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LIFE–HISTORY AND BIOLOGY OF THE OYSTER CRAB, PINNOTHERES OSTREUM SAY

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While the adult female of several species of the pea crab, *Pinnotheres,* has been known since ancient times, it is not clear when the first male was observed and described. The earliest reference available to the present authors was found in a paper by Thompson (1835).

He describes the male of *P. pisum* as being firm in texture, with compressed, hairy appendages and of flatter form and much smaller size than the (adult) globular, soft-shelled female. Such hard-shelled *P. pisum* were generally all thought to be males until Orton (1921) demonstrated the existence of hard-shelled females, which except for differences in the genital apertures and the pleopods proved to be indistinguishable from the males. However, hard-shelled females were known in at least four other species of *Pinnotheres* prior to 1921 (Rathbun, 1918). Possibly, Thompson (1835) was also aware of this in *P. pisum* as he states, "For a considerable time the young females are scarcely to be distinguished from the males, and in this stage both differ so much from the adult, as to render it probable that they have often been taken for individuals of different species, . . ."

Orton (1921) was the first to find a soft-shelled male, which except for the same characteristics as mentioned above resembled the immature female of similar size.

A few years later, Atkins (1926) studied and described all the growth stages of *P. pisum* found in *Mytilus edulis* in English waters. As Orton, she regarded the hard-shelled crabs as free-living, invasive crabs, a point of view which the author later abandoned (Atkins, 1954, 1955). Hence the hard-shelled stage of both sexes was designated as Stage I. In the female, four more stages were described, the fifth and last stage being the mature crab. In the male, only the hard-shelled stage was described, no reference being made to Orton's discovery of a soft-shelled specimen. It was stated, however, that a few abnormal males were found. Soft-shelled males were found also by Mercier and Poisson (1929), who stated that they were abnormal due to the influence of an entoniscid parasite. Later Atkins (1933) disproved this statement and expressed the hope of discussing the matter in a later paper as she still considers these males as abnormal.

Stauber (1945) found and described similar growth stages in *P. ostreum* from the American oyster, *Crassostrea virginica.* He therefore followed Atkins (1926) in designating the hard-shelled stage as the first (invasive) stage, which in the female is succeeded by four more stages as in *P. pisum.* Stauber also found a number of soft-shelled males, evidently corresponding with the finds of *P. pisum* mentioned above. With some reservation, he referred these males to a second stage

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following the hard-shelled stage. This hypothesis does not agree with the general belief that the hard-shelled male is the adult stage of this sex.

Although numerous species of *Pinnotheres* have been described (Bürger, 1895; Rathbun, 1918; Tesch, 1918; and others), knowledge about post-larval stages, other than the adult, is scarce for all species except the two mentioned above. Only in two species has the first crab stage been described, *viz.* in *P. taylori* by Hart (1935), and in *P. ostreum* by Sandoz and Hopkins (1947). In both cases the crabs were reared from the egg in the laboratory, and the stage has never been reported from nature.

The latter paper included a description of the early developmental stages of which there proved to be four zoeal stages, of which the first two had been described earlier (Hyman, 1924), and one megalopa. It therefore almost completed our knowledge of the whole developmental cycle in any pea crab for the first time. The authors, however, pointed out that two or more instars were still unknown as the two crabs reared by them measured only about 0.6 mm. in carapace width while the smallest hard-shelled *P. ostreum* found by Stauber (1945) measured 1.4 mm.

Much to our surprise, the missing instars as well as the first crab stage were found in a number of oyster spat collected in Delaware Bay on August 17th in 1955. This meant that the hard-shelled stage could not be the first invasive stage. The fact that hard-stage crabs of several species of *Pinnotheres* have been taken free in the water (Verrill and Smith,[2] 1874; Rathbun, 1918; Berner, 1952; and others), or trapped between the valves of their host (Orton, 1921; and others), had to be explained otherwise. Two hard-stage oyster crabs were also caught outside their host by the present authors. In addition to the description of the new growth stages, a re-investigation of the biology of *P. ostreum* was therefore decided upon. This seemed especially worth while since Stauber's paper is the only comprehensive work on the biology of any pinnotherid crab. This seems strange considering that the genus *Pinnotheres* alone comprises more than a hundred species, unless, which is very possible, many of them are synonyms. The results of our subsequent studies are the subject of the present paper.

We wish to express our sincere appreciation to Mrs. Grete Møller Christensen, Mr. Donald E. Kunkle and Mr. William Richards for their unfailing interest in our work and for invaluable help in collecting and opening numerous oysters, as well as for help rendered in various other ways. We are much indebted to Dr. Leslie A. Stauber of Rutgers University for reviewing the manuscript, and for giving us access to his collections of oyster crabs as well as his unpublished data on the subject. The director of the N. J. Oyster Research Laboratory, Dr. Harold H. Haskin, gave our work his enthusiastic support for which we express our sincere gratitude. The senior author gratefully acknowledges the grants from the Fulbright Foundation and the Danish State Scientific Foundation which made his visit to the United States possible.

Materials and Methods

The present work on the biology and life-history of *P. ostreum* was carried out at the New Jersey Oyster Research Laboratory, Rutgers University, from August, 1955 to December, 1956.

[2] Judging by their figure, Pl. I, Fig. 2, the species found was *P. maculatus,* and not *P. ostreum* as stated.

Studies on the rate of growth and development, one of the primary objects, were based on extensive collections in the field. Since such factors as the age and size composition of the host populations, as well as the environmental conditions, could be expected to vary from one area to another, it was important to eliminate as many of these variables as possible. We decided, therefore, to find one or two small grounds in Delaware Bay with a good set of 1955 oyster spat and with a high incidence of infestation with oyster crabs. These grounds were then to be sampled at regular intervals throughout the period of investigation. This procedure enabled us to deal with local populations of oysters and crabs of known year-classes. It also eliminated the risk of dealing with oyster populations exhibiting different incidences of infestation, a factor which later proved to be very important to the interpretation of the assembled data.

One ground was selected at Pierces Point about ten miles north of Cape May Point, and another was selected about two miles west of Pierces Point on the Bay Shore Channel Bed, an area where commercial oyster dredging is prohibited. At Pierces Point, oysters were collected by hand at low water when the oysters were exposed. Here a heavy mortality of the 1955 spat occurred late in the winter of 1955–1956, wherefore sampling was discontinued except for a few samples during the summer of 1956, and sampling of 1956 spat in the fall of that year. On the Bay Shore Channel Bed the depth at mean low water is about 6 meters, and here oysters were obtained from the research vessel "Julius Nelson." Little mortality of the 1955 spat was noted on this ground, but some mortality of the crabs occurred in February and early March of 1956 (Fig. 5).

In addition to the regular collections of crabs from 1955 spat (Table I), other collections, which included crabs from older oysters as well as from 1956 spat, were made on the above mentioned as well as other grounds in Delaware Bay. An effort was made to secure a high number of crabs at each collection. As seen in Table I, the lowest number taken in the series of regular samples was 55, and most of the samples contained more than a hundred crabs. Collections began at a time when most of the 1955 crabs were still in the first crab stage, thus enabling us to study the whole post-planktonic life cycle of the crab.

On the Bay Shore Channel Bed, which constituted our main sampling ground, bottom temperatures were determined with a reversing thermometer on each collecting date.

Oysters brought back to the laboratory were, with few exceptions, examined alive and always under a dissecting microscope. Infested oysters, and from time to time also all of the uninfested oysters collected along with them, were measured to the nearest 0.5 mm. in length with vernier calipers. The crabs were measured under the microscope to the nearest 0.1 mm. in carapace width. The smaller crabs were measured with a calibrated ocular micrometer, while the majority were measured on a millimeter glass ruler or by vernier calipers. The amount of error was judged to be the same for the last two methods, as they were checked on several occasions. Unless otherwise indicated, all crab sizes in the present paper refer to the width of the carapace.

Notes on the general condition, amount of gill damage caused by the crab, and other pertinent data concerning the infested oysters were taken on the majority of the collections.

All of the oyster crabs found, except those used for dissections and experiments, were preserved in alcohol, and specimens of the new instars have been deposited in the United States National Museum and in the Zoology Museum of the University of Copenhagen, Denmark.

For various reasons it was decided to reserve a detailed description of the new instars and the necessary revision of the numbering of all the post-planktonic growth

TABLE I

Number and mean size for each collection of oysters and oyster crabs of the 1955 year-class taken at Pierces Point and the Bay Shore Channel Bed, with a column showing the incidence of infestation

Date of collection	Number of infested oysters	Mean length of oysters in mm.	Total number of *Pinnotheres*	Range in carapace width in mm.	Mean carapace width in mm.	Incidence of infestation in per cent
			Pierces Point			
17- 9-55	167	13.8	279	0.6- 2.4	0.69	69.0
1-11-55	101	15.4	107	0.7- 2.1	1.35	60.1
5-12-55	175	18.1	185	0.7- 2.2	1.42	56.6
13-12-55	—	—	215	0.6- 2.0	1.31	—
4- 1-56	127	19.2	130	0.7- 2.2	1.46	64.8
25- 1-56	55	17.4	55	0.8- 2.1	1.51	56.1
23- 2-56	98	18.9	99	0.9- 2.5	1.52	56.4
22- 3-56	85	19.2	86	0.8- 2.2	1.50	43.6
7- 7-56	16	30.6	16	2.5- 4.7	3.10	11.7
			Bay Shore Channel Bed			
14-12-55	192	—	193	0.6- 3.1	1.54	68.3
6- 1-56	120	19.1	130	0.7- 2.6	1.47	72.8
4- 2-56	134	21.7	139	0.7- 2.7	1.59	72.4
5- 3-56	81	22.5	81	1.0- 2.8	1.75	55.1
18- 4-56	127	22.0	127	0.7- 3.2	1.79	52.9
3- 5-56	124	21.1	124	0.9- 2.6	1.63*	59.9
22- 5-56	96	22.6	96	0.9- 2.7	1.75	58.9
5- 6-56	103	24.9	104	0.8- 2.9	1.95	53.1
14- 6-56	110	25.0	110	1.6- 4.2	2.35	62.5
20- 6-56	100	25.4	100	1.1- 5.8	2.46*	58.1
6- 7-56	116	34.3	124	1.8- 7.8	3.64	41.1
11- 7-56	103	35.7	106	1.8- 7.7	4.03	35.7
18- 7-56	108	39.7	113	2.2- 9.2	5.18	35.0
26- 7-56	118	41.6	119	2.5- 9.6	5.76	33.1
1- 8-56	63	44.8	63	2.8- 8.6	6.24	35.0
16- 8-56	118	43.3	119	2.2- 9.6	6.60	28.9
12- 9-56	114	49.2	114	4.4- 9.8	7.41	33.6
9-10-56	100	51.7	100	5.2-10.0	7.68	34.4

* Measurements from formalin preserved specimens.

stages to a second paper. Consequently the present paper only includes such brief notes on the new instars, as well as the previously described stages, as is necessary to the understanding of the following account of the life-history and biology of the crab.

Laboratory experiments and observations were carried out to a limited extent, and some of the moulting experiments yielded valuable information. Holes were chipped in the ventral portion of oysters to insert crabs of known stage, sex and size with the hope that moulting might occur. Although only a small percentage of the crabs moulted, the method proved valuable since crabs kept in Petri dishes did not moult at all except in those cases where the crabs were obviously ready to moult on arrival to the laboratory. Oysters for the above purpose were generally collected from the upper parts of the Delaware Bay Natural Seed Beds where the percentage of oysters infested with the oyster crab was very low. Occurrence of moulting inside the oysters could be detected without opening them since the cast exoskeleton is ejected shortly after a moulting has taken place.

Growth Stages in Pinnotheres ostreum

As indicated earlier, the hard-shelled stage is not the first invasive stage. The true invasive stage is the first crab stage. Proof of this are the following facts: 1. The morphology of the first crab stage shows adaptations both for a free-swimming existence and for entering the host. 2. The first crab stage was found abundantly inside oysters but it was also collected in plankton samples in Delaware Bay. 3. While all subsequent stages were found inside oysters, no earlier stages, such as the megalopa which was suggested by Atkins (1954) to be the invasive stage in *P. pinnotheres,* were ever taken in the host animals.

In the following, therefore, Stauber's (1945) Stage I will be referred to as the *hard stage.* The new instars between the *invasive stage* and the hard stage will be called the *pre-hard stages,* a term which is arbitrarily defined as excluding the invasive stage. To avoid confusion with the earlier literature, and because we have not yet been able to assign pre-hard crabs to definite growth stages, we have adhered to the numbering of the *post-hard stages* as given by Stauber, except for the male in which we found that no post-hard stage exists. In addition to the following remarks, the summary of the main characteristics of all post-planktonic growth stages presented in Table II should be helpful to the reader.

Invasive stage

The mean size of the two crabs reared by Sandoz and Hopkins (1947) was 0.59 mm. while the mean of 183 specimens collected by us at Pierces Point on September 17, 1955 was 0.65 mm. with a size range from 0.59 to 0.73 mm.

The invasive stage is similar to the hard stage in many respects, which is remarkable considering that the pre-hard instars separating these two stages in the developmental cycle have a very different morphology. Both of these stages have a flat carapace, flattened pereiopods with thickened posterior borders, and long, plumose swimming hairs on the third and fourth pairs. They also have, in contrast to all other stages, two characteristic whitish spots visible both on the carapace and on the sternum. These spots seem somewhat larger in the invasive stage than figured by Sandoz and Hopkins, who apparently failed to note them on the dorsal side. However, in proportion to the size of the crab they are much smaller in the invasive stage than in the hard stage. These spots mark the ends of two solid, cylindrical rods connecting the dorsal and ventral side of the body. They consist of a very hard, opaque substance and serve as attachments for many muscles, which probably to a large extent are the heavy musculature needed for the quick swimming movements of the third and fourth pairs of pereiopods. When swimming, only these pereiopods are used while the other pairs, especially the fifth, are kept more or less motionless. Although not as soft-shelled as the pre-hard stages, the invasive stage is not nearly as firm as the hard stage.

We found that the males leave their hosts in the hard stage and proceed to enter other oysters for copulatory purposes, and indications are that the female also may change host under certain circumstances. It is, therefore, not to be wondered that the invasive stage has so many structural similarities common with the hard stage and differing from all other stages. They are all adaptive modifications instrumental for a free-living existence as well as for the invasion of the host.

Pre-hard stages

These are the hitherto undescribed instars between the invasive stage and the hard stage.

Morphologically these stages resemble post-hard crabs. Like these they have a rounded, soft-shelled carapace which yields to the touch. The pereiopods are slender and without swimming hairs. More especially they resemble the second stage described by Stauber (1945). In fact we cannot distinguish with certainty between the last pre-hard and the second stage crab. Although this reflects the morphological adaptation of these stages for life within the oyster, it is still remarkable considering that the very distinctive hard stage separates them in the developmental cycle. As the male seldom, if ever, develops beyond the hard stage, this problem of stage identification applies, however, mainly to the female. It is hoped that future comparative studies of a large number of young females may make a true distinction possible.

As the smallest hard-stage crab, a female, found in our large collection measured 1.3 mm., it seems fairly certain that all soft-shelled crabs smaller than this must be pre-hard crabs. The smallest specimen found measured about 0.75 mm., and several moults, probably at least four, occur with increase in body size and development of the pleopods before the crab moults into the hard stage.

The sexes are indistinguishable except for differences in genital openings and morphology and number of pleopods. By a careful microscopical examination of the latter it was possible to determine the sex of all crabs down to a size of about 0.9 mm. This meant that practically all but the first of the pre-hard stages could be sexed with certainty.

Stauber (1945) showed that hard-stage males were larger on the average than hard-stage females, and this is also true for pre-hard crabs. Admittedly the maximum size, and therefore also the mean, of pre-hard females cannot be stated as long as the last of these stages can be confused with the second stage. Nevertheless, it is bound to be considerably smaller in the female than in the male since the largest hard stage female found measured only 2.7 mm. as against 4.6 mm. for the largest hard-stage male.

The largest soft-shelled male measured 4.2 mm., but Stauber reported one measuring 4.8 mm. With some reservation he referred males of this type to a second stage following the hard stage as he pointed out that they could also be abnormal crabs. This could be due to some sort of parasitism as reported for *P. pisum* by Mercier and Poisson (1929). When these authors found two soft-shelled males they naturally regarded them as abnormal because they differed from the (hard stage) males normally found, and finding that these crabs were infested by the parasitic isopod, *Pinnotherion vermiforme,* they concluded that here was the cause of it. Furthermore, since the two mentioned males as well as an infested, normal male were larger than the uninfested males in their material, they also concluded that the parasite causes an increase in the size of the host. Later, however, Atkins (1933) thoroughly studied the same parasite and found that none of the 8 soft-shelled males in her material were parasitized, but, since such males were scarce, Atkins still regards them as being abnormal. She points out that the parasitized males found by Mercier and Poisson were not larger than many normal (hard stage) crabs. In view of our findings, it is obvious to conclude that these soft-shelled males are normal pre-hard crabs, but, for certain reasons given in the discussion, the possibility that a hard-stage male now and then moults into a soft-shelled crab cannot be omitted. The maximum size of pre-hard males given in Table II may therefore be too high. It should be noted, however, that Stauber's finding of a larger mean size for his soft-shelled than for his hard-stage males is probably due to a sampling error. His material included only 13 of the former specimens, and they were collected over a long period of time.

A few atypical crabs occurred in our samples which combined features from pre-hard and hard stage morphology. Some also had all the characteristics of the pre-hard stages except that the carapace did not yield to the touch. It was brittle, however, and cracked at the slightest use of force. It is hoped to return to the significance of these "abnormalities" in a second paper.

Hard stage

This is the stage described by Stauber (1945) as the invasive stage (Stage I). Many of its characteristics have already been given in the section on the true invasive stage, and there is little to add to Stauber's excellent description.

One point is of particular interest, *viz.* the two cylindrical rods connecting the dorsal and ventral sides of the body. The diameter of these structures is the same as that of the spots on the sternum, while the dorsal spots, as noted by Stauber, usually are somewhat larger and more oval in shape. In proportion to the size of the crab the diameter of a single rod is equivalent to between ¼ and ⅕ of the width of the carapace. Thus the rods account for a considerable part of the endophragmal skeleton. The rods are firmly embedded in the sternum but disconnect rather easily from the carapace.

The hard stage differs markedly from the equivalent stage of *P. pisum,* specimens of which we have had the opportunity to examine. The latter have an arched carapace, possess no spots or rods, and are equipped with long, plumose swimming hairs on all walking legs. Also in contrast to *P. ostreum* the fourth and fifth pairs of pereiopods appear to be the main appendages used in swimming (Darbishire, 1900).

Female hard-stage crabs ranged in size from 1.3 to 2.7 mm., thus slightly extending the range of 1.4 to 2.4 mm. found by Stauber. However, two abnormal females were found which measured 4.1 and 4.6 mm. They had evidently been retarded in development for one reason or another since one had precocious gonadal development with abnormal, gnarled pleopods, and the other had hairy, biramous pleopods which normally do not occur before the crab has moulted into the third stage.

The smallest hard-stage male measured 1.5 mm. or the same minimum as found by Stauber. The upper size range, however, was considerably extended. The largest specimen found by Stauber measured 3.4 mm. while we found many exceeding that size, the largest measuring 4.1 mm. Furthermore, the Bivalve Laboratory possesses a male collected by Mr. Franklin Flower in Delaware Bay on December 18, 1952 which we found to measure 4.6 mm. The fact that Stauber found a soft-shelled male measuring 4.8 mm. seemingly indicates that even larger hard-stage males may occur. As discussed earlier, however, such large soft-shelled males may be abnormal.

It was found that crabs which had reached the hard stage in their first fall, that is, less than two months after invasion of the host, were somewhat smaller on the average than those which had over-wintered in a pre-hard stage and did not develop into the hard stage before growth and development had commenced again the following spring.

Post-hard stages

These are the soft-shelled female growth stages described by Stauber (1945) as the second, third, fourth, and fifth stages, the latter being the mature crab.

They have a thin, membranaceous and rounded carapace which yields to the touch. The slender pereiopods are subcylindrical and possess no swimming hairs. The four stages are primarily differentiated from one another on the basis of the stage of development of the pleopods and the proportional width of the abdomen (Table II).

Stauber's second stage is not clearly defined as his material included a number of pre-hard crabs. Thus he mentions (p. 282) a specimen measuring only 0.9 mm. which could not possibly have been a second stage crab. This mistake was due to the firmly established belief that the hard stage was the invasive stage. Stauber's figures of the second stage, however, agree well with the morphology of the second stage crabs reared by us from the hard stage in the laboratory.

Judging by our data it seems certain that the minimum size of the second stage cannot be less than 1.3 mm. The maximum size, as well as the size ranges of the following growth stages in our collections, agrees fairly well with the figures given by Stauber, except for the fifth stage. Here we found a size range of 4.4 to 15.1 mm. as compared to Stauber's figures of 6.0 to 14.9 mm. All size ranges are given in Table II.

As also pointed out by Stauber, morphological variations occur, a fact which now and then makes it difficult to place a given crab in a certain growth stage.

Invasion of the Oyster and Survival of the Early Stages

As anticipated by Stauber (1945), invasion of the oyster in Delaware Bay takes place during late summer and early fall. In 1955 the first invasive stage crabs were noted on August 17th, but no oysters had been examined especially for the presence of *Pinnotheres* prior to that date. However, a careful check made through the spring and summer of 1956 again revealed no invasive stage crabs before the middle of August, *viz.* on August 16th. Nevertheless, scattered invasions no doubt occurred earlier as 1st stage zoeae were present in plankton samples on July 2nd,

TABLE II

Post-planktonic developmental cycle of Pinnotheres ostreum, based on the combined data of Stauber (1945) and the present authors

Stage of development	Range in carapace width in mm.	Most important external morphological characteristics	Biological factors
Invasive stage (First crab stage)	0.59–0.73	Flattened carapace and pereiopods. Posterior margins of pereiopods thickened, 3rd and 4th pairs have plumose swimming hairs. Two small, white spots on carapace and on sternum. Carapace hard around these spots.	Free-swimming until invasion of host. After invasion it is found in all parts of water-conducting system of the host.
Pre-hard stages	Male 0.75*–4.8 Female 0.75*–2.7*	Rounded carapacc. Thin, flexible exoskeleton. Slender pereiopods. No swimming hairs. Large females practically indistinguishable from 2nd stage crabs.	Found in all parts of the water-conducting system of the host.
Hard stage (I stage of Stauber, 1945)	Male 1.4–4.6 Female 1.3–2.7	Carapace flattened and very hard. Flattened pereiopods with posterior margins thickened and with plumose swimming hairs on 3rd and 4th pair. Two large, white spots on carapace and on sternum. Males larger on the average than females.	Found free-swimming and in all parts of water-conducting system of the host. Copulatory stage. Males die in this stage.
Stage II	1.3*–3.1	Rounded carapace. Thin flexible exoskeleton. Slender pereiopods. No swimming hairs. Abdomen wholly contained in sternal grove. No hairs on pleopods.	Never free-swimming. Predominantly, possibly always, found only on the gills of the host.
Stage III	2.6–4.4	Edges of abdomen extend beyond depression in sternum. First two pairs of pleopods clearly segmented and supplied with a few hairs.	Only found on the gills of the host.
Stage IV	3.6–8.9	Relative width of abdomen larger than in preceding stage, just reaching coxae of pereiopods in most cases. Pleopods almost fully developed and well supplied with hairs.	As in 3rd stage.
Stage V (Mature female)	4.4–15.1	Abdominal edges covers coxae of pereiopods. Pleopods fully developed. The orange gonads may be seen through the thin carapace.	As in 3rd stage.

* Approximate measurements.

and the laboratory studies by Sandoz and Hopkins (1947), as well as our field data, show that only about 25 days or less are required from hatching to the development of the first crab stage, now known also to be the invasive stage. Invasions of oysters in Delaware Bay prior to the middle of August are, however, with little doubt on a very limited scale, at least in years with normal environmental conditions. This is also indicated by the fact that a distinct peak period of invasions occurs in early September. On August 22nd in 1956 only 3 crabs were found in 244 spat collected at Pierces Point, while 136 crabs were found in 199 spat collected on the same ground on September 23rd. Also, of 279 crabs collected there on September 17, 1955, 244 were still in the invasive stage, which indicates that a very recent mass invasion had taken place.

Since the peak period of oyster setting in Delaware Bay generally is in July, most spat will have grown sufficiently large to harbor one or more crabs by the peak of crab invasions.

It is not clear how late in the year invasions may occur as a few invasive stage crabs were found in oysters during all of the winter months. However, since growth and development stops about November 1st (Fig. 1), these crabs were probably late invaders retarded in their development by winter conditions. In 1956 a few ovigers [3] were collected as late as the middle of October. And in 1942, Stauber (1945) collected an ovigerous female as late as October 19th. The embryos were then almost ready to hatch and the first zoeae were liberated 4 days later. Whether the zoeae are able to carry through metamorphosis to the first crab stage that late in the year is perhaps doubtful. The bottom water temperature of Delaware Bay generally falls to about 15° C. by November 1st and to about 5° C. by December 1st, and as it appears that the young immature crabs do not grow and develop at temperatures below the first mentioned level (Fig. 1), the larvae probably do not either.

Surprisingly small spat may be invaded. Thus infested spat of less than 10 mm. in length were often found, and in one case a spat measuring only 4.2 mm. contained two crabs. Up to 7 invasive stage crabs were found in a single spat.

Stauber (1945) observed hard-stage crabs attached to the margin of oysters with their posterior ends towards the bill. This same orientation was also noted for the invasive stage in our laboratory experiments. As free-living crabs are also known to enter enclosures backwards, *Pinnotheres* probably enters its host with the posterior end first.

Once the crab has successfully invaded its host it may be found anywhere in the water conducting system of the oyster where it may stay while developing through to the hard stage, while later stages are found only on the gills. Next to these, the promyal and suprabranchial chambers are the areas usually inhabited by crabs of the early stages.

A preference to invade spat and, secondarily, yearlings rather than older oysters seems apparent from several types of observations. On August 23, 1956 only a single 1956 crab was found in 684 yearling oysters collected in the Cohansey River Cove while the few spat present were all infested, a couple of them with more than one crab. The only extensive comparative data, however, are from the Bay Shore Channel Bed where there was a heavy set of both oysters and crabs in 1956 as there had been in 1955. Two collections, each consisting of three different age groups of oysters were taken (Table III). One was taken on September 12th during the peak invasive period and the other was taken on October 9th. The oysters were all collected in the same dredge hauls, and nearly all the spat were taken directly from yearlings and older oysters.

[3] Oviger = ovigerous female. Term adopted from Ryan (1956).

As seen in Table III, only 21.5% of the older oysters were infested with 1956 crabs on September 12th, while 54.6% of the yearlings and no less than 76.7% of the spat were infested with crabs of that year class. On October 9th the differences were not so striking, a fact to which we return later.

A good number of the yearlings and older oysters were already infested with mature crabs when the 1956 set of crabs occurred (Table III, column 4). This could possibly have been one of the reasons for the preference indicated to invade spat, since the latter for obvious reasons were not already infested. Oysters with and without mature crabs were, however, invaded by 1956 crabs to about the same extent.

Possibly the preference to invade spat is more apparent than real. Failure of hard-stage crabs to invade older oysters was in some cases noted by Stauber (1945), indicating that the invasion is not always easily accomplished. Even if it is, the yearlings and especially the older, larger oysters may possibly still be able to cope with a good number of the tiny invasive stage crabs by enveloping them in mucus and pass them out by ciliary action and clamping of the valves.

TABLE III

Comparison of infestations with P. ostreum in three different age groups of oysters on the Bay Shore Channel Bed during and after the main invasive period

Date of collection	Age group of oyster	Number of oysters examined	Per cent infested with 1955 or older crabs	Per cent infested with 1956 crabs	Per cent of 1956 crabs in hard or post-hard stages	Per cent oyster with two or more 1956 crabs
Sept. 12th, 1956	Spat	167	0.0	76.6	3.1*	31.1
	Yearlings	339	33.6	54.6	47.3*	15.3
	Older oysters	186	50.0	21.5	90.0*	4.3
Oct. 9th, 1956	Spat	180	0.0	77.2	20.9	7.8
	Yearlings	289	34.4	72.7	73.9	27.3
	Older oysters	117	51.3	52.1	82.6	15.4

* An asterisk indicates that only hard stage crabs were found.

Mytilus edulis has been observed to expel inserted megalopa of *P. pinnotheres* by Atkins (1955).

A comparison of the data in Table III, column 5, reveals that the incidence of oysters infested with 1956 crabs rose considerably for the yearlings and older oysters between the two sampling dates while it remained practically constant for the spat. In fact, the absolute number of crabs decreased in the latter group while it increased even more in the other two age groups than the data in column 5 indicate. This is seen in column 7, which shows that the incidence of multiple infestations with 1956 crabs decreased sharply in the spat from 31.1 to 7.8% but increased in the yearlings from 15.3 to 27.3%, and in the older oysters from 4.3 to 15.4%. Considering that the crabs apparently prefer to invade spat these data seem somewhat contradictory. An analysis of these and other data indicates, however, that the apparent paradox can be explained as being due to a higher mortality rate in crabs invading spat than in those invading yearlings and older oysters.

As stated above, only the absolute number of crabs found in spat decreased while the percentage of spat infested remained constant. In other words, the decrease in number of crabs between the two sampling dates was apparently either due to the death or the migration of crabs from spat containing more than one crab. Losses among "single" crabs possibly also occurred; if so, they were made up for by intermittent new invasions of crabs. The same trend that only one crab will survive in the same spat was also noted in 1955 at Pierces Point as well as on the Bay Shore Channel Bed. Only during the peak invasive period in September could spat with 3 and up to 7 crabs be found. A few weeks later only double infestations could be found, and the incidence of their occurrence was less than 10%. By the end of February, 1956 practically no spat contained more than one crab, and even a good number of "single" crabs apparently died during that month (Table I, Fig. 5). These mortalities came after a prolonged period of very low temperatures (Fig. 1), thus indicating that even "single" crabs are easily endangered by adverse environmental conditions.

The increase in number of yearlings and older oysters containing more than one 1956 crab between the two sampling dates (Table III) indicates in itself that the crabs survive better in these oysters than in spat. Further evidence of this is given in the same table (column 6). For both dates it is seen that a much lower percentage of the 1956 crabs had reached the hard and post-hard stages in spat than in the other oysters. This fact, together with the data given on crab-host size relationship in a later section, clearly shows that the crabs grow and develop considerably slower in spat than in larger oysters. In other words, the crabs thrive better in yearlings and older oysters, and it is therefore not surprising that they also survive better. The reasons for this will be discussed later. It is stressed, however, that a quicker rate of growth and development is probably in itself of prime importance for the survival of the crab during its first fall and winter since it is very likely that the earliest stages cannot withstand adverse conditions as well as later stages.

In summing up the data in Table III it may be concluded that intermittent invasions of crabs between the two dates, and a higher mortality rate of crabs invading spat than of those invading other age groups of oysters, constitute the main reasons why the yearlings and older oysters in direct contrast to the spat showed an increase in incidence of infestation on October 9th.

It was also considered whether the data in Table III could be at least partly explained by migrations of hard-stage crabs from spat to other oysters. However, since all the observed differences between the two sampling dates can be explained otherwise, while migrations could explain only little of it, the latter probably did not take place to any large extent. Furthermore, the available data indicate that the "loss" of crabs inhabiting spat occurred at a time when only few of these crabs had developed into the hard stage, *i.e.,* before these crabs were capable of migrating.

Growth and Development

Unless otherwise stated the following statements and discussion of results are based on studies of populations of *Pinnotheres* growing and developing in spat. This point should be kept in mind, because, with other factors being equal, growth and development would differ, depending on the size and age composition of the host population of oysters.