussed, the propensity to infestation of smaller, and probably more rapidly metabolizing, mussels by the early postplanktonic first crab stages.

Finally, the author does not discount the fact that the hazards encountered by these crabs, in settling in deeper water, are much greater and that hence the low levels of infestation found in such conditions may only reflect the loss incurred during the extended settling period.

Houghton (1963:257) reports that there is a correlation between the incidence of infestation of *Mytilus edulis* by *P. pisum* and the tidal level at which the host mussels were collected. He suggests that this is because the first true crab stage of this species is photonegative, and hence it is not likely that mussels found on the shore or at the surface on floats will be invaded.

One further testimony to the delicate balance of this relationship is the fact that double infestations occur only very rarely. As reported elsewhere in this paper only three such cases were noted in this study. This is dramatically different from the condition reported by Stauber (1945:281) and Christensen and McDermott (1958:155), who found that multiple infestations by immature *P. ostreum*, even of spat, were very common during certain periods of the life cycle. However, they did not ever observe two posthard crabs occurring in the same host. Using the same survey techniques as those employed during my investigation of *F. subquadrata*, they recently observed that frequently a single, adult *Mytilus edulis* is infested with up to six prehard *P. maculatus* as well as with an adult female. In this respect, then, the behavior of *F. subquadrata* differs markedly from that of both *P. ostreum* and *P. maculatus*.

The strong tendency toward single infestation observed in the case of *F. subquadrata* certainly suggests some mechanism which selects against multiple infestation of a host organism that is

unable to accommodate the activities of more than one pinnotherid. It appears obvious that, in the case of the *F. subquadrata*-*M. modiolus* relationship, an infestation by two adult crabs would reduce the food gathering surface of the ctenidia to a level below the minimum required to sustain three organisms. Since double infestations are not ever observed between the host and two immature crabs, it would appear that the supposed mechanism operates below the adult level, i.e., at the first stage and/or Stage I levels.

As noted by Wells (1940:34), Stage V females display a marked hostility toward each other when placed together in finger bowls. However, the present investigation has revealed that immature forms (even Stage IV instars), similarly situated, do not demonstrate the marked aggressive behavior which characterizes the adults' relationships. It is notable, however, that when two Stage I crabs are placed in a mussel one, and sometimes both, will immediately vacate the host. This was true in six replicate trials. On the other hand, when a single crab is inserted it will remain within the host.

The relationships between the mussel crab and the alternative, smaller species of bivalve hosts already mentioned are not known as yet. A cursory examination of these hosts did not reveal extensive damage to gills or other parts. The infesting crabs were mostly immature prehard crabs (94 out of 120 such infestations, or 78%), and extensive damage probably would not have had time to occur.

F. subquadrata has also been recorded as occurring in *Mytilus edulis* (Wells, 1928:289), *M. californianus* (Wells, 1928:289; Ricketts and Calvin, 1952:164), and *Saxidomus* sp. (Hart, personal correspondence). Ricketts and Calvin report that the mussel crab is found in 3% of the full grown California mussels. Giles (personal correspondence) has found *F. subquadrata* in only 6 out of 805 *M. californianus* collected from Bodega Bay and Tomales Bay, California. This is less than 1% infestation. The present author has examined some 300 *M. edulis* and 104 *M. californianus* taken from the intertidal zones of San Juan Island without finding a single mussel crab.

Hart (personal correspondence) has collected

F. subquadrata from an unusual bed of intertidal *M. modiolus*. About 18% of the mussels removed from this area (located at Ten Mile Point, Victoria, Vancouver Island, British Columbia) are infested.

DISCUSSION

F. subquadrata, as do the other two pinnotherid species which have been sufficiently studied, *P. pisum* and *P. ostreum*, has a complex postplanktonic life cycle. The anomalous Stage I instar is present in the life cycle; and the prehard and posthard instars, while not identical with those of the two species of *Pinnotheres*, are quite similar. Also, as was demonstrated by Christensen and McDermott (1958:150) for *P. ostreum*, the first true crab stage following the megalops is the invasive stage.

There are extensive differences, however, between the subsequent life cycle of *F. subquadrata* and that reported for *P. ostreum* by the latter authors. Present evidence indicates that the Stage I male oyster crab must leave its host and seek out the female within her host in order to copulate. Following copulation the male leaves the female and perishes, either in the open water or within a secondary host. The results of the present study would indicate that copulation in *F. subquadrata* occurs during a freeswimming period, the swarming, in which both the male and the female participate. There is no indication that the male subsequently perishes. In fact, following the swarming period in late May and June, males are frequently taken throughout the entire summer. Wells and Wells (1961:275) have also noted the continued persistence of males of *Pinnaxodes floridensis* following copulation.³

In addition to the copulatory swarming and persistence of the male following swarming, *F.*

subquadrata does not, at any stage in its life history, engage in the multiple infestations which occur during the early stages of *P. ostreum*.

While previous investigations (Christensen and McDermott, 1958) suggest that swarming is not typical of members of the genus *Pinnotheres*, the recent observations of swarming *P. maculatus* would indicate that at least one species of this group takes part in a copulatory swarming. It is suggested, therefore, that other pinnotherid species should be studied with regard to their reproductive behavior. This is particularly true in view of Sakai's paper (see footnote 2) in which he mentions a swarming or migration as being characteristic of the Asiatic pinnotherid, *Tritodynamia borvathi*. Miyadi (1941) has described a benthic community on the basis of a large number of pinnixid crabs found covering the bottom of certain areas of the Ise-wan, Kii Peninsula, Japan. At one station he reports that these crabs, *Pinnixa rathbuni*, occur in densities of up to 3441/m². They were found associated with several bottom types. Since he thought that such a large number of crabs cannot occupy a bottom area for an extended period of time, he suggested that among other reasons, the crabs could be ". . . in the reproductive period." As both *Tritodynamia* and *Pinnixa* are related in the subfamily Pinnothereliinae it is not improbable that the phenomenon observed by Miyadi was actually a swarming comparable to that observed by Sakai; and, in fact, both might be associated with reproduction. Thorson (1957:518) describes a crab community found in the Persian Gulf as being a parallel of Miyadi's community. The former community has as a dominant a pinnotherid, *Xenophthalmus pinnotheroides*, which occurs in densities of up to 1,500 mature individuals/m². Again, while Thorson suggests that this community is stable, it is not impossible that

³ While at present the genus *Pinnaxodes* is often placed in a different subfamily (the Pinnothereliinae) from both *Pinnotheres* and *Fabia* (which are in the subfamily Pinnotherinae), there is some question as to the validity of this arrangement. Rathbun (1918:179) states that *Pinnaxodes tomentosus* ". . . is very likely a *Pinnotheres*." A thorough study of the life history of the members of this genus will possibly indicate closer affinities with the subfamily Pinnotherinae, including *Pinnotheres* and *Fabia*, than with

the Pinnothereliinae. Members of the latter subfamily, investigated in a recent study (Pearce, 1962b), as well as in the recent descriptions (Wells and Wells, 1961) of the life history and morphology of *Pinnaxodes floridensis*, differ very markedly in their life history from both *Fabia* and *Pinnotheres*. Sakai (1939:582), in his review of the Japanese Brachyryncha, placed the genus *Pinnaxodes*, along with *Pinnotheres*, in the subfamily Pinnotherinae.

the dense population observed is actually a reproductive swarming. To the present author's knowledge neither Miyadi or Thorson was able to study subsequently the respective areas, and hence it is unknown whether or not these populations were maintained.

The present investigations substantiate the finding of Christensen and McDermott (1958:174) that the soft-shelled, posthard females do not normally leave their host. As indicated earlier, however, at least the immediate posthard instars of *Fabia* are able to leave their dying host, and a small Stage V *Pinnotheres pugettensis* has been observed, and photographed, leaving its ascidian host, *Halocynthia igaboja*.

Another aspect which should be investigated further is the size differential between male and female Stage I crabs of at least two species, and the possibly related phenomenon in which males of this stage were observed to moult into soft, posthard forms as reported by the late Dr. Atkins (1958). She regarded these moults as having possible significance in the growth of male crabs. The results reported by both Christensen and McDermott (1958:153) and the present investigation indicate a somewhat larger size for the Stage I male than for the comparable female instar. The former found that the female *P. ostreum* ranges from 1.3–2.7 mm in carapace width, while the male ranges from 1.4–4.6 mm. Female *F. subquadrata* range from 1.5–6.2 and average 3.5 mm (29 individuals), while the males range from 1.3–6.8 and average 4.1 mm (54 individuals). Atkins (1958) stated that hard Stage I males would moult into a soft stage which was frequently followed by two more moults. Thus in *P. pisum*, which Atkins studied, one to three thin-shelled instars intervened between successive thick-shelled or hard forms. Since Christensen and McDermott (1958:164) were unable to keep alive the male Stage I *P. ostreum* under their laboratory conditions, they could not observe such moultings.

Male Stage I *F. subquadrata* survive in the laboratory as long or longer than the same female instar. Such a crab was taken to the Zoology Department of the University of Washington following the end of the normal summer session at the Friday Harbor Laboratories (August 30, 1959). This crab survived, in spite of

no actual feeding or efforts to maintain a normal environmental temperature, in the confinement of a finger bowl until the following spring (May 1960). Similarly, many male Stage I crabs were held throughout the summer months at the Friday Harbor Laboratories. Of particular significance was the fact that eight such crabs did moult into soft, posthard forms. It is thought that the slightly greater size of the male Stage I crabs may be a reflection of a growth moulting which has previously been regarded as anomalous or as not actually occurring.

With regard to the crab–host relationship a number of interesting conclusions can be drawn. There is no doubt that the relationship between *F. subquadrata* and *M. modiolus* is parasitic in nature, especially if the broad definition of Hopkins (1957:413) is used. The extensive, almost ubiquitous, damage to the ctenidia as well as to the underlying mantle and palps cannot be construed as anything but a result of a parasitic relationship. As with some parasitic relationships (Allee et al., 1949) it seems to have developed with a degree of specificity. By this it is meant that many species of pinnotherid crabs, including *Fabia*, are primarily found, at least in the adult instar, in a single host species. There are, however, exceptions to this generalizations, both for *Fabia* and the other pinnotherid species. Although in the waters of Puget Sound adult female *F. subquadrata* almost invariably occur in the definitive or primary host, *M. modiolus*, Wells (1928:289) reports it with both *Mytilus edulis* and *M. californianus* as well as in the branchial sac of the ascidian, *Styela gibbsii*. The crab found in the latter host was noted, however, as being immature. During the present investigation no crabs, of any stage, were found in either *M. edulis* or *M. californianus*. In the more southern extensions of its range adult *F. subquadrata* has recently been found in *M. californianus*. The status of the definitive host, *M. modiolus*, in these waters is not known.

The closely related pinnotherid, *Pinnotheres pugettensis*, which from present information may have a life history very similar to that of *Fabia*, was found only in the large ascidians, *Halocynthia igaboja* and *Ascidia paratropa*. While Wells (1928:286) reports it only from *Halocynthia (Tetbyum) aurantium* collected by

Prof. Kincaid in the Friday Harbor region, the present author was unable to find it in the limited number of specimens which were available for examination. All three of these tunicates are large and quite similar in their basic morphology.

A report by McDermott (1962a:163) also contains information which indicates that, as in the *Fabia-Modiolus* relationship, the oyster crab, *P. ostreum*, may develop through the hard Stage I instar in a secondary host, *M. edulis*. After attaining the hard stage ". . . both sexes leave the hosts and seek some other molluscs (oysters or jingle shells) in which the females may grow to maturity." McDermott suggests, therefore, that it is possible for *P. ostreum* occasionally to utilize two hosts in completing its life cycle.

In the same paper he reported that both *P. ostreum* and *P. maculatus* are able to develop to maturity in the jingle shell, *Anomia simplex*. This is, as he notes, another new record for *P. maculatus*, and emphasizes further ". . . its profound lack of host specificity." This pinnotherid has previously been reported from a wide range of hosts (Rathbun, 1918:76), and since Grey (1961:357) has reported it from the tubes of *Chaetopterus* it must be assumed to be quite widely distributed.

While McDermott finds mature *P. ostreum* in *Anomia* he emphasizes that "the incidence and survival of *P. ostreum* in *Anomia* is not comparable to what we have seen in the oyster. The incidence is much lower as is its survival to maturity."

Representatives of the subfamily Pinnotheriinae, which includes the several species of pinnixids found in Puget Sound, appear to be equally specific in the selection of, or survival in, their hosts. On the tidal flats of False Bay, San Juan Island, two species of lugworm occur and each is associated with a particular species of pinnotherid crab. *Abarenicola pacifica*, a worm living in muddy sand, is almost invariably found with *Pinnixa schmitti*; while *A. vagabunda*, a species dwelling in the clean sandy bars protecting the entrance to False Bay, is usually found with *Pinnixa eburna* (Healy and Wells, 1959:325). However, Healy reports in the same paper an instance in which *A. pacifica* was found in the clean sand substrate favored by the *A. vaga-*

bunda. With three of the former worms he found *P. eburna*. Thus there is an indication that the substratum, not the worm, determines the presence of the crab. During the present investigation, however, several hundred worms of both species were subsequently checked and no anomalies were found in the crab-worm association, i.e., *P. eburna* was always found in association with *A. vagabunda* and *P. schmitti* with *A. pacifica*. One final example of the specificity of the crab-host relationship is the relationship of *Pinnixa faba* and *P. littoralis* to the large lamellibranch host, *Schizothaerus capax*. As with *F. subquadrata*, the juveniles of these two pinnixids are found with a wide range of small bivalve species, although interestingly enough these are never the same species in which the immature *Fabia* occur. The adult *P. faba* and *P. littoralis*, however, are found only in association with *S. capax*. Even though closely related, and similar in size, *Schizothaerus nuttali* never contains the adult pinnixids and rarely the immatures. The reason for this specificity is detailed in a recent paper (Pearce, 1962b:48).

Thus, while many pinnotherid species may occasionally be found in other than the primary host during their early postplanktonic stages, the adults of most species so far studied appear typically to be found in a definitive or primary host species or type. The reasons for this specificity undoubtedly center in the fact that the crabs have evolved in many ways to fit the environment provided by a specific host organism. Apparent exceptions to the general rule, such as *P. maculatus*, must be more thoroughly investigated.

Although at the present time there is not a great body of evidence from which to extrapolate, there are indications that the pinnotherids, as a group, are actively involved in a process of adaptation. For instance, within the subfamily Pinnotherinae there is considerable variation in the use of secondary hosts. *F. subquadrata* utilizes a wide range of bivalve species, of several families, for secondary hosts although, as earlier pointed out, in the waters of Puget Sound the adults have almost invariably been found in the definitive host, *M. modiolus*.

P. ostreum, upon occasion, will infest *M. edulis* and *A. simplex* (McDermott, 1962a),

although it apparently matures only in the latter secondary host, and here there is a noticeable reduction in survival and percentage of infestation when compared to the primary host relationship with *Crassostrea virginica*. In addition McDermott (1962b:2) has observed that there are annual fluctuations in the incidence of infestation of the secondary host bivalves by *P. ostreum*, and these fluctuations should be studied to determine if there are any correlations with fluctuations or relative abundance of the primary host organism, in this case *C. virginica*.

Finally we have the case of *P. pisum* which, according to evidence presented by Christensen (1958), almost always develops, in the Kattegat, first in *Spisula solida* and then undergoes an obligatory host change to *M. modiolus*. In a more recent paper, however, Christensen (1962:6) notes occasional exceptions to this general pattern: he has found an ovigerous female in a *Spisula* and, in addition, has found several new genera which can serve as the initial host. These are *Glycimeris*, *Cardium*, *Laevicardium*, and *Mactra*.

Thus, it would appear that there is a tendency for certain species to fill several niches, at least during the juvenile stages. Whether, in an evolutionary sense, these species are progressing from an original intraspecific or single-host condition to one in which a number of host species are infested is not known. It might be suspected, however, that while the adults of many of the species thus far studied appear to be quite specific in their use of hosts, a definite advantage would accrue to a species which was able to develop in more than one host or niche. This would be especially true of forms living in tropical waters, where a greater speciation has occurred but the total number of any one species, and hence of potential hosts, might not be so great as in temperate or boreal waters. Sakai (1939:589) reports one species of *Pinnotheres* as occurring in at least five different bivalves found in Japanese waters (although there is no statement as to the stages involved); and the tropical species listed by Rathbun (1918) are frequently taken from several hosts. Again, however, there are no statements as to the stage of the crabs. It is of interest that *Pinnotheres maculatus*, which is distributed throughout a wide

range of latitude, is found in association with many different types of hosts, including polychaete worms, mussels, oysters, and scallops.

Even in temperate waters there is an advantage to the infestation of multiple host species, if only by the immature crabs. In the event of an epizootic involving the definitive host, those individual crabs which have infested the secondary hosts during the postplanktonic-hard stage of their development would still be available to reinfest the surviving, previously uninfested individuals of the primary host population.

Intergradations of morphology have been found between comparable instars of the species so far studied. Both the first crab stage and Stage I instar of *P. ostreum* have rigid, well calcified exoskeletons and possess the rod-like structures which connect the carapace to the sternum (Christensen and McDermott, 1958:150). In *Fabia* the first crab stage is not hard, while the Stage I form is; the latter stage of this species does have the well developed columnar structures linking the dorsal and ventral surfaces of the body. Similarly, in *P. pisum* the first crab stage is not hard, while the Stage I instar is.

In addition to these variations in the hosts utilized, and in the morphology of the invasive instars, there are the differences already discussed in the reproductive biology of the various species. *P. ostreum* mates within the bivalve host of the female while, from all available evidence, both *F. subquadrata* and *P. maculatus* engage in a freeswimming swarming during which copulation occurs. While nothing definite is known about this aspect of the biology of *P. pisum*, collections made by Christensen (personal correspondence) indicate simultaneous occupancy of the host bivalves by pairs (male and female) of Stage I crabs. On the other hand, the author is in possession of a female, Stage I *Pinnotheres taylori* taken freeswimming in a midwater plankton trawl.

Because of these intergradations between the various species it is extremely difficult, as suggested by Christensen and McDermott (1958:177), to generalize in any way with regard to the biology of the pinnotherid crabs. The fact that in many species the Stage I female is modified for a freeswimming existence, and yet does

not leave the host during this phase of the development, seems incongruous. It may be that the modified morphology of the Stage I female of *P. ostreum* is an adaptation for the possible host changes which do occasionally occur in this species. Christensen and McDermott (1958:175) point out that when several female *P. ostreum* invade the same host the excessive crabs must either "perish or migrate to other oysters." According to Christensen's (1958) information on *P. pisum*, it may be assumed that this is definitely the case in this species. It seems more reasonable, however, to regard the anomalous Stage I instar, which seems common to many pinnotherids, as a remnant of an earlier ancestral life cycle in which both the male and female were hard and occasionally freeliving, and both simultaneously infested the host organism. Later, during the evolution of the group, when the symbiotic existence was definitely assumed, the female started to moult into the large soft, posthard stages capable of producing the greater number of eggs necessary to the success and survival of a cryptic, parasitic form. At the same time the male became less necessary, and today, in at least some species, seems to be eliminated following copulation. It is suggested that this is a more reasonable hypothesis regarding the evolution of these forms than that proposed by Christensen and McDermott. They state (1958:176) that posthard males, comparable to the existing female stages, probably existed somewhere in the line of evolution. Since to this author's knowledge no known males of any freeliving brachyuran species assumes the soft habitus of the posthard pinnotherid females, it seems unlikely that such males were present in the early evolutionary history of the Pinnotheridae.

Finally, as was mentioned earlier, a definite correlation has been noted between the depth from which the host mussels are collected and the percentage of infestation, as well as between depth and the size of the symbiont crabs. Possible reasons for the correlation between the depth of water in which the mussels are found and the amount of infestation have been discussed previously. It is suggested that the smaller size of the crabs taken from mussels removed from relatively deeper waters (Fig. 1) is the re-

sult of similar influences. A comparative quantitative study of the digestive tract contents of host mussels and their symbiont crabs might be of value in determining whether the limiting factors include total available food.

From the foregoing discussion it is obvious that the investigation of the family Pinnotheridae is still as desirable today as it was several decades ago, when Rathbun (1918:10) made her admonishment concerning the family. It is thought that, particularly from a systematic point of view, a more intensive comparative study of the biology of various species will produce an unsuspected amount of information. Not only will this information be of interest in itself, but it might be profitably applied to the study of benthic and pelagic communities. The effects of the symbiotic crabs on their host organisms would undoubtedly influence the role of the latter within the community. This is especially true when the host is one of the dominants within a community. In fact, *M. modiolus* has been considered a dominant organism in the *Modiolus* faciation of the *Strongylocentrotus-Argobuccinum* biome (Shelford, 1935:287) which is typical of the San Juan Channel. *Pinnotheres ostreum* has been investigated with regard to its effects on the economically important oyster beds of the east coast of the United States (Stauber, 1945; Haven, 1958). Hancock (1962) has reported that infestation by *P. pisum* reduces the average volume of the meats of the edible mussel, *Mytilus edulis*.

More recently a study has been initiated to ascertain the role which *P. maculatus* plays in the benthic mussel communities found in the waters surrounding Cape Cod and the Elizabeth Islands. Some of the preliminary results of this study are contained in this paper.

SUMMARY

1. The postplanktonic stages which succeed the megalopal instar are described and their dimensions given.
2. Like *Pinnotheres ostreum*, *Fabia subquadrate* is shown to invade the host organism during the first true crab stage.
3. "Abnormal" instars of both sexes are described.

4. The external manifestations of ecdysis in *F. subquadrata* are described.

5. Copulation occurs in open water, with both the male and female crabs leaving their symbiont host as the hard, Stage I instar. Following copulation the female crabs return to a host organism to continue their development. Some, if not all, surviving males return to a host.

6. Only during the copulatory swarming have males and females been found together. Only three multiple infestations of the host have been noted; two of these were between two males and the third was between probably incompatible stages of a male and female.

7. Copulatory swarming occurs in Puget Sound during late May. This is followed by a period of 21–26 weeks, during which the precociously inseminated females pass through the five posthard developmental instars. Ovigerous females are first noted in November; the eggs hatch in February.

8. The growth rate of *F. subquadrata* appears to be positively correlated with the growth rate of the definitive host, the horse mussel, *Modiolus modiolus*. Suggestions are given to explain the fact that immature crabs are less commonly associated with the relatively larger host mussels.

9. Four new bivalve hosts are given for *F. subquadrata*.

10. Evidence is presented which suggests that the mussel crab is a true parasite causing extensive physical damage to the host organism.

11. Crabs found in mussels removed from deeper waters tend to be smaller than those removed from hosts taken in relatively shallow waters.

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