OBSERVATIONS ON THE BIOLOGY, ECOLOGICAL RELATIONSHIPS, AND GROWTH

OF THE CURVED MUSSEL, BRACHIDONTES RECURVUS (RAFINESQUE),

IN THE UPPER CHESAPEAKE BAY

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INTRODUCTION

The hooked or curved mussel, _Brachidontes recurvus_ (Rafinesque) is one of the important fouling organisms present on oyster bars in Chesapeake Bay. It has been reported by Frey (1946) as forming much of the cultch on oyster bars in the Potomac River, where most of the marketable oysters were completely covered with mussels. As a result, the oysters were misshapen and twisted from growing among the mussels. Beaven (1947) reported that this species is most abundant on the bars of the upper portion of the Bay and its tributaries, where the salinity is low. While he is of the opinion that it is of minor importance as a hindrance to oyster setting, he does point out that in many cases, a bushel of marketable size oysters will be found to consist of one half bushel of oysters and one half bushel of mussels. Needless to say, this condition will greatly lower the market value of the oysters produced on a bar.

Brachidontes recurvus is a pelecypod mollusk belonging to the family Mytilidae, which is represented in Chesapeake Bay by three species: _Mytilus edulis_ Linnaeus, the edible mussel, occurring as far north as the York River (Galtsoff, Chipman, Engle, and Calderwood 1947); _Volsella demissus_ Dillwyn, the ribbed mussel, growing in marsh areas and the intertidal zone throughout the Bay (Mackin and Menzel 1945, Frey 1946, and Allen and Littleford in press); and _Brachidontes recurvus_ (Rafinesque), the species under discussion, occurring on oyster bars in the upper Bay and its tributaries.

Under the name of _Mytilus recurvus_, this species has been reported by Nelson (1928) as occurring along the New Jersey Coast. Chestnut (1949) noted the occurrence of the curved mussel in North Carolina. Engle (1945) observed that the hooked mussel, _Mytilus hamatus_ Say, was present on oyster bars in Alabama, and later (1948) the same investigator reported the presence of this species on bars in Mississippi and Louisiana. The above observations may be summarized by the statement that the hooked or curved mussel occurs on oyster bars along the Atlantic Coast from New Jersey and Chesapeake Bay southward, and throughout the Gulf of Mexico.

Since this mussel has been referred to under several names in the literature, it is pertinent that its taxonomic position be clarified. The species name _recurvus_ was used by Rafinesque (1820) to designate the hooked mussel which he collected from the vicinity of New Orleans. His original description follows:

> Espèce Mytilus recurvus moule recourbée. Test obovale, cunéiforme, recourbé, à stries longitudinales de trois longueurs; épiderme noirâtre; nacre-violette; becs obliques, à un angle décurrent de chaque côte; bord inférieur et intérieur strié crénate; largeur 7 - 12, diamètre 5 - 12, de la longueur, longueur 1 à 2 pouces. Elle se trouve dans le Mississippi près de la Nouvelle-Orléans. Les stries sont souvent bifides. Partie bâillante oblongue, latérale.

Say (1823) described the same species, which he designated as _Mytilus hamatus_. However, the name _recurvus_ of Rafinesque takes priority over the name _hamatus_ of Say by three years, and therefore is the correct designation of the species.

Swainson (1840) separated certain species from the genus _Mytilus_ and placed them in a new genus, which he designated as _Brachidontes_. He described this genus as follows: "umbones prominent, not term-

inal, valves corrugated; hinge margin considerably angulated; teeth many, small, crenate." Since the species _recurvus_ has the generic characteristics of _Brachidontes_, the correct designation of the curved or hooked mussel is _Brachidontes recurvus_ (Rafinesque).

Despite the wide distribution of this species and its importance as a fouling organism on oyster bars, a survey of the literature reveals that with the exception of the observations on distribution previously mentioned, information is not available regarding its biology and ecological relationships. This situation is in sharp contrast to that existing in regard to other mussels, such as _Mytilus edulis_, _Mytilus californianus_, _Volsella demissus_, and _Volsella_ (_Modiola_) _modiolus_, where considerable information is available on numerous aspects of the biology and ecology of the individual species.

The purpose of this study, therefore, has been to determine certain aspects of the distribution, ecology, development of the gonads, spawning period, and growth of _Brachidontes recurvus_ (Rafinesque) in Chesapeake Bay.

This investigation has been part of a cooperative program between the Department of Zoology of the University of Maryland and the Shellfisheries Investigations of the United States Fish and Wildlife Service, located at Annapolis, Maryland. Appreciation is expressed to Dr. R. A. Littleford for the suggestion and direction of the problem; to Mr. James B. Engle and Staff, of the Fish and Wildlife Service, for the collection of materials and data on temperature and salinity; and to Dr. J. P. E. Morrison, Associate Curator, Division of Mollusks, of the U. S. National Museum, for the identification of mollusks and for numerous suggestions in regard to the problem.

MATERIALS AND METHODS

The specimens of _Brachidontes recurvus_ used in this study were collected from Hackett's Bar, which is located on the western side of the Bay, approximately 2 nautical miles north of the mouth of the Severn River. Hackett's Bar is one half to three quarters of a mile offshore from Hackett Point, in water that varies from 2 to 35 feet in depth. Regular collections of mussels were made from this bar from January 16, 1950 to April 16, 1951. An effort was made to collect samples at two-week intervals during this period, but because of weather conditions and mechanical difficulties with the boat, this was not always possible. All mussels were collected with a standard oyster dredge, from the same area on the bar, at a depth of 16 feet.

The mussels were brought to the laboratory within 24 hours after collection. They were removed from the oyster shells, separated, the byssal threads removed, and then were scrubbed with a steel brush to remove any fouling organisms, such as bryozoans and barnacles. After being carefully washed, they were wiped dry before weighing.

With the shell closed and the specimen held in a lateral position (Newcombe 1936), shell dimensions were measured to the nearest tenth, using a sliding vernier caliper calibrated in millimeters. The definitions of the dimensions used are as follows: length, the greatest distance between the anterior and posterior ends of the shell; width, the greatest distance between the dorsal and ventral edges; and thickness, the greatest distance between the right and left valves.

Total weight, shell weight, and the weight of the soft parts, or wet weight, were determined in grams to the second place. The soft parts were placed in calibrated vials and dried to constant weight at a temperature of 80° Centigrade. Dry weights were carried to the fourth decimal place. All weights were determined by use of an analytical balance.

From each collection made between March 3, 1950 and April 16, 1951, specimens of the entire size range available were selected for microscopic study. These individuals were fixed within the shell by cutting the posterior muscles and then dropping the entire animal into Bouins Alcoholic Fixative (Galigher 1934). After fixation for several days, they were removed from the shell, washed in 70% alcohol, and stored in 80% alcohol. The mussels were dehydrated in alcohol and xylol, and imbedded in tissue mat having a melting point of 54-56° Centigrade. Sections were made at 10 micra, and stained with either Harris' haematoxylin and eosin or Mallory's Triple stain. The staining procedures outlined by Galigher (1934) were followed throughout. After staining, the slides were dehydrated in alcohol, cleared in xylol, and mounted in neutral balsam.

Plankton samples were collected simultaneously with the collection of mussels, by pumping 100 liters of water from just above the Bar through a No. 20 silk plankton net. Each sample was concentrated to 100 ml. and preserved with formalin. Examination of the plankton samples to determine the presence or absence of mussel larvae was made with a Sedgewick-Rafter Cell. The procedure outlined by Littleford, Newcombe, and Shepherd (1940) was followed.

Temperature of the water was obtained by use of a Wecksler re-

versing thermometer and the temperature was recorded in degrees Centigrade. Water samples were collected with a Foerst Water Bottle and the sample placed in a citrate bottle and returned to the laboratory. Salinity was calculated from Chlorinity determined by titration with silver nitrate, following the standard method of Mohr (1856).

Methods used in the analysis of the population and in conducting a survey of the entire Bar are discussed under the proper headings in the observations.

OBSERVATIONS

The curved mussel, _Brachidontes recurvus_, may be distinguished from the other members of the family Mytilidae which are found in the Bay by the rather distinct shape of the shell. The shell of this species is elongate and equivalve, with both valves making complete contact with each other except at the aperture where the byssal threads are extruded. The umbo is narrow and curved toward the ventral surface, giving the shell a beak-like appearance (Fig. 1). The valves are joined at the anterior extremity by the hinge ligament, which extends posteriorly approximately one third the length of the shell, in an almost straight line. The dorsal edge of the shell then bends convexly, straightening out before it reaches the posterior margin, where it curves around to the ventral surface. The ventral surface, as a result, is concave, giving a greater prominence to the umbo region. There is a small rounded elevation on the lateral areas of the umbo.

Numerous striations or ridges completely cover each valve. They originate at the extreme anterior portion of the valve, and radiate in a fan-like arrangement to the edge of the shell. A pronounced ridge is found on the latero-ventral surface of the shell, extending from the umbo region for about two thirds of the total length of the shell. A heavy periostracum completely covers the shell. Under natural conditions, the shell appears to be dark gray, or even black, in color, but upon drying it turns a brown or

Fig. 1. From left to right: <u>Volsella demissus</u> (Dillwyn), <u>Brachidontes recurvus</u> (Rafinesque), <u>Mytilus edulis</u> Linn. Actual lengths are 94.5 mm., 47.7 mm., and 84.3 mm. respectively.

dull gray.

The periostracum at times has dark lines marking the rings that follow the contour of the shell from the dorsal to the ventral edge. These rings may or may not be of significance as regards the age of the individual. The maximum sized mussels encountered in this investigation had attained a length of 62.9 mm. The shell width and thickness of the individuals was observed to vary considerably, depending upon their position in the clusters. This fact also makes a difference in the degree of concavity of the ventral surface of the shell.

The inner surface of the shell varies in color from a grayish purple iridescence to a white margin on the edge. Often there is a reddish purple band all the way around the shell except in the region of the hinge, where the color fades to a paler hue, even to a pink. In this species, the nacreous layer extends nearly to the edge of the shell, even the muscle scars appearing iridescent. The part of the shell containing the body of the animal has a dull white deposit superimposed on the nacreous layer. The entire inner surface of the shell is delicately colored.

The striations observed externally are clearly visible on the inner surface, where they are distinct at the edge of the shell, less pronounced as they approach the umbo, and become invisible in the umbo region. The hinge teeth are small and numerous.

The muscle scars or impressions are easily distinguishable. Two small, more or less spherical scars mark the attachment of the anterior and posterior retractor muscles. The anterior retractor is attached to the dorsal anterior end of the shell, and

the posterior retractor is attached to the dorsal posterior end of the shell. Both are inserted very close to the margins of the shell, with the anterior retractor reaching the extremity. The posterior adductor is marked by a nearly spherical scar at the posterior end of the dorsal region of the shell, posterior to the attachment of the retractor which it joins. An elongate scar at the anterior end of the ventral edge marks the attachment of the anterior adductor muscle. A linear scar which follows the curvature of the posterior of the shell is the attachment of the muscles of the anal membrane. A long narrow scar extending ventrally from the posterior scar and terminating at the umbo marks the attachment of the pallial muscles.

Anatomy. Since the gross and microscopic anatomy of the curved mussel is identical with that of Mytilus edulis as described by Field (1922), no extensive description of the anatomical structure appears to be desirable. However, the more pertinent observations on the gross anatomy, so often used taxonomically, are worthy of mention.

Brachidontes recurvus is enclosed in a mantle which is held to the shell on its outer edge by the pallial muscles. The periostracum, which grows out from the middle fold of the mantle, is in direct contact with it.

The gills consist of two branchial folds located laterally on each side of the viscera, from which they extend ventrally. Each fold consists of an outer and inner lamella, which in turn are composed of filaments. Sections of the filaments demonstrate the presence of lateral, frontal, and latero-frontal cilia on each

filament. The food grooves are located on the ventral edge of the outer and inner lamellae. These grooves are lined throughout their entire length with cilia.

Excurrent and incurrent siphons, as such, are not present in the mussels. The exhalent siphonal opening lies dorsal to the branchial membrane and is surrounded by a tough ring of heavily pigmented tissue, which is brown in color. The space between the mantle lobes lying just below the exhalent siphonal opening corresponds to the inhalent or incurrent siphon of lamellibranchs.

Two pair of labial palps, an inner and outer pair, are observed on the anterior end of the mussel. The ridges of the palps are ciliated and lead directly into the mouth. A short esophagus connects the mouth with the stomach, which has the inner surface lined with cilia and thrown into numerous folds, forming pockets. The crystalline style, which may be recognized by its characteristic appearance, is found in the stomach. The intestine extends from the stomach as a long, oval-shaped tube which runs posteriorly and then bends anteriorly, and finally runs posteriorly again through the pericardial cavity to terminate at the anus, which is located on the dorsal posterior end of the mussel. The inner surface of the intestine is ciliated, and often shows an indentation, which is usually lateral in position.

The alimentary tract is surrounded by the visceral mass, which contains the other organ systems of the animal. Immediately surrounding the stomach and intestine is the so-called liver, or digestive diverticula. The latter structure also extends into the mesosoma, which is an elongate ventral extension of the visceral

mass, except during the period of gonadal development, when the mesosoma is filled with the gonad tissue of the animal.

The foot is small and greatly reduced. The byssal pit is located just posterior to the foot. The byssal threads, with their end plates, are secreted by the byssal gland, which is located at the base of the pit.

Distribution. Previous to this investigation, Frey (1946) reported the presence of Brachidontes recurvus on the oyster bars of the Potomac River, and Beaven (1947) stated that the curved mussel was most abundant in salinities which are low, and was thus found in the upper portion of the Bay and its tributaries. He also stated (Personal Communication) that this species was found between salinities of 8 to 12 o/oo, and therefore was absent in the upper areas of the Bay where the salinity is much lower than 8.00 o/oo. On the basis of oyster surveys conducted during the past three years, J. R. Webster, of the Shellfisheries Laboratory in Annapolis (Personal Communication), reported that this mussel was found on the Western Shore from the Potomac River to the Upper Bay, and on the Eastern Shore from Tangier Sound to the Upper Bay. On both the Western and Eastern Shores, the mussels were most prevalent in the tributaries of the Bay proper.

In the course of this study, the distribution of the curved mussel was investigated in the vicinity of Crisfield, located on the lower Eastern Shore of the Bay. In that area, this species was found occasionally on the oyster bars of Pocomoke and Tangier Sounds. On the other hand, it was observed to be very abundant on the beds located in the Manokin, Nanticoke, and Choptank Rivers.

On the Western Shore, the curved mussel was found to be abundant on all oyster beds investigated, from the Patuxent River to Sandy Point. Because of its abundance on Hackett's Bar, which is located 2 nautical miles north of the mouth of the Severn River (Fig. 2), this population was chosen for detailed study.

The relative abundance of the mussel population on any individual bar was observed to vary from year to year. In some cases, a bar which was well populated one year would show a very sparse population one or two years later. This observation is substantiated by those of R. V. Truitt, of the Chesapeake Biological Laboratory at Solomons (Personal Communication), extending over a period of many years on the oyster beds of the Patuxent River.

From the above information, it may be concluded that Brachidontes recurvus is widely distributed on oyster beds in the Upper Chesapeake Bay and its tributaries between salinities of 12.00 o/oo and at least 8.00 o/oo. While this species has not been reported from the lower Bay, its occurrence in this area should be expected, since it has been reported from southerly coastal areas where the salinity is as high as 30.00 o/oo (Chestnut 1949, Engle 1945 and 1948).

ECOLOGY

Chesapeake Bay has been described by Cowles (1930) as a rather shallow tidal estuary, with a salinity ranging from approximately 30.00 o/oo at the mouth to 6.00 o/oo at the head. The greater portion of the bottom of this estuary is mud, although a few rocky areas exist.

Hackett's Bar is located in the upper region of the Bay on the Western Shore, approximately two nautical miles above the mouth of the Severn River. This bar is situated approximately three quarters of a mile south of Hackett Point, in close proximity to Mill and Whitehall Creeks. The Bar consists of hard bottom, and has a depth range varying from 2 to 35 feet (Fig. 2).

During the period from January 16, 1950 through April 16, 1951, while the mussel population of the bar was under investigation, the bottom salinity at Hackett's showed considerable fluctuation (Table I). The highest salinity of 16.24 o/oo was recorded on October 9, 1950, and the lowest salinity of 2.85 o/oo on February 19, 1951. From the graphical presentation of salinity in Fig. 3, it will be observed that the lower salinities occurred during the spring and summer, whereas the higher salinities prevailed during the fall and winter. The extremely low salinity of February 1951 may be considered unusual. It contrasts sharply with the higher value of 11.60 o/oo of the previous year. Significantly, this low salinity, which was apparently the result, in part at least, of unusually heavy spring rains, was accompanied by an excessive mor-
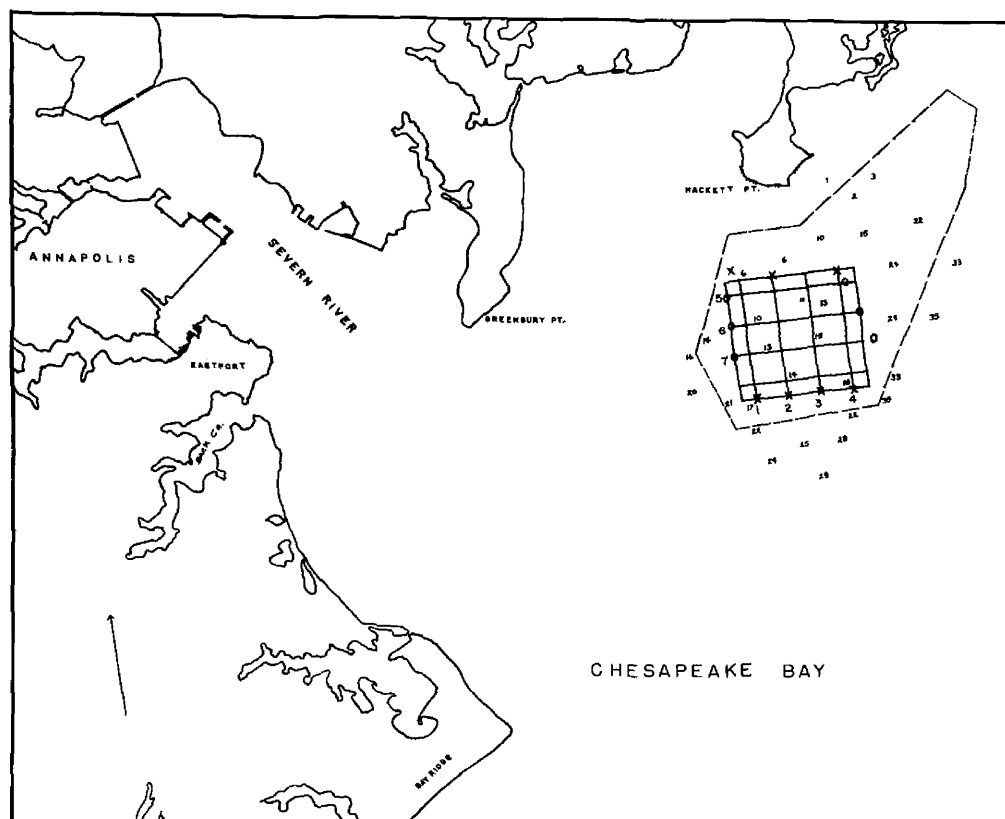
Fig. 2. Outline map showing the location of Hackett's
Bar. The grid designates the planned area covered in
the population survey on October 17, 1951. S-N runs.
are 1, 2, 3, 4; W-E runs are 5, 6, 7.

tality of the mussels, which practically wiped out the entire
adult population.

The data on bottom temperature for the same period are pre-
sented in Table I. The range of temperature was between 1.8° to
24.5° C. As would be expected, the higher temperature prevailed
during the summer period and the lower temperature during December,
January, and early February of each year. The graphical presenta-
tion of the temperature data may be observed in Fig. 4.

Growth Habits. The curved mussel grows in clusters attached
to the shells of living oysters; on single valves, planted on the
bar as cultch; and on "boxes". The oysters are often completely
covered with mussels, one valve supporting several hundred. By
means of the byssal threads and their end plates, the mussel
attaches with the umbo or anterior end of the shell pointing down-
ward and the posterior end of the shell rising vertically (Fig. 5).
The largest mussels are usually located in the center of the cluster,
with the smaller mussels graduating toward the periphery of the sub-
stratum. The adult mussels are attached toward the anterior end of
the oyster shell, away from the open valves.

The spat set in cracks, perforations, crevices, or depressions
on the oyster shell, as many as 15 to 20 individual spat having
been observed adjacent to each other in crevices less than one
half inch in length. Some of the set may be noted attached to
larger mussels. Usually, in such cases, the attachment is near
the center of the cluster. Large numbers of spat attach in the
crevices between the junctions of the shells, in those cases where
several oysters are found fused to one another. If the spat sets

TABLE I

BOTTOM TEMPERATURE AND SALINITY AT HACKETT'S BAR
JANUARY 16, 1950 THROUGH APRIL 16, 1951

Date	Temperature ° C.	Salinity o/oo
1950 – Jan. 16	6.8	10.10
Feb. 16	5.7	11.60
Mar. 1	2.7	13.60
13	3.6	12.70
27	6.1	9.30
Apr. 10	7.0	5.20
24	10.3	7.50
May 8	13.6	7.90
22	13.3	10.10
Jun. 5	17.7	8.00
19	19.0	8.64
Jul. 3	22.5	9.64
17	23.5	9.63
31	24.5	8.51
Aug. 14	23.5	12.05
28	24.3	13.44
Sept. 11	22.8	10.75
25	20.4	15.41
Oct. 9	19.5	16.24
25	17.4	15.81
Nov. 13	11.6	13.28
27	7.2	8.86
Dec. 11	6.8	8.77
1951 – Jan. 2	3.1	7.48
15	3.6	9.47
29	2.1	3.84
Feb. 5	2.1	3.48
19	1.8	2.85
Mar. 5	5.3	6.91
19	5.2	8.21
Apr. 2	8.4	5.44
16	9.6	5.84
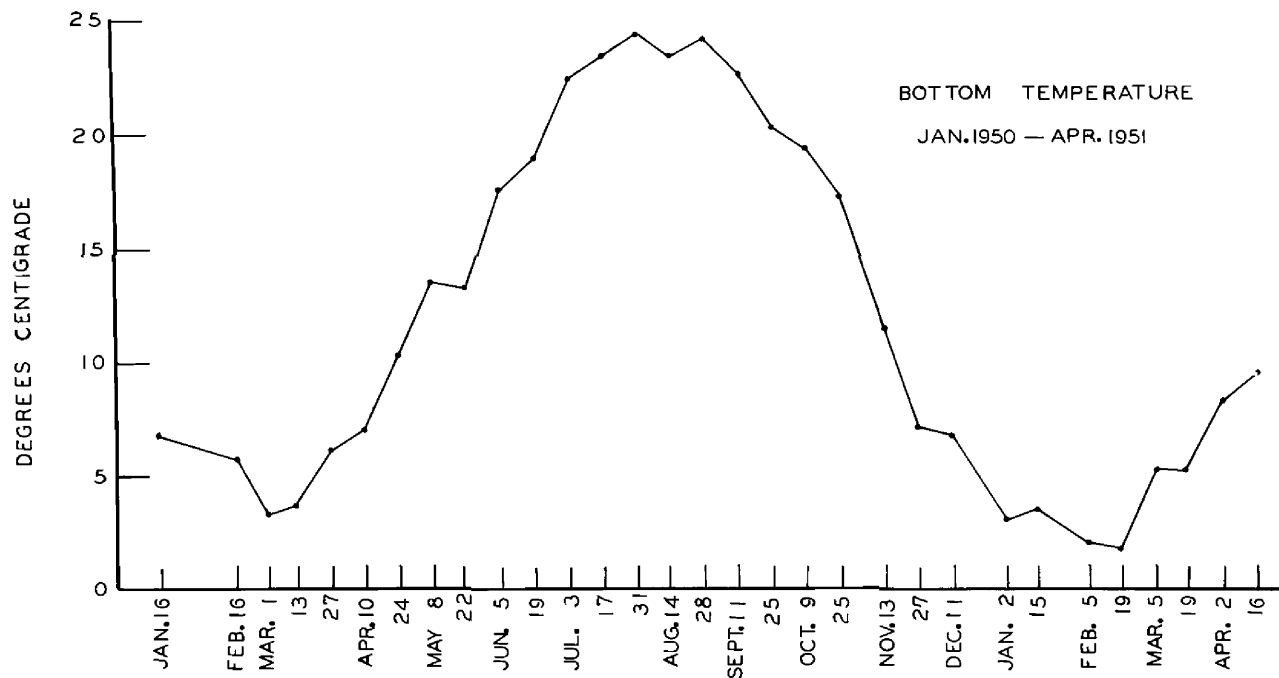
Fig. 3. Bottom temperature of Hackett's Bar from
January 16, 1950 through April 16, 1951.
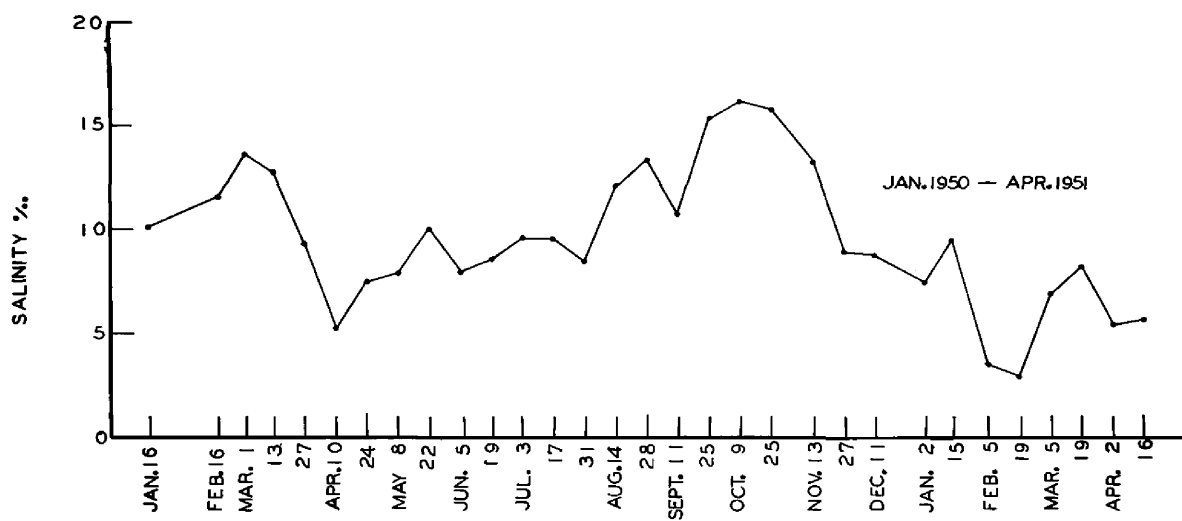
Fig. 4. Bottom salinity of Hackett's Bar from
January 16, 1950 through April 16, 1951.

Fig. 5.   Small group of mussels attached to oyster
shell.

on unprotected areas of the shell, it takes a lateral position
and appears to have attached horizontally.

Some of the individual mussels are misshapen as a result of
crowding in the clusters, and considerable variation in shell
width and curvature is associated with this crowded condition.

Size Variation and Density of the Population. Length measure-
ments of 2,941 mussels, not including those of a survey of Hackett's
Bar made on October 17, 1951, showed that the maximum size at-
tained was 62.9 mm. in length. The length-frequency distribution
and percentage of the population is presented in Table II.

An analysis of the data presented in Table II demonstrates
that 21% of the population has a size range between 0.00 and 30.00
mm., while 38% of the population is between 30 and 39.99 mm., and
32% of the population is between 40.00 and 59.99 mm. in length.
Approximately 10% of the population has a size range above 50 mm.
in length, with only 0.2% being above 60 mm.

In the data on distribution of the mussels, no significant
variation in size is observed in association with the dates of col-
lection. The larger number of small mussels observed in January
1950 would be expected since, as is reported later, the period of
setting extends late into the fall. Similarly, it should be noted
that the collection from July 1950 precedes by approximately two
months the time of attachment of the majority of the mussel spat.
On the other hand, the absence of small mussels in the April 1951
collection may be associated with the widespread mortality noted
in the mussel population at that time.

TABLE II

LENGTH-FREQUENCY DISTRIBUTION
OF THE POPULATION

LENGTH INTERVAL IN MM.	January 16 1950	July 17 1950	April 16 1951	TOTAL NUMBER MUSSELS	PERCENT TOTAL POPULATION
	NUMBER OF INDIVIDUALS				
0.00 - 9.99	49	9	0	58	1.97
10.00 - 19.99	42	19	45	106	3.60
20.00 - 29.99	141	156	101	398	15.53
30.00 - 39.99	330	504	292	1,126	38.28
40.00 - 49.99	238	532	192	962	32.71
50.00 - 59.99	57	175	52	284	9.65
60.00 - 62.99	0	6	1	7	0.23
TOTAL	857	1,401	683	2,941	

DATE:-

On the basis of the data presented in Table II, it is suggested that the life span of _Brachidontes_ _recurvus_ extends over a period of five years, with the exception of a small number of individuals that survive somewhat longer. The existence of such a short life span probably accounts for the yearly variation in relative abundance of the mussel population on oyster bars.

One of the important problems associated with the fouling of oysters by _Brachidontes_ _recurvus_ is the number of individuals that attach and survive on individual oysters. A count of the number of mussels present on a single valve of an oyster shell was made on over 300 individual valves. The results of this observation showed that between 8 and 251 individual mussels may be attached to a single valve.

In order to ascertain the density of the mussels on an oyster valve, the total number of mussels enumerated was divided by the number of valves. On this basis it was found that an average of 102.5 mussels was attached to a single valve.

In an effort to determine whether a relationship existed between the size of the oyster shell valve and the number of mussels present, 24 valves, covering the size range observed, were selected at random. The relative size of these valves was obtained by determining the greatest length and width of the valve in mm. The number of mussels on each of the valves measured was then counted. The results are presented in Table III.

On the basis of the results in Table III, it becomes obvious that a relationship between the size of the substratum and the number of mussels does not exist. Considering the fact that the

TABLE III

RELATIONSHIP BETWEEN THE SIZE OF THE
OYSTER SHELL VALVE AND THE NUMBER OF MUSSELS

SIZE OF VALVE IN MM.	NUMBER OF MUSSELS	SIZE OF VALVE IN MM.	NUMBER OF MUSSELS
35 x 35	35	90 x 48	94
55 x 45	23	92 x 56	62
55 x 50	35	94 x 55	60
60 x 45	82	100 x 60	108
63 x 40	15	100 x 90	40
65 x 40	128	105 x 65	186
78 x 56	127	112 x 70	125
80 x 53	67	113 x 60	48
85 x 40	90	115 x 70	251
85 x 65	183	115 x 75	166
86 x 55	227	120 x 75	155
87 x 62	81	120 x 80	101

oysters grow at many different angles on the bar and thus present different areas of actual surface available for attachment, such a result is not unexpected. Consequently, a small oyster with its entire valve surface exposed has a greater area of available surface for setting than does a larger oyster which, because of its position on the bar, has a limited surface area available.

The surface area of the individual valves was determined by use of the planimeter (Gray 1909, Wheatley 1903). The number of mussels present on the valve was then divided into the surface area so obtained, in order to determine the density of the population per unit of area. The resulting figures show that the greatest density of the population was 1 mussel per 7.6 square mm. of area, as compared to the lowest density of 1 mussel per 225 square mm. The average density for the entire 24 clusters reported in Table III was 1 mussel for every 44 square mm. of surface area.

In order to determine the variation in population density with respect to depth on the oyster bar, a survey of Hackett's Bar was carried out on October 17, 1951. This particular date was chosen in order to include the set of mussels for 1951, and also to determine the extent of the mortality of the mussel population which had been observed during the spring.

Casual observations had shown that while the entire bar was covered with mussels, the population was more abundant on the southern end and the inshore portions. Because of the draft of the boat used in the survey, the inshore portion of the bar was eliminated from consideration, and it was decided to confine the

study to an area approximately 1,440,000 square yards located on the southern portion of the bar.

Before the survey was initiated, a grid 1200 x 1200 yards was plotted on the map of the bar (Fig. 2) and buoys were set out to mark the beginning and end of each planned transect of the area. Four transects from West to East and three transects from South to North were completed. The positions of these runs are designated by the numbers 1 to 7 on Fig. 2.

In conducting the survey, the dredge was lowered at the edge of the transect, hauled for one and one half minutes, and then raised. A three minute running period elapsed between successive dredge samplings. Depth soundings were made at the beginning and end of each haul to determine the average depth of the station. At the conclusion of each run, the position of the boat was determined and the deviation from the plotted course was entered on the map. These deviations are indicated on Fig. 2 by X in the case of the S-N transects and O in the case of the W-E transects. The distance traveled in yards and the running time of the boat was recorded so that the approximate location of each dredge sample was available. Samples were secured from 35 stations in the area.

The deficiencies of the dredge as a sampling device are well recognized and have been pointed out by Winslow (1882), Stevenson (1894), and Frey (1946). In general, the dredge gives a sample that is entirely too low when compared with more accurate but less feasible methods (Frey 1946). However, as the same author points out, the comparative data are valid, and in respect to marketable-

sized oysters, the sample obtained is reasonably accurate. Since
little choice was possible in this investigation, and since mar-
ketable-sized oysters and shells were desired, the dredge was
utilized for the sampling.

From each dredge haul, a half bushel sample of oysters and
shells was collected, placed in a burlap bag, and returned to the
laboratory for analysis. The samples were separated and all or-
ganisms present were counted, or in the case of some forms, such
as the Bryozoans, the relative abundance was estimated. The mus-
sel population was found to consist of living individuals, gener-
ally of small size, and large numbers of empty shells which were
still attached to the substratum by the byssal threads. In order
to get an analysis of the past as well as the present population,
both living mussels and empty shells, when attached, were counted.
The data on the distribution of mussels in respect to depth is
presented in Table IV.

Considering the distribution of the mussels in relation to
depth, the data show that with increasing depth there is a de-
crease in the relative abundance of the population. A total of
2033 individuals were collected from 5 stations at a depth of 9
feet or less. This number may be compared with 990 individuals
from 15 stations at a depth range of 10 to 14 feet, 661 from 12
stations in 15 to 19 feet of water, and 60 mussels from 3 stations
at a depth of 20 feet or more. The average number of mussels per
station at the respective depth range is as follows: 9 feet or
less, 406.6; 10 to 14 feet, 66; 15 to 19 feet, 55.08; and 20
feet and over, 20.

TABLE IV

DISTRIBUTION AND DENSITY OF THE
POPULATION OF BRACHIDONTES RECURVUS ON
HACKETT'S BAR – OCTOBER 1951

RUN	STA.	DEPTH IN FEET			NUMBER OF MUSSELS	NUMBER OF SHELLS "BOXES"
		INITIAL	END	AVERAGE		
S - N I						
Distance 1300 yards	1	19	17	18	52	58
	2	17	16	16.5	8	0
Elapsed Time 20 minutes	3	14	13	13.5	33	79
	4	11	10	10.5	54	50
	5	9	8	8.5	601	30
S - N II						
Distance 1125 yards	6	19	19	19.0	45	87
	7	17	15.5	16.25	24	154
Elapsed Time 19 minutes	8	15	14.5	14.75	23	70
	9	12	11	11.5	21	49
	10	9.5	9	9.25	694	338
S - N III						
Distance 1075 yards	11	19	19	19	65	4
	12	19	18	18.5	18	48
Elapsed Time 24 minutes	13	16	16	16	59	213
	14	14.5	14	14.25	78	372
	15	16	18	17	25	460
	16	17	10	13.5	37	210

TABLE IV (CONT.)

RUN	STA.	DEPTH IN FEET			NUMBER OF MUSSELS	NUMBER OF SHELLS "BOXES"
		INITIAL	END	AVERAGE		
S - N IV						
	17	20.5	21	20.75	25	2
Distance						
1200 yards	18	16.5	18	17.25	34	21
Elapsed	19	14	14.5	14.25	108	89
Time						
15 minutes	20	14	15	14.5	124	74
W - E V						
	21	11	10	10.5	201	47
Distance						
1125 yards	22	9.5	9	9.25	207	345
Elapsed	23	9.5	10	9.75	531	200
Time						
18.5 minutes	24	9	13.5	11.25	177	92
	25	15	19	17	181	107
W - E VI						
	26	13	13	13	37	138
Distance						
1200 yards	27	13	12	12.5	31	226
Elapsed	28	12.5	15	13.75	28	357
Time						
19.5 minutes	29	14	15	14.5	19	70
	30	14.5	16	15.25	37	185
W - E VII						
	31	16.5	17	16.75	75	10
Distance						
1325 yards	32	14.5	15	14.75	19	84
Elapsed	33	16	16.5	16.25	38	94
Time						
19 minutes	34	19	21	20	23	57
	35	23	26	24.5	12	4

An examination of the number of empty shells shows results similar to those obtained on the mussels. In a depth of 9 feet or less we have an average population of 182.6 empty shells, as compared to 133.8 for depths between 10 and 14 feet. The population density continues to decrease, as indicated by an average of 120.8 at depths between 15 and 19 feet, and 21 at depths 20 feet and over.

Reference to Table IV shows that in the case of the individual transects, there is a general tendency for the population to decrease with increasing depth along the transect. This is particularly true of the S-N transects, where, in general, the depth of the water over the bar tends to decrease toward shore.

It is also evident that the population density is greater on the western end of the bar, regardless of depth, than it is on the eastern end. In this connection, it may be observed that the eastern end of the bar approaches the deeper water of the Bay, and therefore probably is subject to greater tidal action than the western end. Such an influence conceivably could determine the area of the bar over which the greater proportion of setting occurs.

On the basis of the data, however, the general conclusion may be drawn that on Hackett's Bar the population density of Brachidontes recurvus is greatest in water less than 10 feet in depth, while below 20 feet the distribution of the species may be considered sporadic.

Population Cycles. As has been pointed out, general observations in the Bay area by a number of investigators, as well as the author, have shown that the mussel population on any given bar is

subject to periods of abundance and scarcity. Clements and Shelford (1939) point out that these periods of variable abundance, so common to marine organisms, particularly bivalves and sedendary forms, are often considered abnormal and referred to as excessive mortality, chaotic changes, or "crash" periods, when in reality they represent normal fluctuations in abundance brought about by adverse conditions, such as lack of food, failure to reproduce, short life cycles, alteration in the physical environment, and other ecological factors. Therefore, the mortality of the mussel population observed during March and April 1951 is considered as representing a phase in the population cycle of the curved mussel.

From January 1950 through March 1951, the mussels on Hackett's Bar grew in large clusters attached to oyster shells. Monthly examinations of the population during this period showed little fluctuation either in the relative numbers of individuals or in size variation. Dead mussels were not common, and the mortality never exceeded 1 or 2 % of the population.

During the same period, the salinity at Hackett's fluctuated considerably (Table I, Fig. 3), as would be expected in any estuary. It reached its highest point on October 9, 1950, at which time it was 16.24 o/oo, and its lowest value on February 19, 1951 was 2.85 o/oo. At approximately the same time the preceding year, February 16, the salinity was 11.6, and during that spring, the salinity did not go below 5.2 o/oo.

Following the low salinities of January and February, a noticeable mortality was observed in samples collected from March 5 through April 16, 1951. A count of a bushel of oyster shells with

attached mussels showed a mortality of 54.94 %; that is, out of a total of 628 mussels, 283 were alive and 345 were dead. At the time of the survey in October 1951, less than 1 % of the population on the bar was greater than 35 mm. in length, the majority of the mussels observed at this time representing the set of 1951.

Even though the salinity value rose to 6.91 o/oo by March 5, the importance of the sudden drop in salinity, as a possible causative factor in producing the mortality, was recognized. The effects of lowered salinity on oyster mortalities in the upper Bay are well known (Beaven 1946, Engle 1946). However, as Beaven (1946) points out, exposure to a brief period of lowered salinity seems to have little permanent effect on quality and survival of oysters.

In an effort to determine the relative importance of lowered salinity on the survival of the curved mussel, a series of laboratory studies were devised. Groups of mussels still attached to the oyster shells from the collection of April 16, 1951 were placed in 6 gallon, aerated, glass aquaria, containing water from just above the bar and water from the same area which was diluted with distilled water so that the salinity ranged from 6.5 to 0.9 o/oo. The aquaria were kept at room temperature, which fluctuated between 18° and 21° C. The duration of the experiment was 36 days. Salinity was determined daily by the titration method.

Each aquarium contained 4 gallons of water and between 40 and 50 mussels. No selection for size was made, in that the mussel clusters were used as obtained. The range of size investigated was between 35 and 55 mm. in length. The criterion for failure to survive was the inability of the individual to close the valves

when touched or removed from the water. The aquaria were examined daily, and the dead mussels were removed once each day.

The results of the experiment showed that a mortality occurred in any salinity below 6.00 o/oo, with a constant increase in the per cent mortality with decreasing salinity. The summarized results are presented in Table V.

TABLE V

PER CENT MORTALITY OF B. RECURVUS
ASSOCIATED WITH LOW SALINITY

SALINITY RANGE o/oo	TOTAL NUMBER OF SPECIMENS	NUMBER DIED	PER CENT MORTALITY
6.0 - 6.5	135	0	0.00
5.6 - 5.9	184	11	5.97
4.6 - 5.5	144	22	15.22
3.6 - 4.5	216	212	98.01
0.9 - 3.5	165	165	100.00

The data in Table V show that in the salinity range, including 2.8 o/oo, observed over Hackett's Bar, a 100 % mortality occurred. Likewise, it may be noted that a mortality of 98 % is associated with salinities below 4.5 o/oo. This leads to the conclusion that the critical low salinity for the survival of Brachidontes recurvus is 4.5 o/oo.

The greater number of deaths in all salinities occurred during the first 7 days. This was followed by a decreasing mortality ex-

tending over the next two weeks. The mussels surviving at the end of the three week period continued to live until the termination of the observations. The data is presented in Table VI.

TABLE VI

NUMERICAL SUMMARY OF THE
MORTALITY OF B. RECURVUS
BY DAYS

SALINITY o/oo	5.6 - 5.9	4.6 - 5.5	3.6 - 4.5	0.9 - 3.5
DAYS		NUMBER OF DEATHS		
3	3	5	64	80
5		5	16	24
7		7	32	20
10	2	3	48	8
12		1	24	12
14		1	20	12
16	3		12	8
19	1			1
21	2			
TOTAL DEATHS	11	22	212	165

From an examination of Table VI, considerable individual resistance to low salinities is apparent. In the salinity range of 0.9 - 3.5, the greater number of early mortalities is associated with the lower end of the range.

It should be noted that a rather striking correlation exists

between the experimental data and the observed salinity and mortality on Hackett's Bar. On February 5 the salinity (Table I) had dropped to 3.48 o/oo, which is well within the range of the experimental data where 98 % mortality occurred. Thus, the mussels on the bar were exposed to critical salinity conditions for a sufficiently long period to account for the observed mortality. The rise in salinity to 6.91 o/oo by March 5, continuing upward to 8.21 o/oo by March 19, apparently was insufficient to prevent the mortality of the population observed in March and April. It is concluded, therefore, that a part of the observed mortality in the mussel population was the result of the lowered salinity during January and February 1951. The lower per cent mortality of 54.94 noted in the mussel population may have been associated with the fact that low temperatures prevailed simultaneously with the low salinities (Figs. 3 and 4, and Table I).

Community Relationships. The survey of Hackett's Bar offered an opportunity to study its community relationships. The oyster bar community has received considerable attention in ecological discussions because the concept of the community as a natural assemblage of organisms was first recognized by Mobius in 1877, as a result of his studies on oysters. Mobius stated that "every oyster bed is .... a community of living beings, a collection of species, and a massing of individuals, which find everything necessary for their growth and continuance" (Allee et al. 1949).

The community, as it exists at Hackett's, will be referred to as the Balanus-Brachidontes Association, on account of the relative abundance and permanency of these two forms. An adult population

of mussels of any consequence is not always present, as mentioned earlier in connection with the observations concerning the population cycle, but the presence of a young population indicates the importance of this species as a dominant member of the community (Shelford 1930).

The mussel, Brachidontes recurvus, and the barnacle, Balanus crenatus Bruguiere, were present at all stations, and in all cases were the two most abundant members of the community. The two species of bryozoans, Membranipora crustulenta (Pallas) and Acanthodesia tenuis (Desor), (Osburn 1944) are considered the subdominants of the association. These two species were collected from 25 of the 35 stations investigated, and in all cases ranked from common to abundant in relation to the other forms present. Given ideal circumstances as regards setting and growth, either or both of the species of bryozoans probably could become the dominants of a community. They are very common on oyster bars in Chesapeake Bay, and often form a complete blanket-like crust over the oysters and shells on the bar (Osburn 1944). It is possible that in other circumstances, or in deeper water, an association dominated by these species replaces the Balanus-Brachidontes Association in the oyster community.

A number of other species present in the community are considered as influents of the association. Their small number and occasional distribution mitigate against assigning any higher rank to these forms. Following the definition of influent as used by Dexter (1947), the following species are considered to be the influents of the association: the mussel, Congeria leucophaeta;

the snail, Odostomia trifida; the limpet, Crepidula convexa; and

mud crabs of the genera Rhithropanopeus and Eurypanopeus.

Incidental forms present, species of no significance in the

economy of the community (Dexter 1947), include Nereid worms,

Anemones, and miscellaneous crustaceans, of which Callinectes

sapidus was the most common.

The relative rank and the general distribution of the species

observed in the community are presented in Table VII.

TABLE VII

RANK AND DISTRIBUTION OF THE SPECIES
IN THE BALANUS - BRACHIDONTES ASSOCIATION

RANK IN ABUNDANCE	SPECIES	NUMBER OF STATIONS PRESENT
1	Balanus crenatus	35
2	Brachidontes recurvus	35
3	Membranipora crustulenta	25
4	Acanthodesia tenuis	25
5	Nereid Worms	26
6	Miscellaneous Crustaceans	12
7	Anemones	24
8	Rhithropanopeus and Eurypanopeus	26
9	Congeria leucophaeta	20
10	Odostomia trifida	11
11	Crepidula convexa	3

DEVELOPMENT OF THE GONADS AND SPAWNING

The gonadal tissue of _Brachidontes_ _recurvus_ consists of a series of ducts or canals, lined with germinal epithelium, which end in pockets or follicles. The mature tissue occupies almost the entire mantle and mesosoma to the edge of the foot, and penetrates into the digestive diverticula, where it is found adjacent to the so-called liver canals, the stomach, and the direct and recurrent intestine. It appears that the early development begins in the mantle and then spreads into the mesosoma. The vesicular tissue which fills in between the follicles is replaced by the gonadal tissue as it matures. Thus, when the sex cells are mature, nearly the entire structure of the organism is devoted to reproduction. As sexual maturity approaches, the mantle and mesosoma become either a bright yellow or a stippled brown in color.

The curved mussel is dioecious, and of the 896 specimens examined, there was no indication of the existence of hermaphroditism or alternation of sex. The gonads of both male and female show parallel development in time and in the position of the gonads. From those studied, it appears that the sex ratio is evenly distributed, with perhaps a slight leaning toward a greater number of females. The reproductive potential of the mussels is determined by their size rather than by their age. Gonadal studies were made of those forms which were as small as 20 mm. in length, and their gonadal tissue had the same appearance as that of the larger forms. It might be said, then, that they produce as many

reproductive cells as their anatomical structure will allow. It also leads to the conclusion that sexual maturity occurs the summer following setting, regardless of size.

Seasonal Development in the Male. The male follicles vary a great deal in size, depending on whether the immature or the mature condition is observed. From January until mid-April, the follicles are found in the mantle (Figs. 6 and 7), and to a lesser degree, in the mesosoma. They appear at this time to be loosely filled with cells, but by mid-April they become more dense in appearance and they take a deeper and darker stain (Fig. 8). As they mature, the follicles become filled with spermatozoa, which radiate from the periphery of the follicle toward the center (Fig. 9). These cells appear as small oval or spherical bodies which are packed too closely together for their detailed structure to be clearly visible. They mature by June and remain mature until October (Figs. 10 and 11). Observation of the density of the sex products in the follicles leads one to believe that spawning may occur from the mantle first, then proceed from the mesosoma. However, the appearance indicates that the animal could very well spawn simultaneously from both areas. The spawning extends over a considerable period of time from each follicle, so that some do not have the appearance of being spent, while others are mature. As the follicles mature, there are light, radiating areas, which under increased magnification show that the cells adjacent to these areas are concentrated in short rods, apparently similar to the condition observed in Mytilus edulis (Field 1922).

As the follicles increase in size and maturity, the supportive
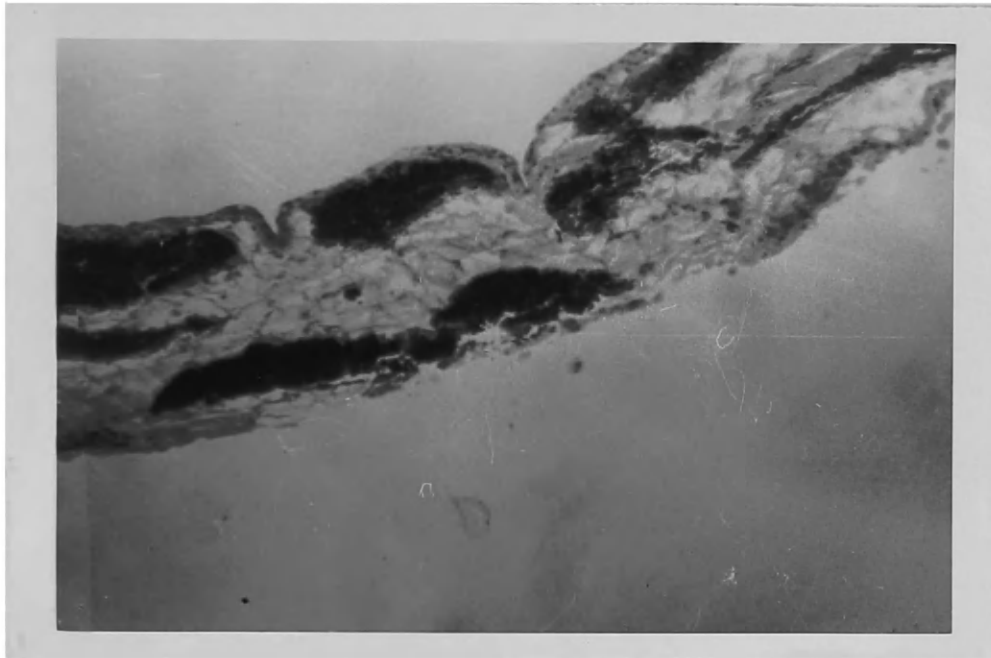
Fig. 6. Cross section through mantle showing the
presence of the male reproductive tissue in the
edges of the mantle. Note the presence of vesic-
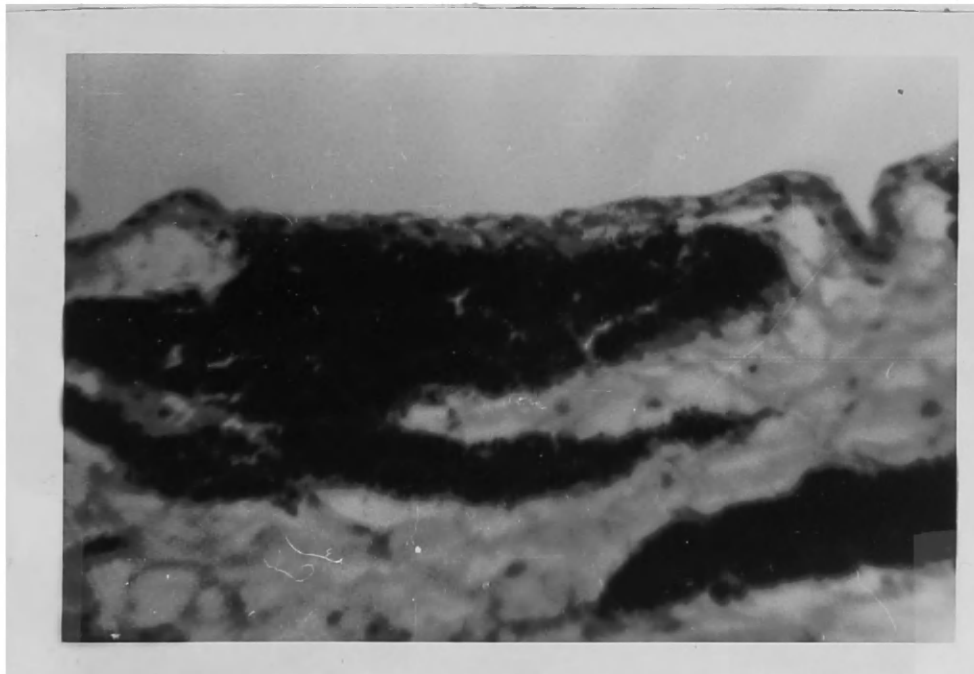ular tissue. Mallory's Triple stain. X100.

Fig. 7. Same as Fig. 6. X200.

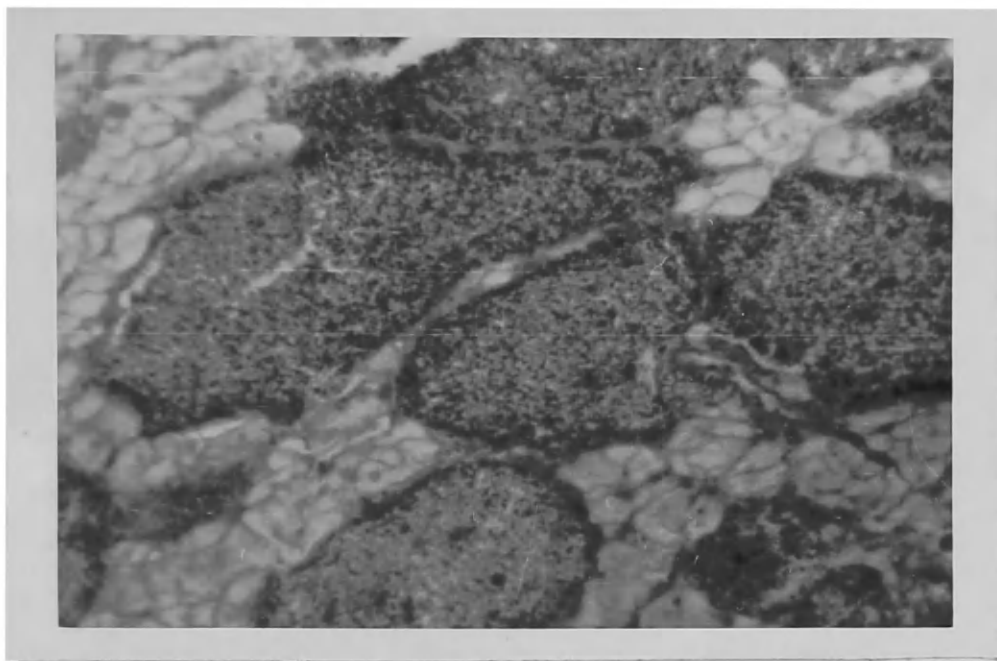Fig. 8. Immature follicles of the male gonad in Mid-April. H. & E. stain. X200.
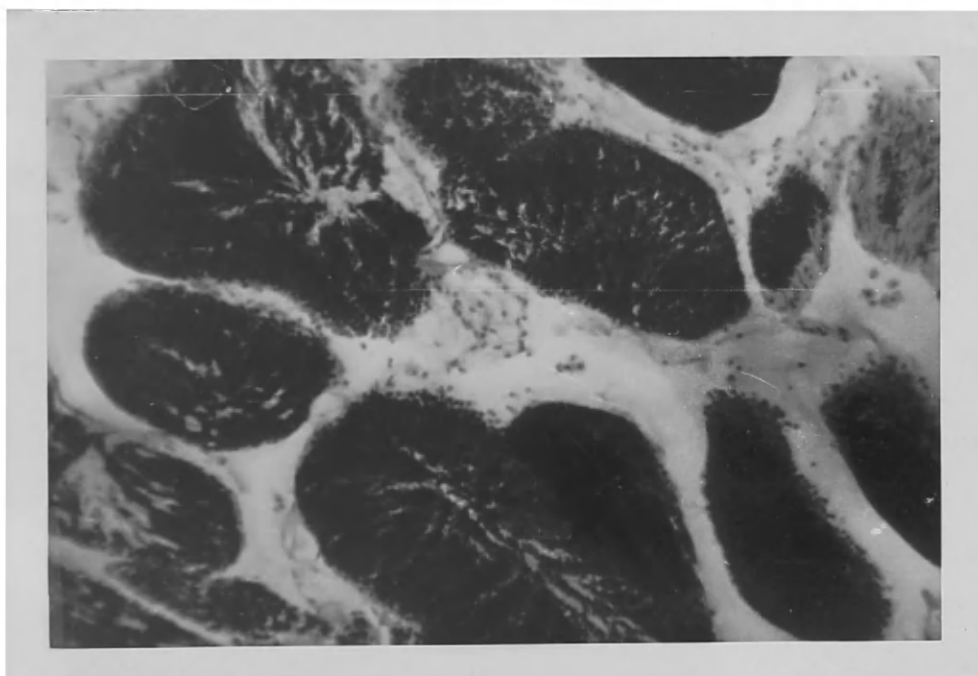

Fig. 9. Male follicles filled with spermatozoa in June. Note the radiations from periphery of follicle to center. Cross section through mesosoma. Mallory's Triple stain. X200.
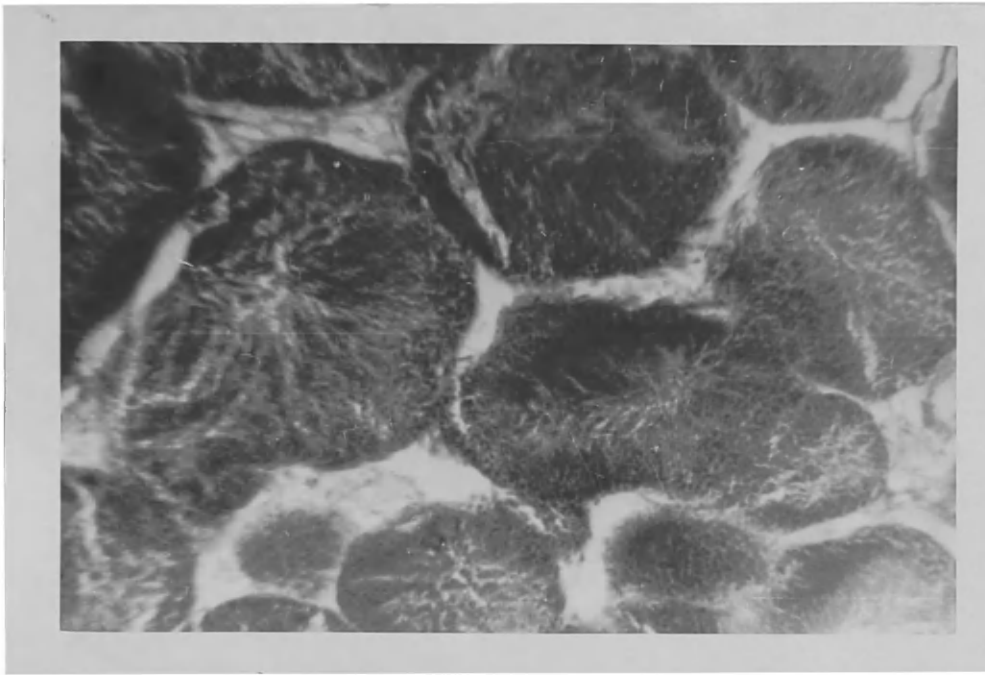
Fig. 10. Mature male follicles as they appear in July.
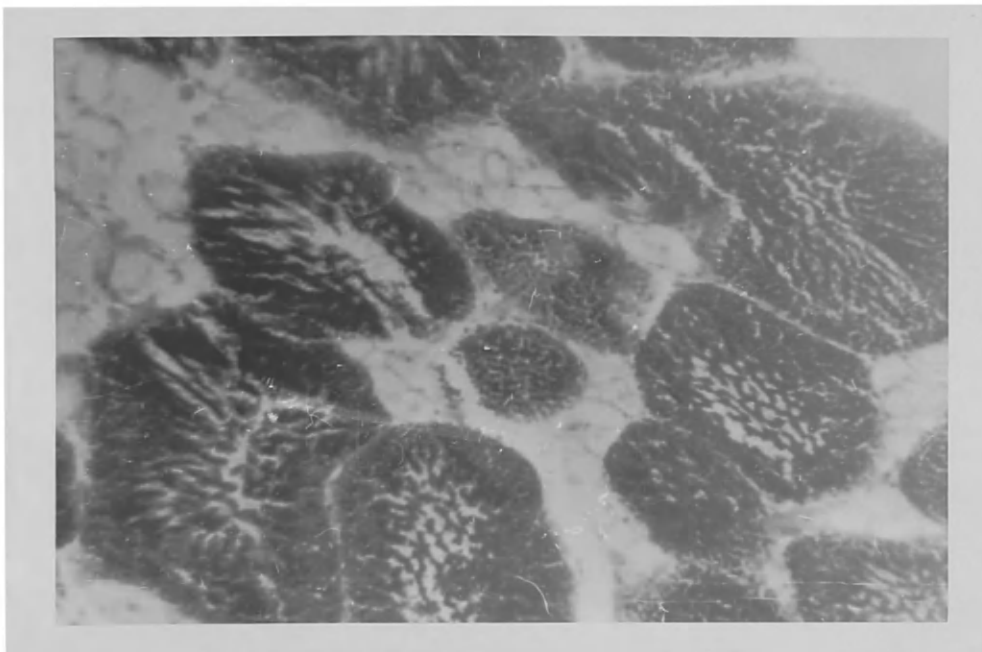H. & E. stain. X200.

Fig. 11. Mature male follicles as they appear in August.
H. & E. stain. X200.

vesicular tissue surrounding them gradually disappears almost completely. After spawning, this supportive tissue again appears, filling the spaces between the spent follicles.

Seasonal Development in the Female. The immature follicles of the female are separated by vesicular connective tissue and vary in size. By the first week in May (Fig. 12), the follicles are lined with small cells containing nuclei which stain a dark blue with H. & E. By the third week in May (Fig. 13), the cells have increased in size so that the prominent nucleoli can be seen, but the cells are still immature. By mid-June, the mantle and the mesosoma are occupied by follicles which are filled with mature and immature eggs (Fig. 14). Figure 15 shows that some of the vesicular supportive tissue is present, but has decreased or disappeared considerably as the eggs approach maturity. It will be noted that the eggs vary a great deal in size and that the nucleoli are large and prominent. When the eggs mature, they break from the follicle and are moved along by the ciliated ducts. The eggs are not considered as mature until they break free from the follicle. As is the case in the male, the female gonadal tissue penetrates into the digestive diverticula and is in close proximity to the liver canals (Fig. 16). In Figure 17, which is the section of the mantle near the gills and shows the general structure, the presence of large numbers of eggs of varying sizes, and even shapes, and the nuclei and nucleoli can be seen. The ova appear to be misshapen, rather than oval or spherical. This condition may be due to the crowding as the eggs mature, and also to the fact that they are closely packed after breaking loose
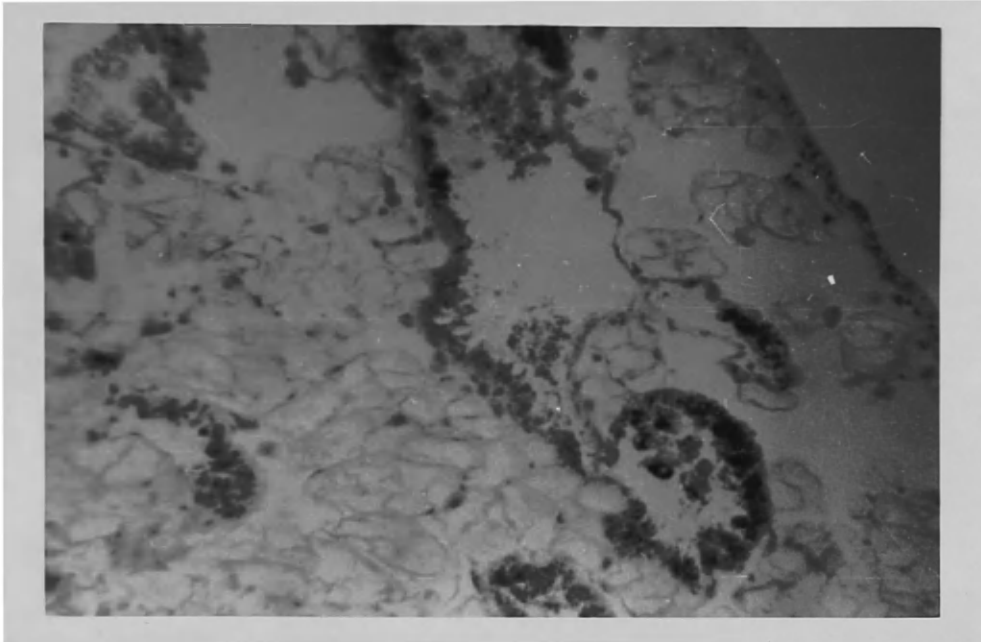
Fig. 12. General view of cross section through mantle, showing the appearance of the female follicles during the first week in May. H. & E. stain. X100.
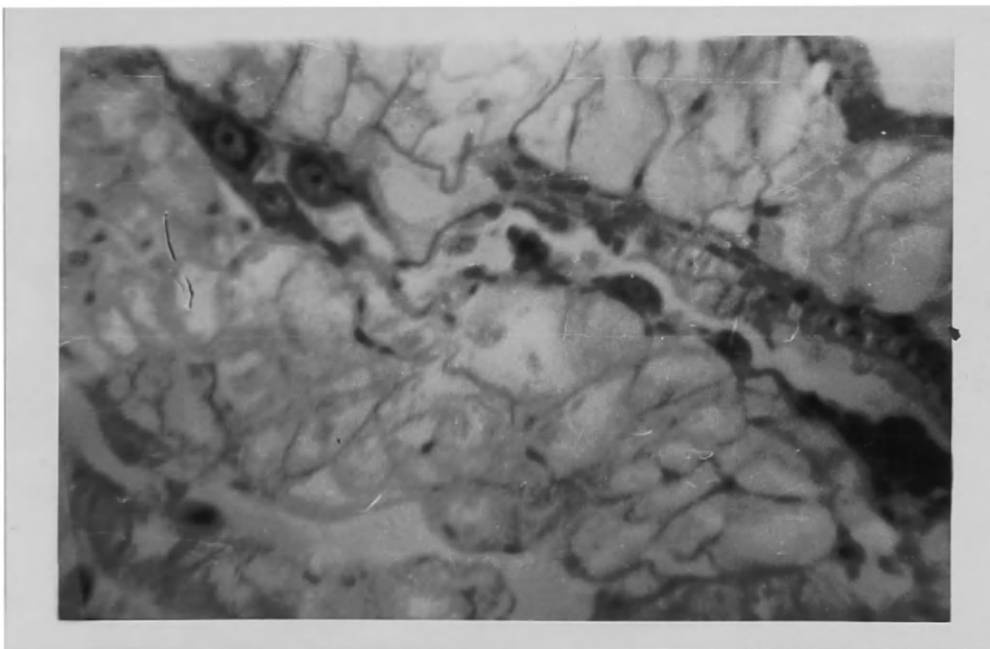
Fig. 13. Section through mantle, showing small, immature eggs as they appear in late May. H. & E. stain. X200.
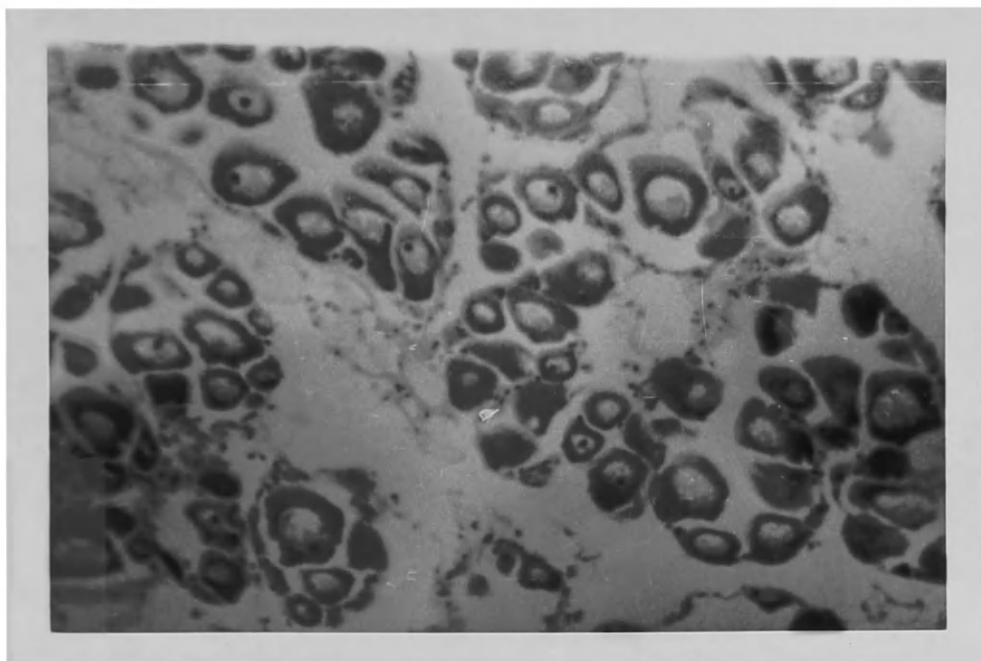
Fig. 14. General view of mantle in mid-June, showing presence of mature and immature eggs. H. & E. stain. X100.
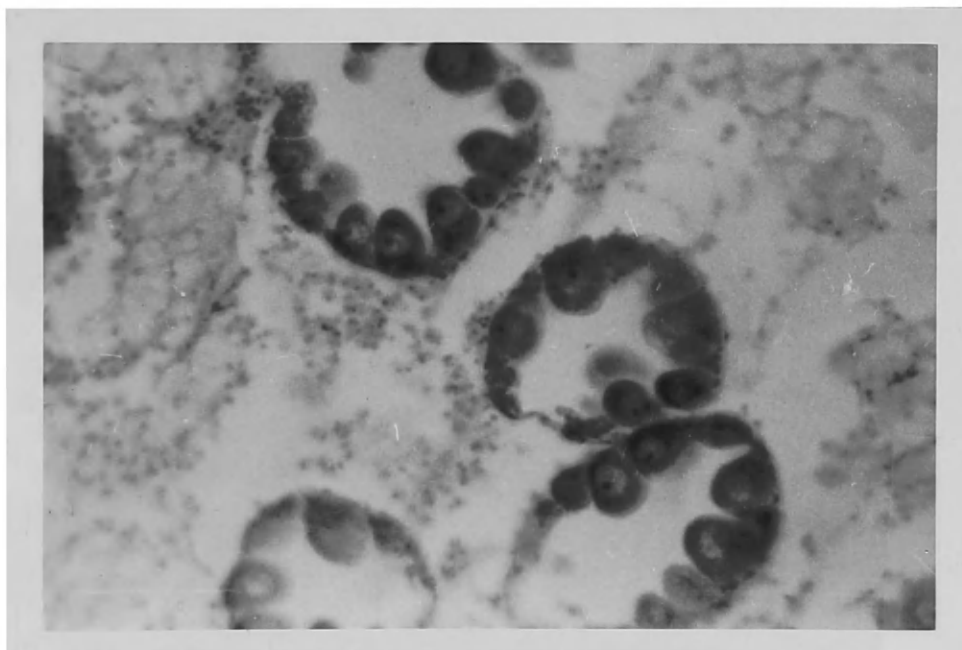
Fig. 15. Female follicles in mid-June. Note the prominent nucleoli and the disappearing vesicular tissue. H. & E. stain. X200.
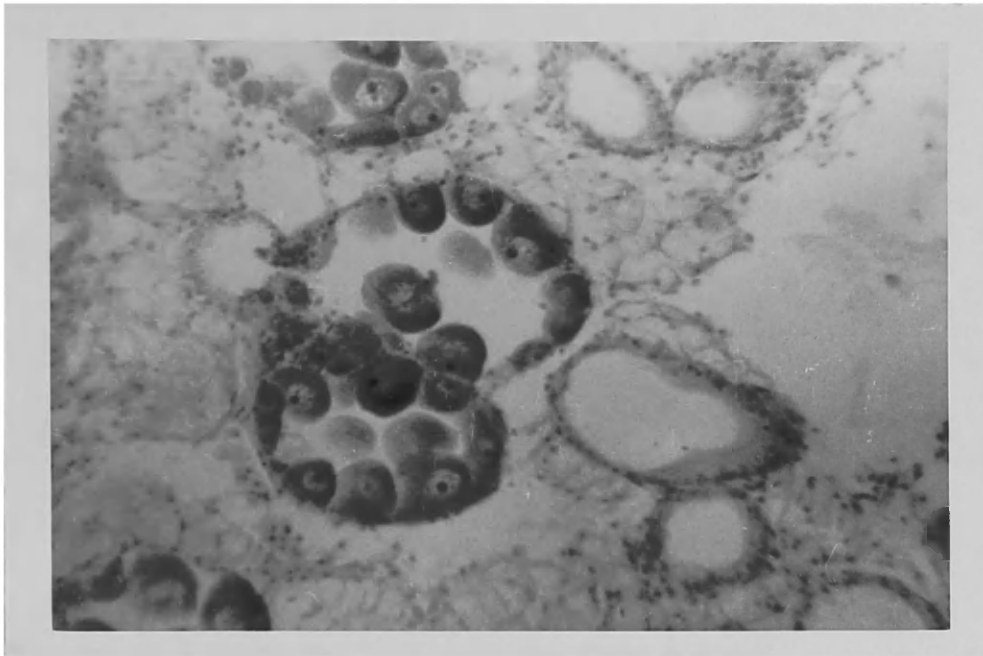
Fig. 16. Mature female follicles adjacent to the so-called liver canals in the digestive diverticula. Mid-June. H. & E. stain. X200.
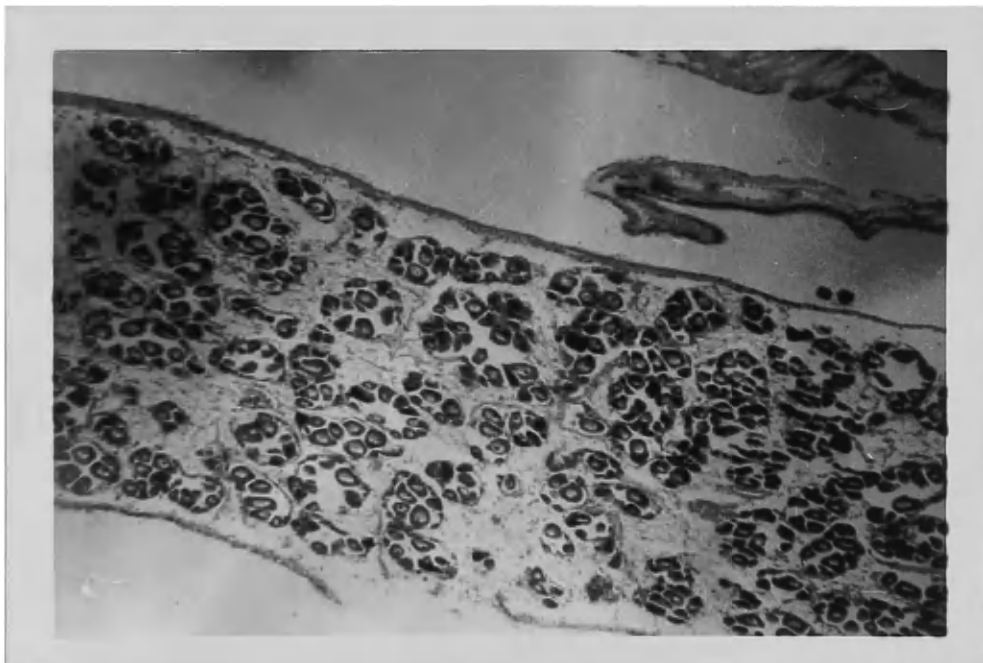
Fig. 17. General view cross section through mantle in the region of the gills. Note presence of mature and immature eggs. July. H. & E. stain. X50.
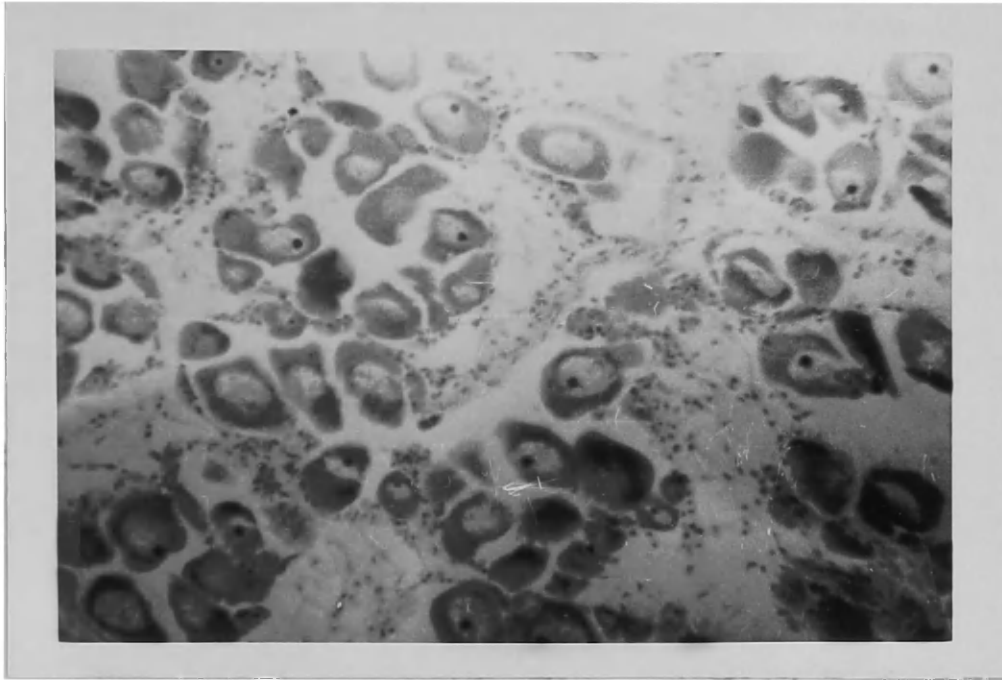
Fig. 18. Female follicles in July. Note mature and immature eggs, shape of eggs, and prominent nucleoli. H. & E. stain. X100.
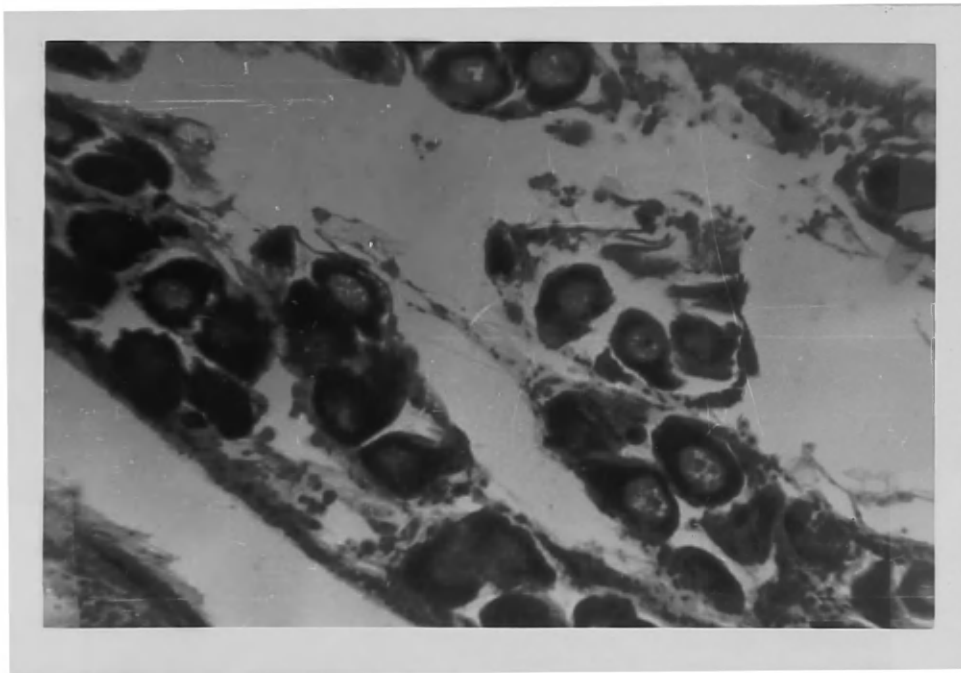
Fig. 19. Female follicles as they appear in October. H. & E. stain. X200.

within the follicle. The condition of the gonad from July (Fig. 18) to October is similar to that in June. After October, the ova are not as numerous (Fig. 19), but some retain the same appearance as those of June.

On July 3, the small eggs appeared in the mantle and the larger ones in the mesosoma. In August, the mantle was not as densely packed as was the mesosoma, which contained many follicles. In one specimen from the September group, one side of the mantle contained only a few eggs, while the other side of the mantle and the mesosoma were dense with eggs. Although the condition of the maturity of the ova is such that the entire gonadal tissue is subject to spawning at the same time, the intensity of spawning and the time of spawning of these different areas depends upon the individual.

Mature eggs are present in December (Fig. 20), but show evidences of degeneration or death, as shown by the condition of the nucleus, the absence of nucleoli, and the general appearance of the cytoplasm. While the destruction of the gonadal tissue appears evident, there is no similarity to the comparable mechanism of resorption noted in some pelecypods by Loosanoff and Davis (1951).

The development of the gonads indicates that the state of sexual maturity exists from June through October. Release of the sex products occurs over a relatively long period of time, from early June through October, and in some cases through November. Individual follicles develop independently of each other in both sexes. In other words, the gonads do not reach a high peak of maturity and immediately spawn out.
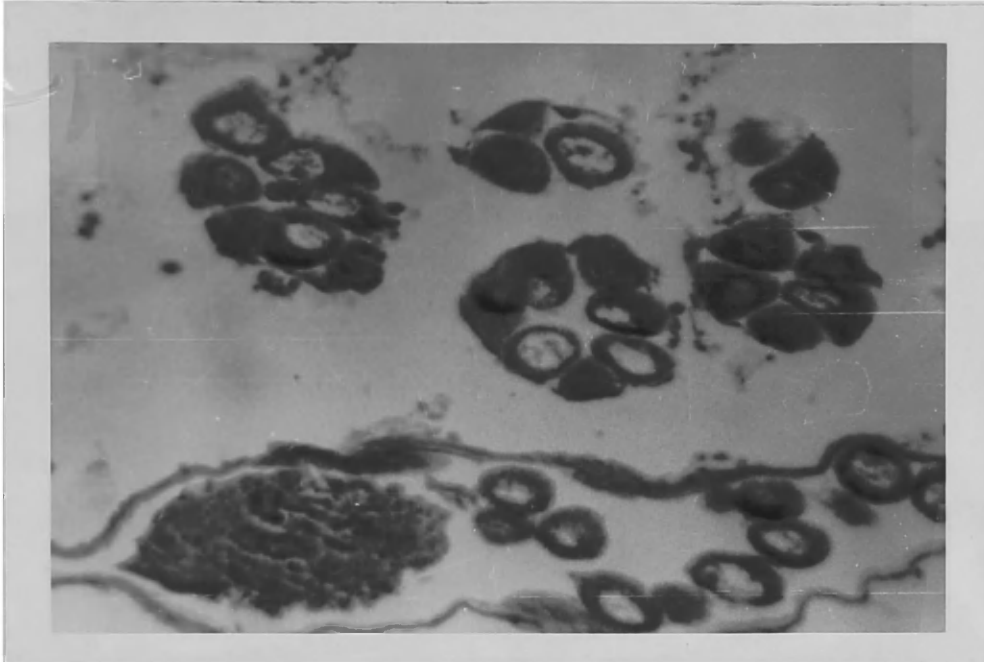
Fig. 20. Note presence of mature eggs in December, but
also their degenerate nature. H. & E. stain. X200.

Seasonal distribution of the larvae. Plankton samples col-
lected from January 16, 1950 through April 16, 1951 were examined
to determine the presence, relative abundance, and stages of de-
velopment of the larval forms of Brachidontes recurvus.

Since the rate of development of the larval stages shows con-
siderable variation, in part, at least, because of the protracted
spawning period, it was decided to divide the forms present into
three groups: pre-hinge stage, hinge stage, and post-hinge stage.
The hinge stage was defined as "the straight-hinge-line embryonic
shell" (Field 1922), in between the circular immature larval stage
and the triangular ovate form of the more mature larva. In the
area of Hackett's Bar, the larval stage of this species could be
confused only with the larval stages of Congeria leucophaeta,
Crassostrea virginica, or possibly with Tagelus plebeius and Mya
arenaria. However, as is pointed out by Sullivan (1948), careful
examination will show numerous diagnostic differences between the
mussel larvae and other lamellibranchs. Therefore, the larval
stages of different groups may be easily separated from each other,
although some confusion might possibly arise in regard to the larvae
of Brachidontes recurvus and that of Congeria leucophaeta. However,
considering the rare occurrence of the latter form on Hackett's Bar,
such confusion should not invalidate the data.

The results of the observations on larval distribution are pre-
sented in Table VIII. The relative abundance of the various larval
forms is expressed as present, common, abundant, and very abundant,
rather than by using some numerical statement. It was felt that
such an expression of results had more validity than an exact numer-

TABLE VIII

SEASONAL OCCURRENCE OF MUSSEL LARVAE
IN PLANKTON SAMPLES - 1950

Date	Tide	Pre-hinge	Hinge	Post-hinge
June 5	High	Present	Present	Absent
June 19	Ebb	Common	Common	Present
July 3	Ebb	Common	Common	Common
July 17	Medium	Absent	Present	Present
July 31	Ebb	Abundant	Present	Absent
August 14	Low	Common	Common	Absent
August 28	Low	Abundant	Abundant	Abundant
Sept. 11	Flood	Very Abund.	Very Abund.	Very Abund.
Sept. 25	Flood	Common	Present	Common
Oct. 9	Low	Present	Absent	Common
Oct. 25	Low	Absent	Absent	Present
Nov. 13	Low	Present	Common	Common
Nov. 27	Low	Absent	Absent	Present
Dec. 11	High	Absent	Absent	Present

ical expression, since the method of collection was not susceptible to exact quantitative analysis (Littleford, Newcombe, and Shepherd 1940).

The larvae appeared in the plankton for the first time on June 5, 1950, when pre-hinge and hinge forms were observed in the samples. By the middle of June, the pre-hinge and hinge stages had quadrupled in number over the earlier part of the month. The post-hinge stage was observed for the first time on June 19, 1950. During July and August there was, generally speaking, a continued rise in abundance of the larval stages. However, the pre-hinge stage was not found on July 17, 1950 and the post-hinge stage was not observed in the collections of July 31 and August 14. All three stages were present in large numbers in the collection of August 28, and the peak of their numerical abundance in the plankton was observed on September 11, 1950.

Some idea of the relative seasonal abundance of the larval stages may be obtained from the fact that the number of pre-hinge stages in June was 27.50% of the total number observed on September 11. Similarly, the number of the hinge stage in June was 15.15% and the number of the post-hinge stage was 0.54% of the numbers observed on September 11.

By reference to Table I, it may be observed that spawning occurred at a temperature of 17.7° C. or lower and continued throughout the summer and fall, at least until the middle of November, when the temperature had dropped to 11.6° C. The older larvae present during December were able to survive a temperature as low as 6.8° C., recorded on December 11.

The data presented with respect to larval distribution leads to the conclusion that the spawning period of B. recurvus extends from early June until November. The greater number of larval stages were observed in late summer and fall, which leads to the conclusion that the greater percentage of setting takes place during late August and September. This observation is supported by the observations on the development of the gonads and the small size range of the mussels collected during the survey in October.

The data on tides presented in Table VIII were calculated by use of the Tide Tables for the Atlantic Coast (U. S. Coast and Geodetic Survey, 1950). It will be noted that there is no evidence that the relative abundance of the larvae is influenced by the height or direction of the tide.

The distributional data on the larval stages also point to the existence of three relatively distinct periods of spawning: an early spawning in June, a mid-season spawning in late July and August, and a late spawning in November. It will be noted (Table VIII), in following the seasonal variation of the pre-hinge stage, that the larval stages increase during June and early July, but are then absent from the plankton. They occur in abundance during August and September, but are again absent in late October. Finally, they are present in mid-November. This seasonal pattern of distribution is followed also by the hinge and post-hinge stages. Acceptance of the three distinct spawning periods would explain the absence of the post-hinge stages during late July and early August.

Explanation of three such periods on the basis of environmental factors is not possible. Whedon (1936) and Young (1942, 1946) re-

ported similar observations on <u>Mytilis</u> <u>californianus</u>. Numerous

other investigators have made similar observations on other species

of pelecypods, and it has been shown that either a rise or a drop

in temperature may induce spawning in these forms (Berner 1935).

In lamellibranchs, spawning is usually associated with rising temp-

erature. The conclusion of Pelseneer (1935) and Nelson (1928a) is

that when a critical temperature is reached, spawning occurs above

that point, but below that temperature it does not occur. Galtsoff

(1938 and 1940), however, points out that . . . .

> There exist several "critical" temperatures for spawning
> of males and females, apparently determined by their
> physiological conditions. . . . . The idea (therefore) of
> a single critical temperature effective in inducing
> spawning in all oysters of a given population . . . .
> should be abandoned.

It is possible, considering the long period of sexual maturity

of the gonads in <u>B</u>. <u>recurvus</u>, that physiological conditions result

in different spawning periods for individual mussels.

AGE AND GROWTH

The determination of age in lamellibranchs has been approached either by counting the annual rings which follow the contour of the shell, or by rearing marked specimens under natural conditions. In this investigation it was not possible to rear the curved mussel under natural conditions, since Hackett's Bar is a public oyster bar, subject to tonging operations during the entire oyster season. Therefore, it was necessary to resort to the use of "annual" rings in the estimation of age.

In a previous portion of the observations, it has been pointed out that on the basis of length-frequency, we have what appears to be five rather distinct years of growth. Examination of the annulations of 5,027 individuals shows that in the case of 3,129, or 62.61% of the population, the annulations appear well defined and are apparently rings associated with age. In the remainder of the population, the determination of the annulations is more difficult because a number of marks or "rings" appear in between the primary ones that indicate age.

Following the observations of Mossop (1922) on <u>Mytilis</u> <u>edulis</u> and Wiborg (1946) on <u>Modiola</u> (actually <u>Volsella</u>) <u>modiolus</u>, it was decided to consider only those annulations that continued around the shell in the region of the hinge, as annual rings. The remainder of the markings may be considered as lines of "arrested growth" (Mossop, 1922), for which no definite reason is assigned. Mossop prefers this terminology, since it does not postulate any

particular cause for the slowing down of growth. Considering the growth habits of the curved mussel, it would be difficult, in many cases, to offer any one specific reason for growth interruption.

The results of the examination of the population to determine age distribution are presented in Table IX.

TABLE IX

AGE DISTRIBUTION ACCORDING TO
LENGTH FREQUENCY

Length Interval in MM	Number Of Mussels	Per Cent Distribution of the Population: Year of Growth						
		1	2	3	4	5	6	Misc.
0.00 - 9.99	96	100						
10.00 - 19.99	212	82	17				1	
20.00 - 29.99	880		72	25				3
30.00 - 39.99	2016			92	4			4
40.00 - 49.99	1458				46	52	1	1
50.00 - 59.99	356					96	1	3
60.00 - 62.99	9						100	

The data on population distribution show that the mussel may reach a length of 19.99 mm. before the end of the first growing season. Many of them do not grow this rapidly, as is shown by the fact that 17% of the individuals between 10 and 19.99 mm. in length have already passed through their first period of growth cessation. Like-

wise, it may be noted that each "year class" observed includes a wide range of length distribution. The fact that the mussel spawns over a period extending from June through November explains the wide range in length distribution for a given year of growth. Similar observations have been reported on Modiola modiolus by Wiborg (1946).

It is probable that the annual rings are laid down during the period from December to March, when the temperature of the water is below 7° C. (Table I). While the lowest temperature at which the curved mussel will feed has not been determined, it has been shown by Coe and Fox (1944) that Mytilis californianus will not feed below 7 to 8° C., and Wiborg (1946) observed that growth almost ceases and the winter rings are formed in Modiola modiolus between December and April, during which period the water temperatures are low.

A number of individuals were found to show a very slow rate of growth as compared to the general population. For example, one mussel with a length of 14.6 mm. had 5 clear annulations. Eight annulations, found on two specimens, was the largest number observed. It seems apparent that the average length of life of Brachidontes recurvus extends over a period of five years, with a small percentage of the population living beyond that time.

Additional information in regard to growth of the curved mussel was obtained by an investigation of the linear measurements of length, width, and thickness, and the weights of the shell, soft parts, and dry weight. Because of the overlapping age distribution of the population, no attempt was made to compare these data with

age of the mussel. In order to compensate for the fact that considerable individual variation was observed in all size intervals with respect to the above measurements, the results are given in 5 rather than 10 mm. intervals.

Following the suggestions of Simpson and Roe (1939), the mussels used for the determination of growth indices were collected over as short a period as possible during the early summer of 1950. This period was chosen in order to limit the data to a single growing season and to avoid the period of maximum spawning. In order to clarify the comparison of the smaller variates, length and weight indices, with length intervals, the graphical presentations are made on semilogarithmic paper (Simpson and Roe 1939).

The data on width and thickness in respect to length in the curved mussel are presented in Table X. These data show that there is considerable variation in the width range in all length intervals between 25 and 54 mm., as would be expected on the basis of the variability in age of the samples and the growth habits of the mussel. It has already been pointed out, that the position of the individual in the cluster determines the available room for normal growth, and that therefore many of the mussels are misshapen or have a peculiar growth form because of their immediate environment. Significantly, this variation is slight in the smaller individuals, where growth continues uninhibited by crowding, and in the larger forms where age variation is not so great as in the general population.

Despite the wide differences in width range in the linear groups, the mean widths of the mussel show a comparable and expected

TABLE X

VARIATION IN WIDTH AND THICKNESS, WITH
RESPECT TO LENGTH INTERVALS, EXPRESSED
IN MILLIMETERS

LENGTH RANGE	NUMBER SPECIMENS	MEAN LENGTH	WIDTH RANGE	MEAN WIDTH	THICKNESS RANGE	MEAN THICKNESS
10.0-14.99	29	11.888	6.0- 9.0	7.550	3.0- 5.0	4.555
15.0-19.99	30	18.600	10.0-16.0	12.140	4.0-13.0	9.120
20.0-24.99	48	22.185	10.0-19.0	14.098	7.0-18.0	11.020
25.0-29.99	108	27.095	10.0-30.0	17.079	7.0-18.0	12.944
30.0-34.99	220	32.122	13.0-29.0	19.240	9.0-21.0	14.496
35.0-39.99	284	37.115	12.0-35.0	21.183	9.0-25.0	16.008
40.0-44.99	311	41.769	15.0-30.0	22.268	11.0-25.0	17.611
45.0-49.99	221	46.725	17.0-35.0	24.127	13.0-30.3	19.610
50.0-54.99	141	51.565	18.0-33.0	25.613	14.0-27.6	20.565
55.0-59.99	34	56.211	27.0-35.0	27.905	17.0-25.0	21.679
60.0-62.99	6	60.766	25.1-34.0	28.483	20.0-27.0	23.350

increase with added length. This width increase is, in general, progressively less as the population grows in length, showing that the growth increment becomes smaller as the individual becomes older.

The variation in thickness occurring in any length interval also shows a relatively wide range. However, in this case, a constant increase in this variability may be observed until the mussels are over 55 mm. long. In these latter groups, the range of width is considerably reduced and is comparable to the range that may be observed in the smaller members of the population.

The graphical presentation of this data shows that there is a correlation between length and width, length and thickness, and width and thickness. The alteration in the direction of the curve between 22.18 mm. and 27.09 mm. in length is associated with the development of the curved or hooked appearance of the mussel. The smaller individuals have first an elongate appearance, which is followed by a somewhat triangular shape that immediately precedes the development of the characteristic hooked form of the larger specimens.

The relative positions of the two lines representing width and thickness, with respect to the interval separating them, may also be associated with morphological changes in the mussel (Fig. 21). Associated with the wide interval observed between 27.09mm. and 46.73 mm., there is a corresponding variability in shape and relationship between thickness and width in the individuals comprising the population.

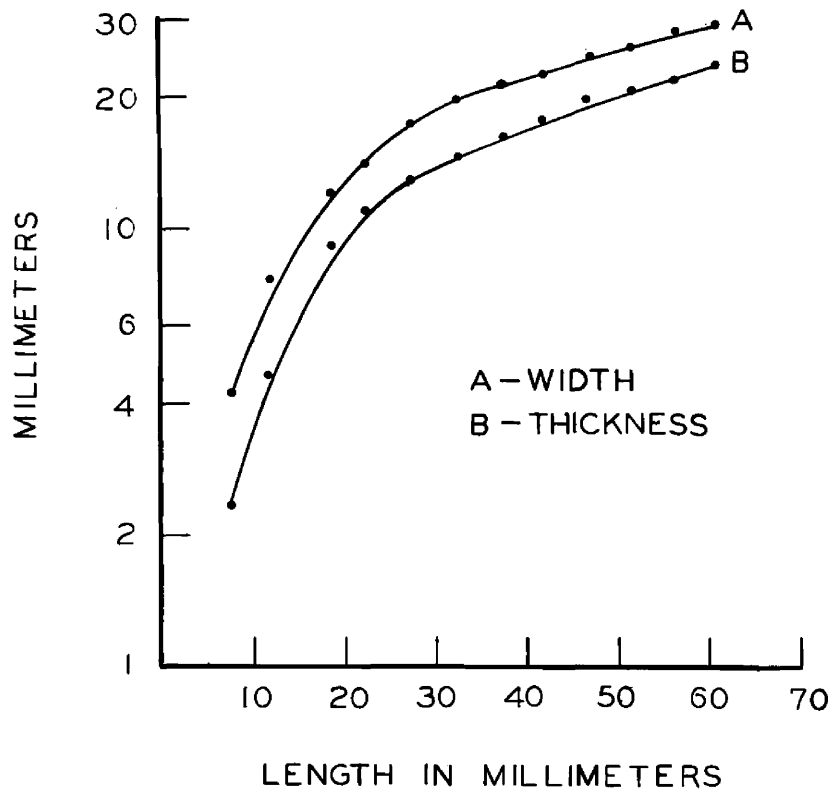On the basis of the data in Table X and Figure 21, it may be

Fig. 21. The relationship between width and thickness with respect to length in Brachidontes recurvus.

observed that the greatest increment in linear growth takes place in the size range below 25 mm. After that size has been reached, growth slackens. These observations are comparable to those of Wiborg (1946) on _Modiola modiolus_, a much larger species, in which the most rapid growth is shown by individuals less than 55 mm. in length.

Investigation of the total weight, shell weight, and wet weight of the mussel shows that there is wide variation in these indices among individuals of a given length interval. Tabular presentation of this data may be noted in Table XI, while the curves of weight indices are presented in Fig. 22. By reference to the data, it will be observed that the weights under discussion are proportional to each other throughout the entire length variation of the mussel.

The most rapid increase in weight of each category under consideration occurred in the smaller mussels. Similar to the results observed in the case of the linear indices, the increase in growth slows perceptibly between the mean lengths of 22.18 and 27.09, indicating that the greatest increment of growth takes place below 25 mm. On the basis of the data presented, it may be noted that the weight indices show a linear progression.

The data on dry weights may be observed in Table XI and Fig. 23. It will be noted that the increment of growth was greater in the dry weights, in proportion, for successive length intervals than in any other group of weights. From Fig. 23 it may also be observed that the slope of the curve continues upward for a longer period than that of the curves of the other weight indices.

TABLE XI

SUMMARY OF TOTAL WEIGHT, WET WEIGHT, SHELL
WEIGHT, AND DRY WEIGHT, IN GRAMS, WITH
RESPECT TO LENGTH INTERVALS

| NUMBER INDIVIDUALS	MEAN LENGTH	TOTAL WEIGHT RANGE	MEAN TOTAL WEIGHT	WET WEIGHT RANGE	MEAN WET WEIGHT	SHELL WEIGHT RANGE	MEAN SHELL WEIGHT	DRY WEIGHT RANGE	MEAN DRY WEIGHT
29	11.888	0.09- 0.28	0.160	0.05-0.21	0.138	0.03-0.15	0.120	0.012-0.015	0.0134
30	18.600	0.50- 0.75	0.721	0.27-0.41	0.370	0.23-0.39	0.350	0.019-0.051	0.0229
48	22.185	0.70- 1.50	1.025	0.35-1.10	0.530	0.30-0.90	0.489	0.027-0.073	0.0390
108	27.095	0.90- 3.20	1.630	0.40-2.00	0.867	0.40-1.20	0.756	0.026-0.107	0.0540
220	32.122	0.90- 3.70	2.345	0.40-2.20	1.236	0.50-1.60	1.207	0.013-0.209	0.0902
284	37.115	1.60- 5.40	3.262	0.70-3.40	1.765	0.65-2.35	1.490	0.035-0.551	0.1310
311	41.769	2.90- 6.90	4.839	1.60-4.60	2.651	1.18-5.30	2.177	0.017-0.573	0.1934
221	46.725	3.90-10.40	6.582	2.20-6.40	3.712	1.10-4.45	2.850	0.032-0.654	0.2343
141	51.565	5.10-12.20	8.007	2.80-7.70	4.576	2.30-4.70	3.401	0.129-0.636	0.2892
34	56.211	7.70-13.00	9.835	4.20-7.70	5.529	2.20-5.30	4.265	0.019-0.485	0.3152
6	60.766	11.60-15.68	14.400	6.10-9.78	8.675	5.40-5.90	5.650	0.337-0.424	0.3807
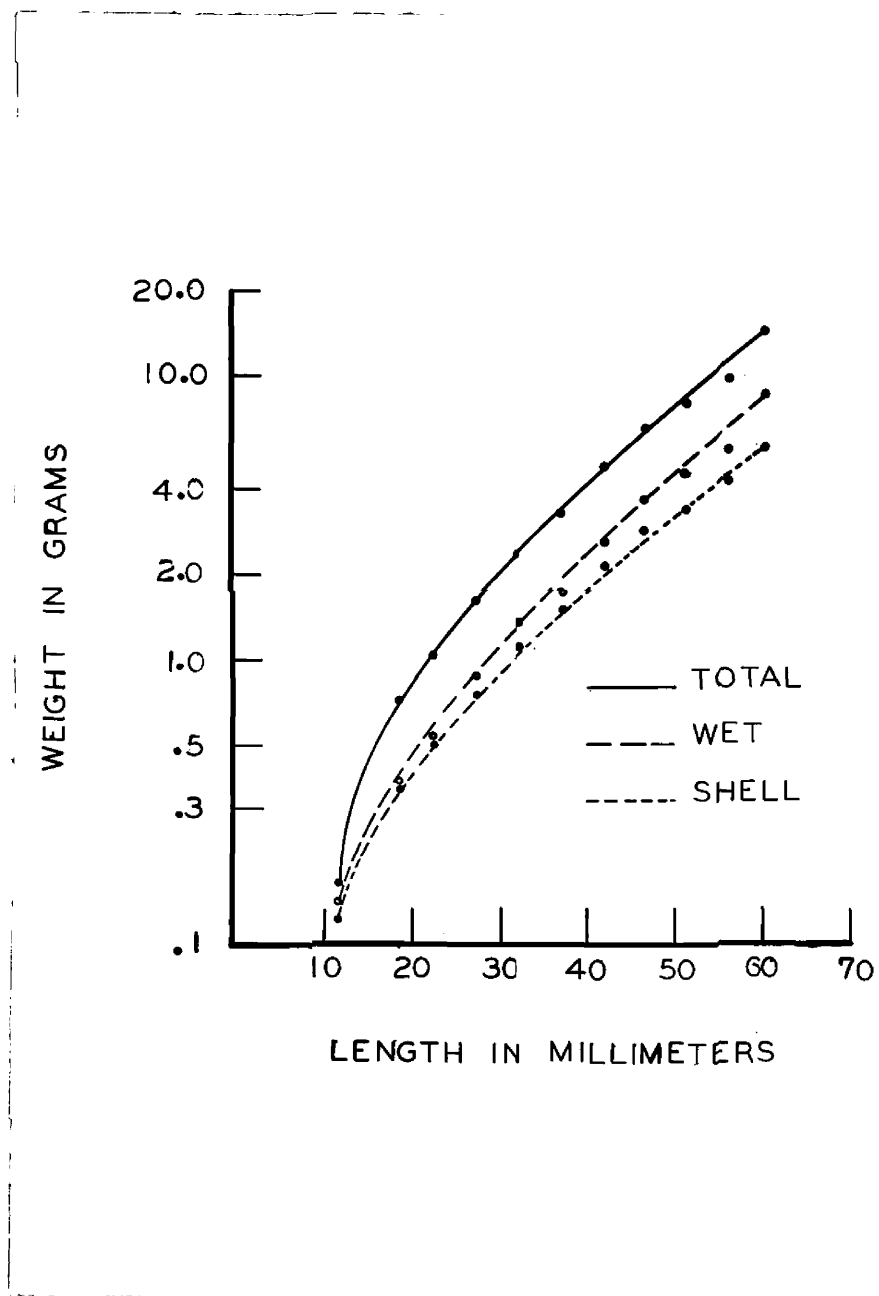
Fig. 22. Showing the relationship of total weight, shell weight, and weight of the soft parts, with respect to length in Brachidontes recurvus.
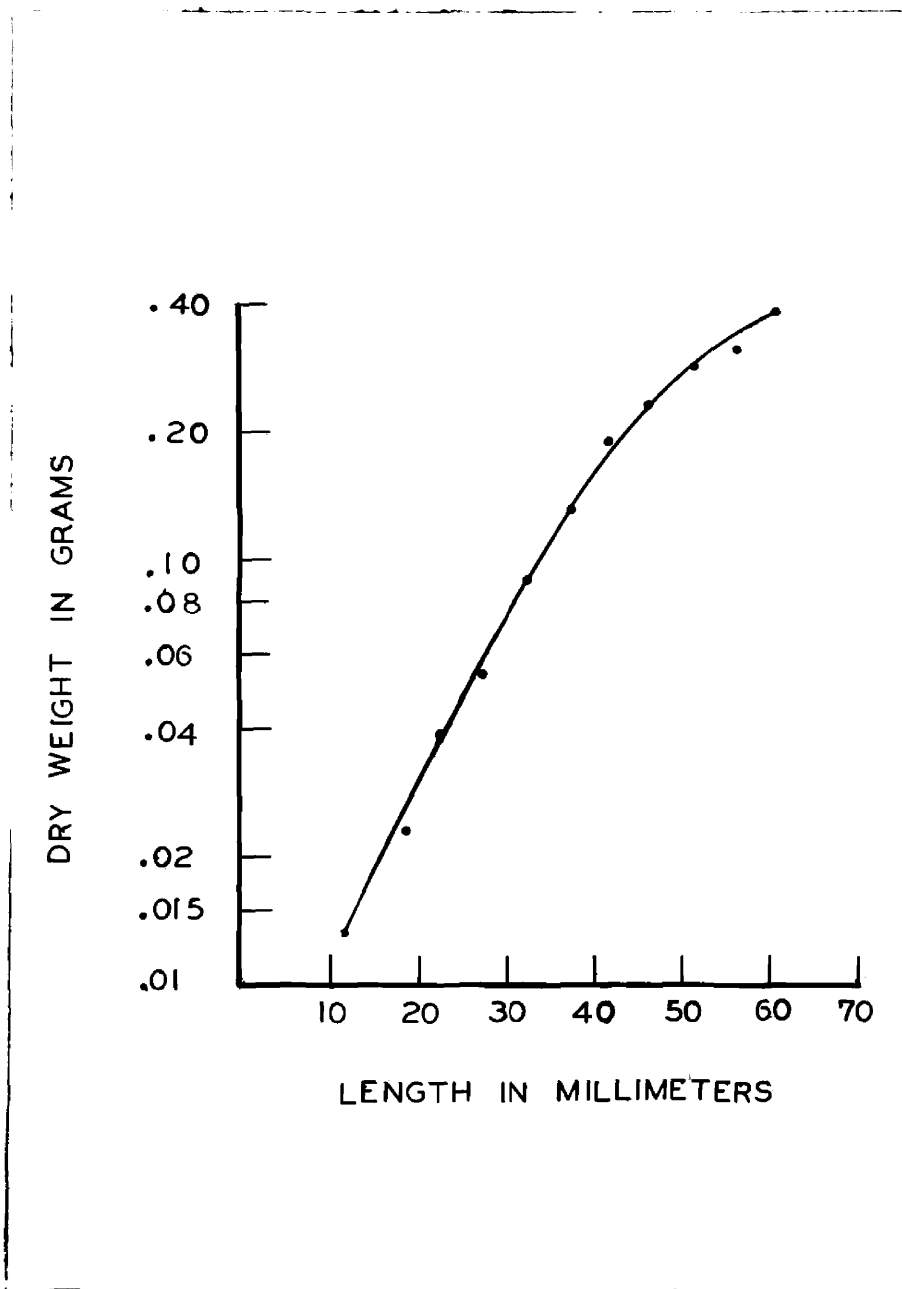
Fig. 23. Showing the relationship between dry weight and length in Brachidontes recurvus.

The data on growth summarized in the preceding tables and graphs show that the process of growth in <u>Brachidontes</u> <u>recurvus</u> is linear, as has been reported for numerous other lamellibranchs. The width and thickness and the weights of the individuals increase proportionally with an increase in length which has been used as the basic index of growth. The greatest increment of growth takes place below 25 mm., after which time it tends to decrease with increasing length. The greater percentage of the total weight of the mussel is wet weight, or weight of the soft parts.

Basing the determination of age on the use of annual rings, it may be said that the weight increases with increasing age. However, since the age composition of any given length interval consists of individuals of different "year classes", the exact relationship between age and growth is difficult to determine. It is probable that much of the individual variation within the range of width and thickness, as well as weight, observed in each length interval, is the result of the difference in age. This variation is undoubtedly the result of the protracted spawning period of the mussel, which results in considerable variation in length at the end of the first growing season.

DISCUSSION

The family Mytilidae includes the sea mussels, a group of bi-valves that is world-wide in distribution. All of them, without exception, are inhabitants of either the intertidal or the sub-tidal zone. Usually they are found in great numbers and form beds of considerable extent. Needing some firm substratum for attach-ment, they are found abundantly on rocky shores; they also live attached to the roots of aquatic plants, or subtidally on boulders, gravelly bottoms, or firmly attached to some other shell bearing form, such as the oyster.

In North America this family is represented by four widely distributed species: Mytilus edulis, which is either intertidal or subtidal in distribution; Mytilus californianus, which is found on rocky shores in the intertidal zone of the West Coast; Volsella demissus, which is associated with Spartina, and is found inter-tidally along the entire Atlantic Coast; and Brachidontes recurvus, which is strictly subtidal and is attached to oyster shells on sub-merged bars.

In European waters, Mytilus edulis and Modiola modiolus are the two most widely distributed forms. The horse mussel, Modiola modi-olus, lives under conditions very similar to those of the curved mussel, Brachidontes recurvus (Wiborg 1946).

ECOLOGY

Despite the general similarity of these different species as far

as distribution and basic ecology are concerned, each of them dif-
fers widely in individual habits of growth and relationship to
salinity and tide levels. Mytilus edulis, the edible mussel, dwells
in the intertidal zone and extends subtidally (Field 1922, Newcombe
1935). The distance below the mean low tide level to which Mytilus
edulis extends varies with the locality. The mussel beds of New
Brunswick, Maine, and New Hampshire are situated near the low tide
mark. Huntsman (1918), Mossop (1922), Newcombe (1935), and Warren
(1936) believed that the presence of predators such as starfishes,
sea urchins, welks, and drills limited the downward extension of
the mussel beds in this area. Scattergood and Taylor (1950) ob-
served that the mussel beds in Buzzard's Bay and other southern
New England localities are located in over 40 feet of water. They
also noted the presence of the same predators as existed farther
north, and therefore suggested that these predators were in such
small numbers that they did not prevent the establishment of beds,
or that perhaps "factors other than predators influence the depth
at which mussels grow".

The horse mussel, Modiola modiolus, according to Wiborg (1946),
is common in northern waters and along the western and northern
coasts of Norway, where it extends from just below the littoral
region to about 80 meters in depth. In general, the mussel beds
are more extensive and better developed in narrow waters with
strong tide currents than in more quiet areas.

The other two species, Mytilus californianus and Volsella
demissus, are intertidal in their distribution. Mytilus californ-
ianus is found on rocky shores where the mussels are exposed at low

tides (Clements and Shelford 1939, Fox et al. 1936, and Hewatt 1935). _Volsella demissus_, the ribbed mussel, is usually found in the intertidal zone attached to the roots of _Spartina_, where it forms large clumps, tumps, or mats (Allen and Littleford in press, Dexter 1947, Frey 1946, Mackin and Menzel 1945, and Newcombe 1947). Occasionally this species may occur subtidally, where it is attached to pilings (Allen and Littleford in press), or on the outer edges of marshes (Mackin and Menzel 1945), and it has been reported on oyster beds in the York River by Galtsoff, Chipman, Engle, and Calderwood (1947), although it is possible that these authors have confused _V. demissus_ with _B. recurvus_.

Brachidontes recurvus, by contrast, is strictly subtidal in its distribution, although limited to relatively shallow water. Engle (1945, 1948) observed that this species was present on oyster beds in Mobile Bay and Mississippi Sound, in water from 2 to 18 feet deep. Likewise, Chestnut (1949) and Frey (1946) noted the presence of the curved mussel on oyster bars in shallow water. In this investigation, it was observed that the mussel was in relatively shallow water, with the greatest abundance of the population at depths of 9 feet or less. It is also of interest that the curved mussel appears to be confined to oyster bars, there being no reports of beds of the curved mussel, such as exist in the case of _Mytilus edulis_ and _Modiola modiolus_.

The growth habits of _Brachidontes recurvus_ were found to be similar to those reported for other species, regardless of their distribution in the intertidal zone or subtidally. In all cases, the species attach to each other if a suitable substratum is not

available. Therefore small individuals are found attached on, between, and in some cases, inside of larger mussels. The curved mussel, however, is the only species in which characteristic clusters are produced. These clusters are built up from the sub-stratum in such a fashion that many more individuals are able to utilize the available space than is true of other species.

A number of environmental factors have been reported as influencing the distribution, population cycles, and physiological properties of various species of mussels. In attempting to determine which one of many factors may be important, it is well to consider the point of view of Shelford (1931), who has pointed out that the same factor is not always of major importance; that at times the biotic factors of the environment exert the greater influence, and at other times the physical factors control.

In this investigation, attention was given to salinity, since the mussel was found abundantly in areas of relatively low salinity. Mytilus edulis exists quite satisfactorily along the ocean coast and in estuaries where the salinity is relatively high and which are not too distant from the influx of water of high salinity during the tide changes (Dexter 1947). This fact probably explains why this species is not found in Chesapeake Bay above the mouth of the York River (Galtsoff, Chipman, Engle, and Calderwood 1947). Similarly, Mytilus californianus is confined to salinities from 17.00 o/oo and above. While this species can tolerate a salinity of 45.00 o/oo, values from 12.00 o/oo to 0.00 o/oo were fatal within 7 days (Fox et al. 1936).

Since Brachidontes recurvus has been reported from salinities

as high as 30.00 o/oo (Chestnut 1949, Engle 1948), it does not appear likely that high salinity is a factor in limiting the distribution of this species in the Bay. It is more likely that depth of the water, which may be associated with feeding habits, tidal action, enemies, or any number of biotic or physical factors are determining factors in regards to the presence of this species on oyster bars. On the other hand, the influence of low salinities is well marked. Experimental data show that mortality of the curved mussel is common below 6.00 o/oo and that 4.50 o/oo apparently represents a critical point of salinity. This fact would limit the upstream distribution of the curved mussel, and probably explains why it is not found at the head of the Bay. Frey (1946) observed that this species was not common on oyster bars in the Potomac River above Swan Point and below Piney Point. His observations correlate with the observations made above as to the influence of salinity and depth on the distribution of the mussel.

One of the important observations in this study was the disappearance of the mussel community during the spring of 1951. It is pointed out that this condition was accompanied by a drop in salinity during the early part of the same year. The length of life of mussel beds is an important fact when the species is of economic importance, as is Mytilus edulis, or an important fouling organism, as Brachidontes recurvus. Field (1922) observed that the length of life of the average mussel bed of Mytilus edulis was three or four years. He cites several instances in which the entire mussel population was completely wiped out in a matter of 10 days or less. In one case reported, the destruction was caused

by heavy storms, during which the tidal currents and wave action stripped the shellfish from the bottom and carried them to distant points. According to Field, other factors which will account for the destruction of mussel beds are "freshets, shifting sand and ice, freezing of mussels exposed at low tide, depredations of enemies, and suffocation from the mussel's own excrement".

Viallanes (1892) noted similar conditions in _Mytilus edulis_ and pointed out that the total amount of excrement produced by a mussel is 3 times as much as that produced by a Portuguese oyster and 18 times as much as by a French oyster. This excrement is primarily diatom shells and detritus, and results in a thick layer of mud on the bed, which ultimately suffocates the mussels.

Observations of mussels on oyster beds in the Bay show that the mussel community has a definite life span. The commonly held opinion is that this life span is short, probably no longer than three or four years at most. Considering the data on the effects of low salinity presented in this paper, and correlating these facts with the observations of Beaven (1946) and Engle (1946) on the fluctuations of salinity in the upper Bay, it is apparent that low salinity plays an important role in determining the length of life of the mussel community, and therefore the population cycle of the mussel. On the other hand, it should be remembered that _Brachidontes recurvus_ has a relatively short life cycle, and this fact, coupled with failure of spawning or the setting of spat during any one year, would also contribute materially to the destruction of the mature community.

While there was no evidence, during the period of this study,

of the collection of mud in excessive quantities on the bed, the possibility of such a condition producing deleterious effects cannot be ignored. However, considering the location of the beds of the curved mussel as compared to the location of the beds of the edible mussel, it is not likely that such a factor would be of major significance in the case of Brachidontes recurvus. The fact that Mytilus edulis lives at the edge of tidal flats would allow for the deposition of this material more readily during periods of low tide. The tidal action over the oyster beds in deeper water would tend to be more uniform and scouring in character.

The more recent studies on the aggregations of marine life have tended to emphasize the structure of the community and the particular role that organisms may have in this organization. The modern approach to ecology was well stated by Shelford (1929) that "modern ecology may be stated to be the science of communities". Similarly, Allee (1934) has pointed out that "the distinctive contribution of ecology to biological complex has been the emphasis on the fact that organisms live in communities".

With this point of view in mind, an approach was made during this study to form some definite concept of the community on the oyster bar of which Brachidontes recurvus is a part. Following the system of naming communities after the dominant or characteristic species (Peterson 1918), it was decided to call the community the Balanus-Brachidontes Association. The oyster was not considered a part of this community, as it forms the substratum to which the mussels and barnacles attach. This approach follows the

general reasoning of Clements and Shelford (1939), Newcombe (1935), and Shelford and Towler (1925), that the various mussel communities or barnacle-mussel communities are formed on some relatively firm substratum.

The mussel, Brachidontes recurvus, qualifies for the position of dominant in that it fulfills the general definition of such a form. It is the species which controls and characterizes the community directly and through its efforts on the habitat (Dexter 1947), and it occupies the available surface (Shelford, Weese, Rice, Rasmussen, MacLean, Wismer, and Swanson 1935). Balanus crenatus was present in large numbers at all stations, where it was observed to be attached to the shells of the mussel and on whatever available space was left by the mussel on the oyster shells. In many cases it showed a greater numerical abundance than Brachidontes recurvus. Considering the fact that the presence of this species prevented the growth of the bryozoans, and that it competed with the mussel for space for attachment, it was decided to consider it as a co-dominant of the community.

The bryozoans, Membranipora crustulenta and Acanthodesia tenuis, are considered the subdominants of the community because they lack the uniform distribution of the dominants and yet may replace the dominant species under certain circumstances or in certain areas. Since April 1951, an increase in the extent and distribution of these two forms has been observed. The absence of mussels during this period has enabled these two species to cover the oyster shells more completely than during the period of the study.

Because of the small numbers of the other species present and

the relatively short duration of the observations, no definite position could be assigned to them in the community. It was arbitrarily decided to consider the forms that were important to the activities of the community as influents. As a matter of fact, they may actually deserve the rank of subinfluents or even secondary forms.

The exact relationship of this association to the communities described for the marine environment is difficult to determine. Dexter (1947) pointed out that any designation of marine communities in the present state of our knowledge must be regarded as provisional. Actually, we know little of the subtidal marine communities, and even the general extent of the major intertidal communities on the Atlantic Coast has not been determined. Therefore, the designation of this community as the Balanus-Brachidontes Association is provisional.

The relation of this association to the oyster community of which it is a part may be a subject for some debate. It is recognized that oysters are true dominants, which build up the communities and the habitats which they control (Clements and Shelford 1939). Petersen (1908) pointed out that oysters can reproduce in conditions resulting from their own presence. Likewise, they can widen their own area by lateral extension due to the growth of shells at the periphery. In a very real sense, the oyster community may be considered a climax community.

The exact ecological position of this community, however, is in no sense clear. Clements and Shelford (1939) consider it as a fragmented faciation. If this definition is to be accepted, then of course, the Balanus-Brachidontes community would have to be

considered part of this faciation. Petersen (1908) noted that with reduction in numbers of oysters by fishing, the beds in the Lim Fjord become covered by cockles and mussels.

The oyster beds on the Atlantic Coast are similar in many respects to those of Europe, although the oyster in question is another species, Crassostrea virginica. Truitt, quoted by Clements and Shelford (1939), stated "that in the brackish waters of the Chesapeake Bay, the oyster builds up a community which includes a number of species that are of uncommon occurrence outside the oyster-dominated area".

Since the mussel does not occur on all oyster beds in the Chesapeake Bay, it does not appear desirable to consider it as a co-dominant with the oyster in a community. Therefore, for the present, the community is designated as the Balanus-Brachidontes Association of the Oyster Community.

GONAD DEVELOPMENT AND SPAWNING

Coe (1943) observed that the majority of the pelecypods have separate sexes, with an occasional hermaphrodite making its appearance. He found that a study of the juveniles of Venus and Ostrea was necessary in order to ascertain the sexual condition of the species. In addition to these forms, examination was made of specimens of Volsella demissus, Mytilus edulis, and Mytilus californianus. In none of these species did he find any evidence of ambisexuality except in undifferentiated gonads and an occasional hermaphrodite. None of these species has a distinctly juvenile phase of sexuality, and the occurrence of males and females was

about equal. Wiborg (1946) found that the sexes of Modiola modiolus are separate, with hermaphrodites occurring in 2 to 8% of the individuals. The proportion of males to females in this species is usually 1 to 1, but on some occasions more males than females may be found among the smaller individuals, and more females among the larger ones.

In Brachidontes recurvus resemblance to the above forms was evident in that the sexes were approximately evenly divided and no ambisexuality was noted. Hermaphroditism was not observed in the forms examined.

The protracted spawning period of Brachidontes recurvus is similar to conditions reported in Mytilus californianus Young (1946), even though different seasons of the year are involved. The question of critical temperatures and spawning of the curved mussel has already been considered. The observations reported in this study support the findings of Young and others on Mytilus californianus. They are in direct contrast to those of Nelson (1928a), who reported that lamellibranchs fall within the group which breed at a definite temperature. The same author's observation that the curved mussel spawns at a temperature of 25° C. is obviously inconsistent with the facts.

AGE AND GROWTH

In this investigation the determination of age was based on the presence of the annual rings, or "growth rings". The validity of these rings as actual indicators of age is by no means accepted for all lamellibranchs under all conditions of growth and survival.

Massey (1914) observed that rings on the European oyster had some value as indicators of age. Mead and Barnes (1904) questioned the validity of similar rings in the determination of Mya arenaria. Newcombe (1935b), on the other hand, noted that some rings on Mya arenaria in the Bay of Fundy region were annual in character and thus indicative of age. However, he also pointed out that they were not of equal validity throughout the life of the animal. The same author (1936) noted the absence of annual rings on the same species in Chesapeake Bay and later (1936a) suggested that regional differences in the shell of pelecypod mollusks might determine whether "annual growth rings" were produced or not.

In mussels, little attention has been given to the question of annulations, since most of the growth studies carried out did not consider age or used a population of known age. Wiborg (1946), however, demonstrated the existence of growth rings that were annual in character in Modiola modiolus. The rings observed in Brachidontes recurvus could easily be divided into two types, those that were obviously "lines of arrested growth" (Mossop 1922), and those for which no valid explanation except that of annual rings was possible.

On the basis of the estimations of growth, it is noted that Brachidontes recurvus has a rather short life span, particularly when contrasted with Modiola modiolus, which has a life span of 18 years or longer. Information on the probable life span of the other species of mussels is unavailable. Newcombe (1947) suggested that in the case of Mytilus edulis and Volsella demissus, the life span certainly would exceed that of the curved mussel. Personal observa-

tions on <u>Volsella</u> <u>demissus</u> in Chesapeake Bay indicate that the

life span is between 10 and 20 years.

SUMMARY AND CONCLUSIONS

Brachidontes recurvus (Rafinesque), the curved mussel, is an important fouling organism on oyster bars of Chesapeake Bay that are located in shallow water of low salinity and in the adjacent tributaries. In an effort to elucidate some of the more important aspects of the biology, ecological relationships, and growth of this important bivalve, the present investigation was conducted from January 1950 through April 1951.

The mussel population on Hackett's Bar, which is located on the Western Shore of the Bay approximately 2 miles above the mouth of the Severn River, was chosen for study. Collections of mussels were made every two weeks for the duration of the study.

A group of mussels representing the size range observed at each collection from March 1950 through April 1951 was fixed in Bouins and stained with Haematoxylin and Eosin and Mallory's Triple Stain before examination of the gonads and the internal anatomy.

Plankton samples were collected simultaneously with the collection of mussels, in order to determine the seasonal distribution and relative abundance of the larval stages. At the same time, determinations of temperature and salinity of the water just above the oyster bar were made.

Mussels brought to the laboratory within 24 hours after collection were scrubbed, washed, and dried. These specimens were used for the determination of linear and weight indices of growth.

On the basis of this study, the following conclusions may be made:

1. While the shell of <u>Brachidontes</u> <u>recurvus</u> shows a characteristic appearance and shape, the anatomy is identical with that of <u>Mytilus</u> <u>edulis</u>, as described by Field (1922).

2. The curved mussel is widely distributed on oyster bars in the upper Bay and its tributaries between salinities of 12.00 o/oo and 8.00 o/oo.

3. The growth habits of the mussel result in considerable variation in shell width and curvature, as well as misshapen individuals.

4. The size range of the population extends from less than 0.50 mm. to a maximum size of 62.9 mm., the major portion of the population being between 30.00 and 59.99 mm. in length.

5. While there is no relationship between the number of mussels and the size of the shell of the oyster serving for attachment, the average density of the mussel population was found to be 1 mussel for every 44 square mm. of surface area.

6. There is an inverse relationship between density of the population and depth of the water. The greatest abundance of the population occurs in less than 10 feet of water, and in over 20 feet of water the distribution was occasional and sporadic.

7. The presence of cycles in the life history of the population has been established. This probably explains the fluctuation in abundance of the population on oyster bars.

8. The importance of low salinities as a cause of mortality and population cycles has been established.

9. The critical low salinity for survival of the mussel is 4.50 o/oo, at a temperature of between 18.0 and 21.0° C.

10. The mussel community established on the oyster substratum is designated as the Balanus-Brachidontes Association. The co-dominants of this community are Balanus crenatus and Brachidontes recurvus. The subdominants are Membranipora crustulenta and Acanthodesia tenuis.

11. It is concluded that the Balanus-Brachidontes Association is a major entity of the Oyster Climax Community.

12. The gonadal tissue of both sexes of the mussel, when mature, occupies the entire mantle and mesosoma, and penetrates into the digestive diverticula, where it is found adjacent to the liver canals.

13. The curved mussel is dioecious and does not show alternation of sex or hermaphroditism.

14. Sexual maturity exists from June through October, and perhaps longer in some cases.

15. It is concluded that spawning takes place from June until November, with the greater proportion of spawning occurring in late summer and early fall.

16. Spawning is independent of the height or the direction of the tide, and no single critical temperature influences it.

17. On the basis of annual rings interpreted as being indicative of age, it is concluded that the maximum age for the majority of the mussels is 5 years, with a small proportion of the population living beyond that time.

18. The size variation with age extends over a wide range be-

cause of the varying rates of growth and the protracted period of setting, which extends from June through November.

19. Investigation of the indices of growth, width, thickness, and weight, as compared to length, show that growth is a linear process.

20. The data show that the greatest percentage of growth takes place under 25 mm. in length.

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