THE GROWTH, SEXUAL DEVELOPMENT AND INCIDENCE OF INFECTION OF *MALACOBDELLA GROSSA* IN THE RAZOR CLAM, *SILIQUA PATULA*

by

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INTRODUCTION

The commensal nemertean worm *Malacobdella grossa* inhabits several Lamellibranchs on the coast of Europe, on the Eastern Coast of North America, and the razor clam, *Siliqua patula*, on the Western Coast of North America. The unusual mode of life has stimulated research on this unique genus in an effort to determine its relation to free living nemerteans. The ultimate aim of establishing its taxonomic position has led to a number of investigations on the taxonomy of the species within the genus, the embryology, morphology and histology, and the nature of the existence within the host. Other than a few records of incidence of infection, size at maturity, and conflicting descriptions of the spawning period, little has been written on the later life history.

The majority of work on *Malacobdella* has been done in Europe. With one exception American investigators have been concerned only with the taxonomy of the species.

Blanchard in 1845, according to Riepen (9, p.327), made the first detailed observations on the morphology of *Malacobdella grossa*. Hoffmann in 1877-78 (4, pp.1-27) contributed additional information on the morphology and described early development as far as the 14-day old larva. Von Kennel in 1877-78 (5, pp.305-381) carried on a very similar investigation to that of Hoffmann. Gering in 1911

(1, pp.673-720) also continued the investigation on morphology and early development through the cleavage stages. Riches in 1893 (8, p.5) made brief observations on the spawning period of Malacobdella in collections of nemerteans taken from Plymouth Sound. Hammarsten in 1918 (3, pp.1-95) described in great detail early development and the spawning period for Malacobdella at the Bergen Biological Station in Norway. Riepen in 1933 (9, pp.323-496) described completely the histology and morphology of Malacobdella grossa and reviewed briefly the work of earlier authors on larval development and spawning period.

The only description of Malacobdella from the razor clam, Siliqua patula, was made by Guberlet in 1925 (2, pp.1-14) from specimens taken on the Washington Coast. Guberlet's investigation included the identification of the Pacific Coast species, incidence of infection, and host-commensal relationship.

Very little of each above investigation is devoted to aspects of the later life history of Malacobdella. The maximum sized Malacobdella found were recorded by the following authors. Riepen (9, p.331) stated that Blanchard found Malacobdella in Mya truncata as long as 40 mm. Guberlet, (2, p.6) working with Malacobdella from Siliqua patula on the Washington Coast, reported the largest specimen to be 50 mm. long and 11 mm. in width. The largest specimen taken from Cyprina in the Kieler Förde by Riepen (9, p.331) was 30 mm. long.

There is a considerable disagreement amongst past investigators over the question of when spawning takes place in Malacobdella grossa. Hoffmann (4, p.1) thought spawning occurred from November or earlier until March in the North Sea of Europe. Riches (8, p.5) described finding ripe individuals from late summer until the middle of December. Gering (1, p.701) believed the spawning period in the "Ostsee" off Norway to start in July and continue until September. In August he placed specimens of Malacobdella in an aquarium, and spawning occurred followed by fertilization; development proceeded as far as the first cleavage stage. Hammarsten (3, p.4) found spawning to occur from the middle of March to the middle of April, but he believed any yearly spawning time would vary with the particular winter temperature. Hammarsten found developing stages of Malacobdella in the plankton from March through April in the vicinity of the Bergen Biological Station in Norway. His investigation was not carried on through the summer months.

Riepen (9, p.486) made no attempt to describe the spawning period. His specimens were stimulated to spawn under aquarium conditions. It was Riepen's belief that local environmental conditions caused variations in the spawning time in the findings of the previous authors.

Gering (1, pp.675-676) recorded incidence of infection in three size groups of Cyprina islandica in the "Ostsee." The large clams had an incidence of infection of 71.5 per cent. For the medium sized clams the incidence of infection was 69 per cent, and for the smallest clams examined 32 per cent were found to be infected. These clams were not segregated on the basis of age. Therefore only a general comparison of incidence of infection can be made. Gering did not examine clams smaller than 2 cm. in width. In Kieler Föhrde, in another group of "Cyprinen" examined, the incidence was 47 per cent. In the same area von Kennel (5, p.312) found an incidence of 58 per cent.

Guberlet (2, p.2), in specimens of razor clams from the Washington Coast, found in September of 1924 3 out of 14 clams infected. In two other groups, 7 out of 42 clams and 30 out of 50 clams were infected. Guberlet stated that McMillin found 57 out of 65 infected in a group of clams washed up by a storm. Guberlet also recorded in one instance finding more than two Malacobdella in a clam. However, Guberlet does not state the size of the specimens found or in what size or age of clam they were found.

MATERIALS AND METHODS

All collections of *Malacobdella grossa* were made along the Clatsop County beaches of Oregon from Tillamook Head south of Seaside, Oregon to the Columbia River. The specimens were collected from the razor clam, *Siliqua patula*, between February 1950 and February 1951. All razor clams were dug on the beach and removed to the laboratory. There the clams were opened, the specimens of *Malacobdella* were removed, fixed in flat position between cover slip and glass slide, and stored in AFA fixative. A record was kept of the worms taken from each clam.

The razor clams were later measured for length. The age was determined from annual winter checks by the method specified by McMillin (6, pp.1-52) and (7, pp.1-7), Weymouth, McMillin, and Holmes (11, pp.201-236), Weymouth and McMillin (10, pp.543-567), and substantiated for the species in Oregon by the writer.

Because the extent of contraction of the nemertean worm was variable at fixation, measurements of either length or width alone were inadequate for a comparison of sizes. To avoid errors resulting from this fact, a system was devised for the measurement of area. Thirty specimens including all sizes were selected. Projections of the worms were made, and the outline of each worm was traced. Each outline was measured for total length and width. The width was taken across three regions of the body: head, middle, and posterior immediately anterior of the posterior sucker. The area enclosed by the outline of the worm was then measured with a planimeter.

The length multiplied by the average width gave a rough rectangular area pattern. When the rectangular area was divided into the area obtained from the planimeter reading for each worm, a constant was derived. The final constant of 0.956 was an average of that obtained for all the thirty outline drawings.

Each nemertean was then directly measured for length and width in an identical manner to that used on the outline drawings. The area was obtained for each specimen by multiplying the length times the average width and then by the constant 0.956 as shown in the following formula.

Length X Average Width X Constant = Area

Since Malacobdella are sexually dioecious it was necessary to determine the sex of each worm. In the larger females this was possible by examination of gonad smears under a microscope. With the males and immature stages this was impossible. Microscopic sections were taken through the region of the gonads to detect the stages of development and the sex of all worms in which the sex could not be determined by direct examination. After all measurements were made a portion of each worm was embedded in paraffin, sectioned, and stained in iron hematoxylin. The slides were examined to determine the sex and the stage of sexual maturity.

PRESENTATION OF DATA

The age classes of the razor clam can be defined in the following manner. The number one age class from February 1950 to February 1951, the interval over which these collections were made, consisted of clams having one annual winter check. This age class had set on the beach during the previous late summer and fall. Their ages from setting would vary from about 6 months in February of 1950 to 18 months in February of 1951. The second year class clams were one year older than the previous class with an age of 18 months in February 1950 to 30 months in February 1951. The third year class clams were one year older than the second year class, with an age of 30 months in February 1950 to 42 months in February 1951. The fourth year class were one year older than the third year class and were marked with four annual winter checks. Their ages from setting were 42 months in February 1950 to 54 months in February 1951.

It was common to find considerable variation in size at any particular date within each year class, since the time of setting varies with individual clams from midsummer to midfall.

Seasonal Infections of the Host

The months for the yearly infection of the host by Malacobdella grossa can be estimated from Graphs 1 and 2 and Table 1. The first definite indication of an infection in the one year class of razor clams occurred in August (Graph 1, A to E). A few small Malacobdella were first collected about the middle of August. The total size-frequency by month for all age classes combined indicates this same time of initial infection (Graph 2). In Table 1 the August incidence of infection was slightly greater than that of May and June in both the one and two year classes of razor clams. The small specimens continued in the majority during November and December and through January and February. Likewise there occurred a continual increase in the incidence of infection in the first year class of the razor clam. In March and April from the second, third, and fourth year class, small Malacobdella still were found; but they were slightly larger than those taken during the preceding months, making it doubtful that new infections continued to occur. It appears as though March, April, May, June, and July are the months in which no new infections occur. From the data obtained it was impossible to determine whether the infections of the clam by Malacobdella were continuous or occurred in a series of periodic invasions.

It cannot be known whether or not any of the smaller specimens were missed in the examinations of clams. Hammarsten (3, p.7) states that he found none smaller than 5 mm. in length inhabiting "Cyprinen" on the Norwegian Coast. Von Kennel (5, p.312) found in Cyprina a partly developed form only 0.509 mm. in length and several 3 to 4 mm. long, which he called young Malacobdella.

The examination procedure the author employed certainly recovered almost all the specimens of 7 or 8 mm. or longer. Many smaller than 5 mm. in length were detected with the naked eye.

In the first year class of the razor clam two specimens of Malacobdella were found before the August infection occurred, one in March and one in May (Graph 1, A and B). An examination of the clams harboring each of these shows, that although both seem to be of the first year class, they were larger than the average for the particular month. This suggests that they may have been members of a small group of clams that were first found on the beach in late July and August, at least two months ahead of the peak of the yearly setting of young clams. In these clams infection must have first occurred during the previous fall.

An attempt was made to examine a number of the clams of the 1950 set during January 1951. The specimens available were unfortunately all of a small size group from a later fall set. Of the six specimens examined with the aid of a dissection microscope, none yielded specimens of Malacobdella grossa.

Relationship of the Age of the Host to the Size of Malacobdella grossa

The previous analysis of infections in the first year class of razor clams suggested that the first infection possible was preceding the formation of the first winter growth check. The maximum size Malacobdella in any year class of razor clam would then have an age dating from this first fall infection. In the first year class of razor clam the maximum age of Malacobdella (Graph 1, A to E) would be 4 to 7 months in March and April of 1950 and 14 to 17 months in January and February of 1951. Following through a graph where a continuous series of months are shown for the various age classes of razor clam, maximum sizes of Malacobdella can be associated with a definite maximum age of the host, provided that the samples are large enough.

The mature males of Malacobdella were known, as discussed below, to average smaller than the mature females. Therefore the growth of each sex was analysed separately.

The sizes of the females that are believed to represent maximum growth are: November (Graph 3, A) area 136.7 mm.^{2} and length 45.0 mm., at an age of 18 to 21 months; and November (Graph 3, K) area 431.0 mm.^{2} and length 46.5 mm., at an age of 36 to 39 months. The maximum rate of growth for the females is plotted in Graph 5.

The sizes of the males that are believed to represent maximum growth are: May (Graph 4, A) area 92.5 mm.^{2} and length 21.5 mm., at an age of 6 to 9 months; April (Graph 4, E) area 202.0 mm.^{2} and length 27.9 mm., at an age of 16 to 19 months; and November (Graph 4, L) area 426.0 mm.^{2} and length 43.5 mm., in a four year old clam at an age of 46 to 49 months. The maximum rate of growth for the males is plotted in Graph 5.

The age of specimens older than 18 to 21 months in the females and 16 to 19 months in the males is questionable. The samples are not of an adequate size to necessarily include the larger specimens. It appears as though the growth rate of males is initially faster than that of the females, but that the growth rate declines steadily thereafter. The growth rate of the female, although slower than the initial rate of the males, continues unchanged to a greater size than that of the male. The maximum size specimen found of each is approximately equal, but it probably takes the male longer to reach a maximum size.

To further check the maximum size, a series of five clams of ages between 5 and 8 years were checked for larger specimens of Malacobdella. None were found larger than those from the two and three year age group.

A further confirmation of the growth rates may be had from following predominant size groups through a series of consecutive monthly samples. In Graph 3, A to G of the females this is clearest. The predominant group of every monthly sample from November and December in the first year class to November and December in the second year class increased in size. The growth rate can be followed beyond the one year level stated above, to August in the third year class of razor clams, although in most of the monthly samples, the size group is represented by only one specimen.

Growth in the males is impossible to follow from an increase in size of predominant size groups (Graph 4). If growth between monthly size groups exists, the samples are not large enough to demonstrate it.

From the data on growth rates it can be estimated that the female Malacobdella reach a maximum size in about three years. The males reach the same size somewhat later between three and four years of age. The total duration of the infection is unknown.

The yearly increment of growth in males for the first three years varies between 100 $mm.^2$ and 140 $mm.^2$ This is actually a decrease of growth rate with each succeeding year of age. The females during the first year make an approximate growth of 100 $mm.^2$ and during the second year over 200 $mm.^2$ of growth. Further growth in the females is much slower.

Observations on Spawning

Each month during which large females were collected, ova were seen in the ovary that were indistinguishable from mature eggs. From August to February in nearly every sample of Malacobdella collected, occasional specimens placed in sea water at room temperature would discharge eggs. Specimens placed on a slide in preparation for fixing frequently discharged eggs when a slight pressure was applied. The eggs examined appeared mature in every instance.

Early stages of oögenesis were present in the ovary from March until August. The developing oögonia began as a few cells differentiating from the epithelium of the ovary walls in March and April. In August a large amount of the ovary consisted of developing oögonia. A few ripe eggs were present in the lumen, and appeared to be the products of the first differentiating ova rather than older eggs undergoing degeneration.

From a study of the gonad sections it was impossible to limit the actual period of spawning. The only positive method of determining the spawning period would be to obtain the eggs and young

Malacobdella free in the ocean. In the plankton tows that were made, the author found it impossible to identify either eggs or larval stages of Malacobdella. Sperm were present in the testes for every month of the year during which collections were made.

Size at Maturity

Guberlet (2, p.7) stated that Malacobdella are found sexually mature with a length of less than 20 mm. This would correspond to an area measurement of about 80 to 90 $mm.^2$

The first certain identifications of male Malacobdella were made when sperm could be seen in the testes. The minimum size of mature males in the samples was about 10 $mm.^2$ Immature individuals were found up to 20.5 $mm.^2$ in which sex differentiation had not occurred.

The minimum size at which the gonads were distinguishable as developing ovaries varied from 13 to 16 $mm.^2$ Specimens as small as 30 $mm.^2$ had one or two eggs in the last stages of development in each ovary. The smallest specimen definitely observed to have mature eggs was 78.3 $mm.^2$

In the larger females the ripe ovaries fill the largest part of a cross section of the adult animal (Fig. 1). The testes vary in size from minute sacks (Fig. 3) in the smaller specimens containing a small quantity of loosely packed sperm, to organs densely packed with sperm (Fig. 4) and as large in cross section as a large ovary.

Incidence of Infection

For the details of the incidence of infection by month and in the various year classes see Table 1. The over-all monthly incidence increased from February of 1950 through January and February 1951. The increased incidence of infection is greater in the one and two year class clam, as would be expected. The February 1950 samples were not separated so that incidence of infection of the year classes could be determined. However, these clams probably were nearly entirely members of the first and second year classes. As indicated there were five of the clams collected that harbored two worms. In each clam at least one of the nemerteans was very small and immature.

Table 2 is a listing of the specimens found in each age class of clam for various months. The specimens are divided into immature, females, and males. For every year class of razor clam except the second, the ratio between males and females can be considered to be on a 50-50 basis. This also applies to the total incidence.

DISCUSSION

Since the lapse of time between spawning and infection is unknown, it is very difficult to relate the two seasonal occurrences. None of the embryological investigations of Malacobdella carried the development from the egg to the size of Malacobdella first found to infect the razor clam. Although the ovaries were full of ripe ova during the winter months and the ovary walls were free of developing eggs, spawning probably does not occur until spring. Spawning must certainly take place from March through May if not over a longer period. A spring spawning period would seem more logical on the basis of the first infection occurring in August. The ripe eggs are probably held over the winter months until warmer spring temperatures.

The small immature specimens between 1.5 $mm.^2$ and 4 $mm.^2$ were considerably larger than the largest Malacobdella described by Hammarsten in his embryological study. Intermediate stages are unknown.

It is doubtful if the small forms between 0.3 and 0.4 mm. long found by von Kennel (5, p.312) were Malacobdella. The description given does not distinguish them from intermediate stages of trematodes often found inhabiting clams during this investigation. Riepen (9, p.480) considered von Kennel's forms to be Turbellarians.

Thus two important questions remain unanswered: (1) the length of time of development from the egg to the smallest stages found in the clams, and (2) the mode and place of existence of Malacobdella before infection.

The data are inadequate to accurately determine the time interval in growth from the smallest specimens to the mature individuals.

It is impossible to state exactly for how many months each year new infections of the clams take place. The continual recovery of small Malacobdella through January and February may be the result of a slower rate of growth for the winter months, rather than infections recently acquired.

From a comparison of the growth rates and the size at maturity, it is estimated that the females live through 2 or 3 spawning seasons. The uncertainty of the age of the large specimen found, made it difficult to predict the maximum age of survival and thus the total number of spawnings that might occur. The males mature earlier and at a much smaller size. The largest male Malacobdella collected could have lived through four yearly spawning seasons.

All size records of authors cited except Guberlet's (2, p.6) are smaller than the maximum size found in this investigation. When both length and width are considered the maximum size found by Guberlet is almost identical to the maximum size recorded in this investigation.

The figures on incidence of infection point to the accumulative effects of successive yearly infection in the older clams. The incidence of infection does not occur at a constant rate through successive year classes. This may result from several limiting factors. (1) The percentage of incidence of infection may differ from year to year. (2) An appreciable mortality rate may exist during the entire life span of the nemertean. (3) The infection of the clam may vary with age. All of these factors may be operative and any one of them may be most influential.

SUMMARY

1. Periodic collections of Malacobdella grossa were made from the razor clam, Siliqua patula, from February 1950 to February 1951. The nemertean worms were measured and the age of each host was determined.

2. Yearly infections, evident by the finding of small size Malacobdella, occur from August to February. Nothing is known of the manner and characteristics of the first infections.

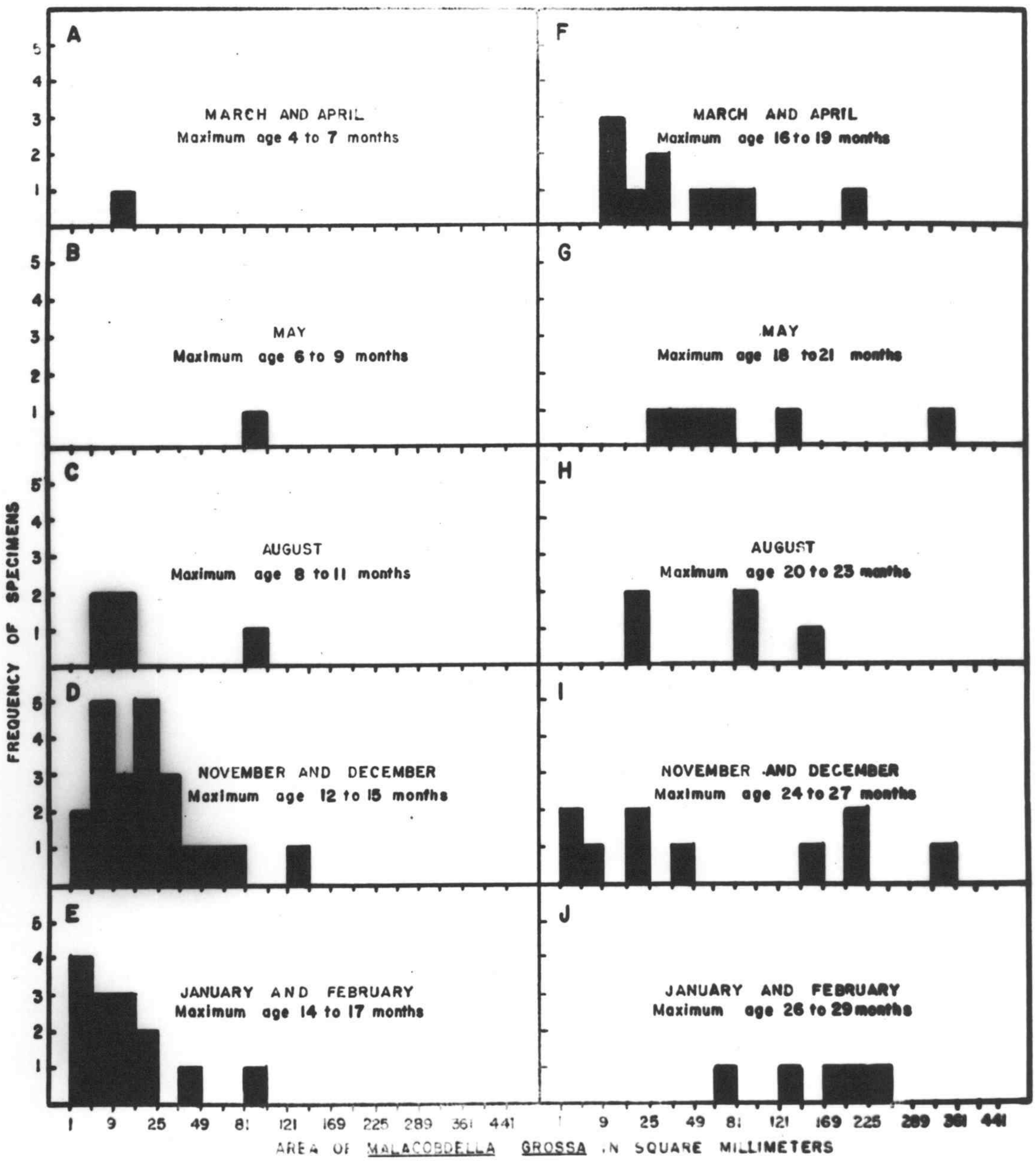
3. The sexes were found to have different growth rates. The females reach maximum size in 2 or 3 years: a rapid constant rate of growth continues for about 18 to 21 months to an area of about 340 $mm.^2$ The male has a very rapid initial growth continuing for about 6 to 9 months, and the rate of growth decreases thereafter. The maximum size is attained at about 3 or 4 years of age. The maximum size was the same for both sexes, about 420 $mm.^2$ in area and 46 mm. in length.

4. Malacobdella with apparently mature eggs were found throughout the year. The maximum number of mature eggs in the ovary occurs from November through May.

5. Mature males were recorded with an area of 10 $mm.^2$ and a length of 7 or 8 mm. The smallest female with definitely mature eggs had an area of 78.3 $mm.^2$ and a length of 16.3 mm.

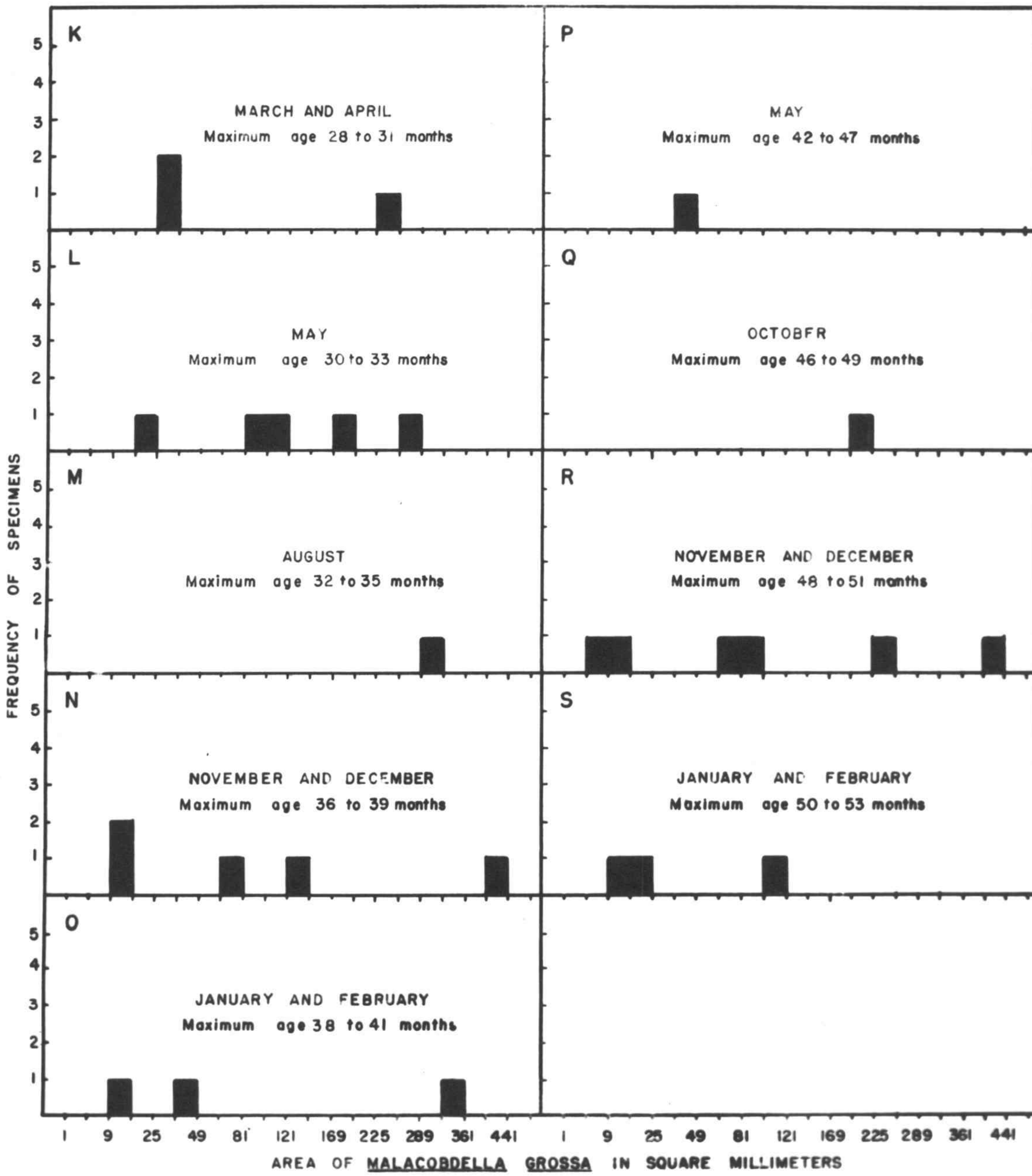
6. The incidence of infection and the number of immature, female, and male Malacobdella are recorded by month and by year class of the host in Tables 1 and 2.

GRAPH I



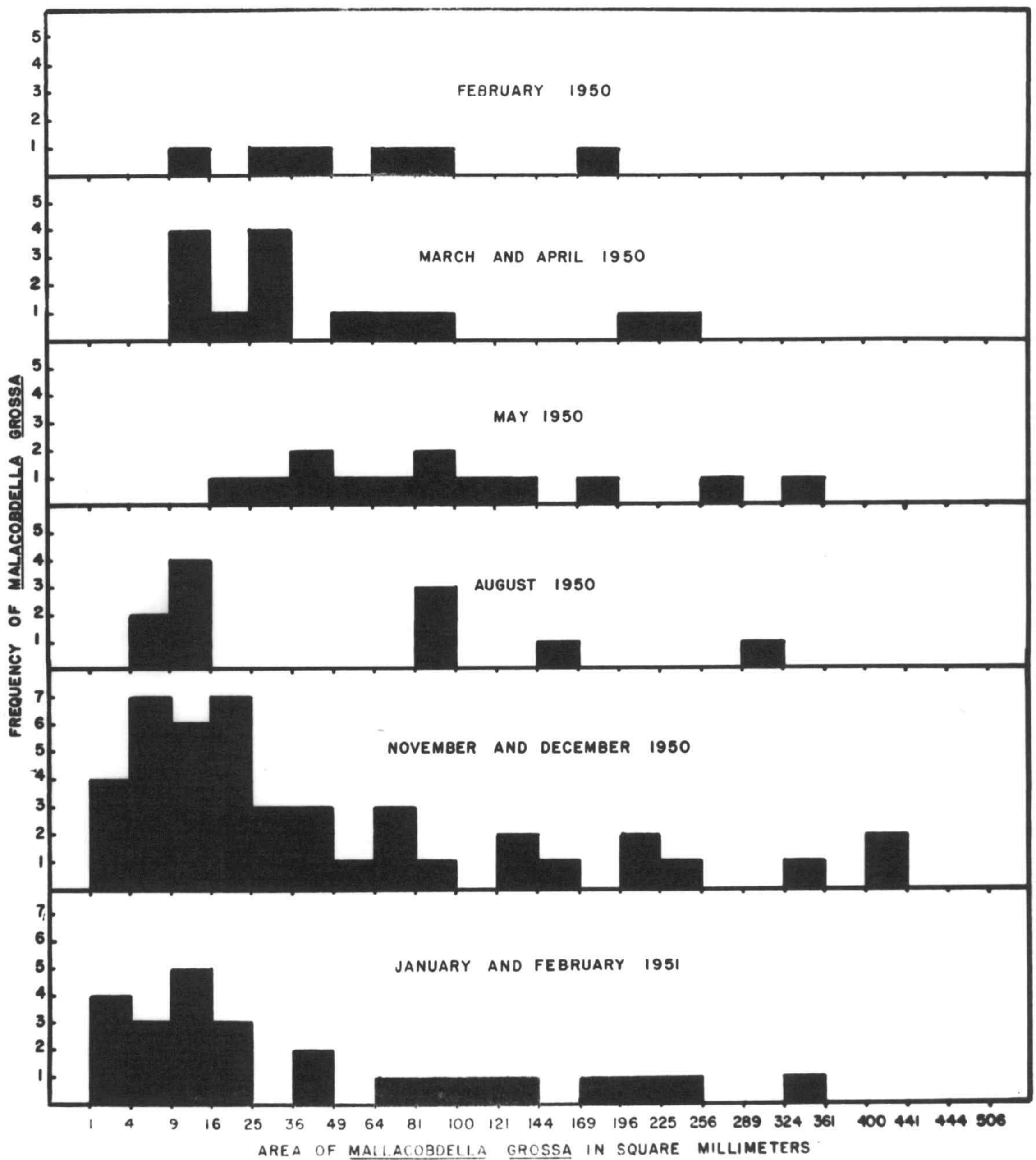
Size—frequency relationship of *Malacobdella grossa* for designated months from March 1950 to February 1951. A to E are from razor clams in the first year class, and F to J are from razor clams in the second year class. Continued on the following page.

GRAPH I (CONTINUED)



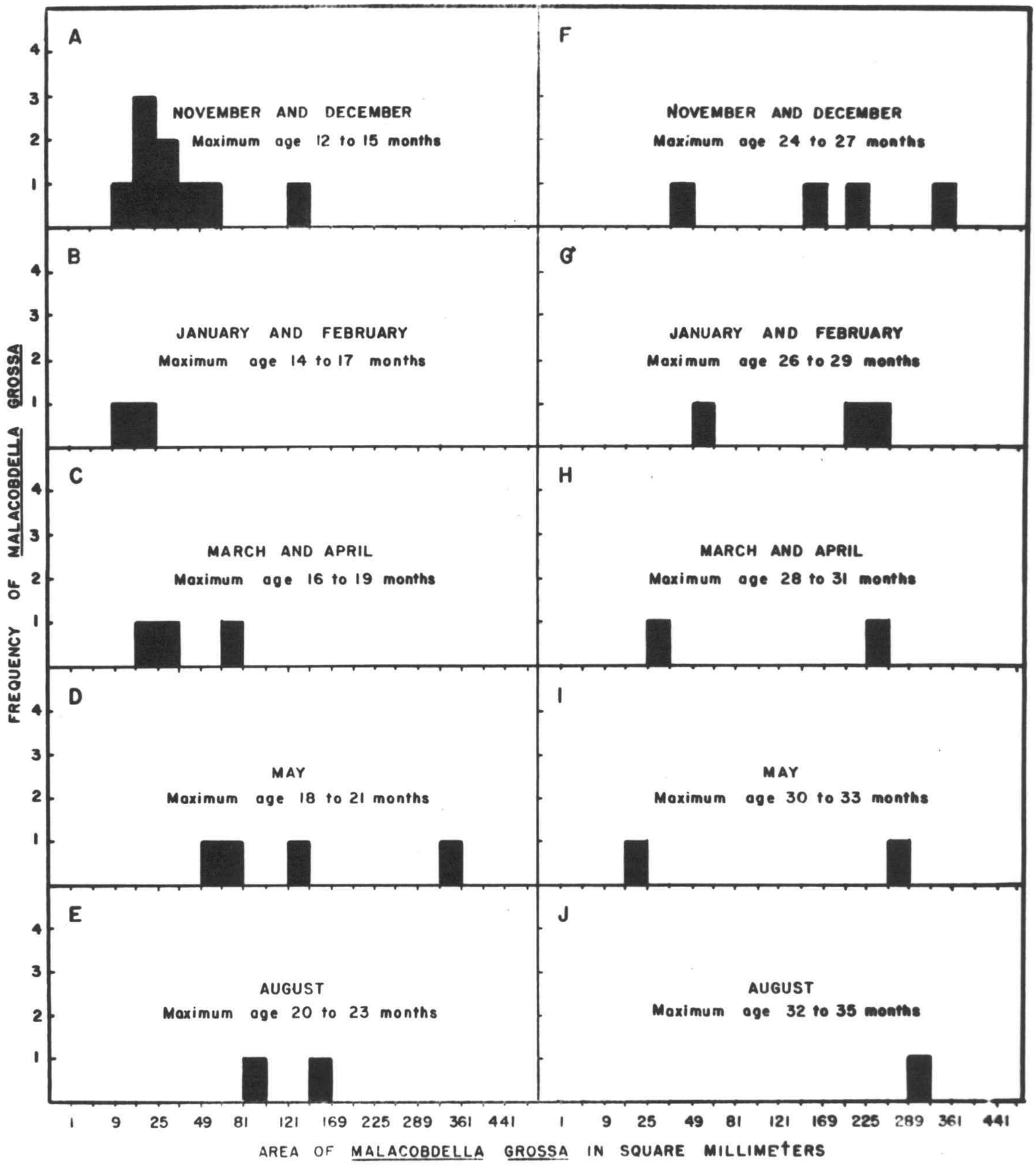
Size-frequency relationship of *Malacobdella grossa* for designated months from March 1950 to February 1951. K to O are from razor clams in the third year class, and P to S are from razor clams in the fourth year class.

GRAPH 2



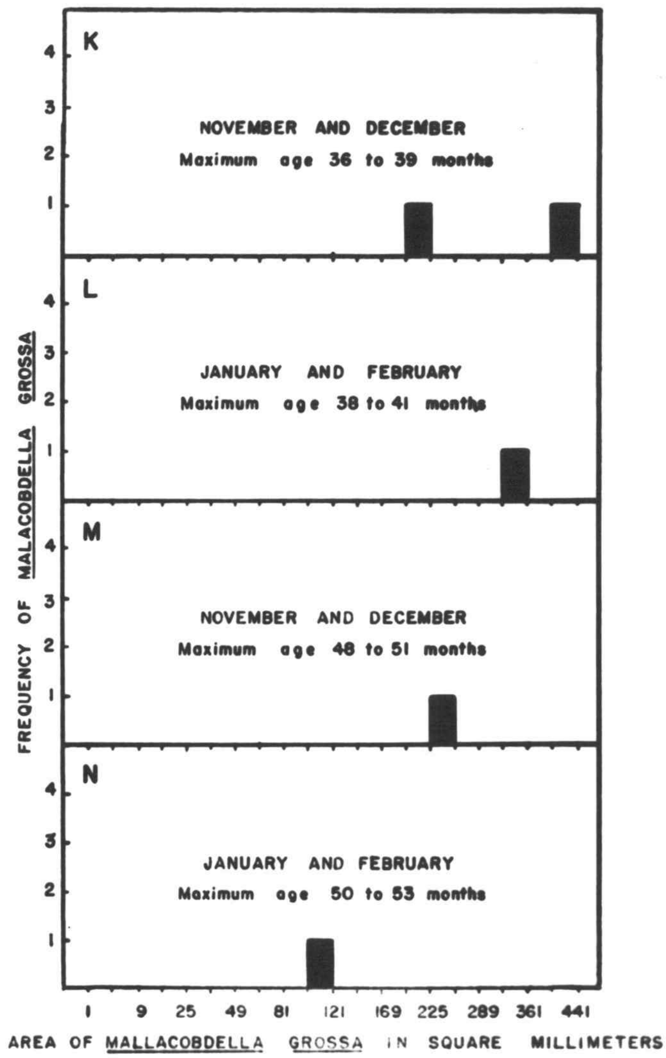
Size-frequency relationship of Mallacobdella grossa for designated months from February 1950 to February 1951.

GRAPH 3



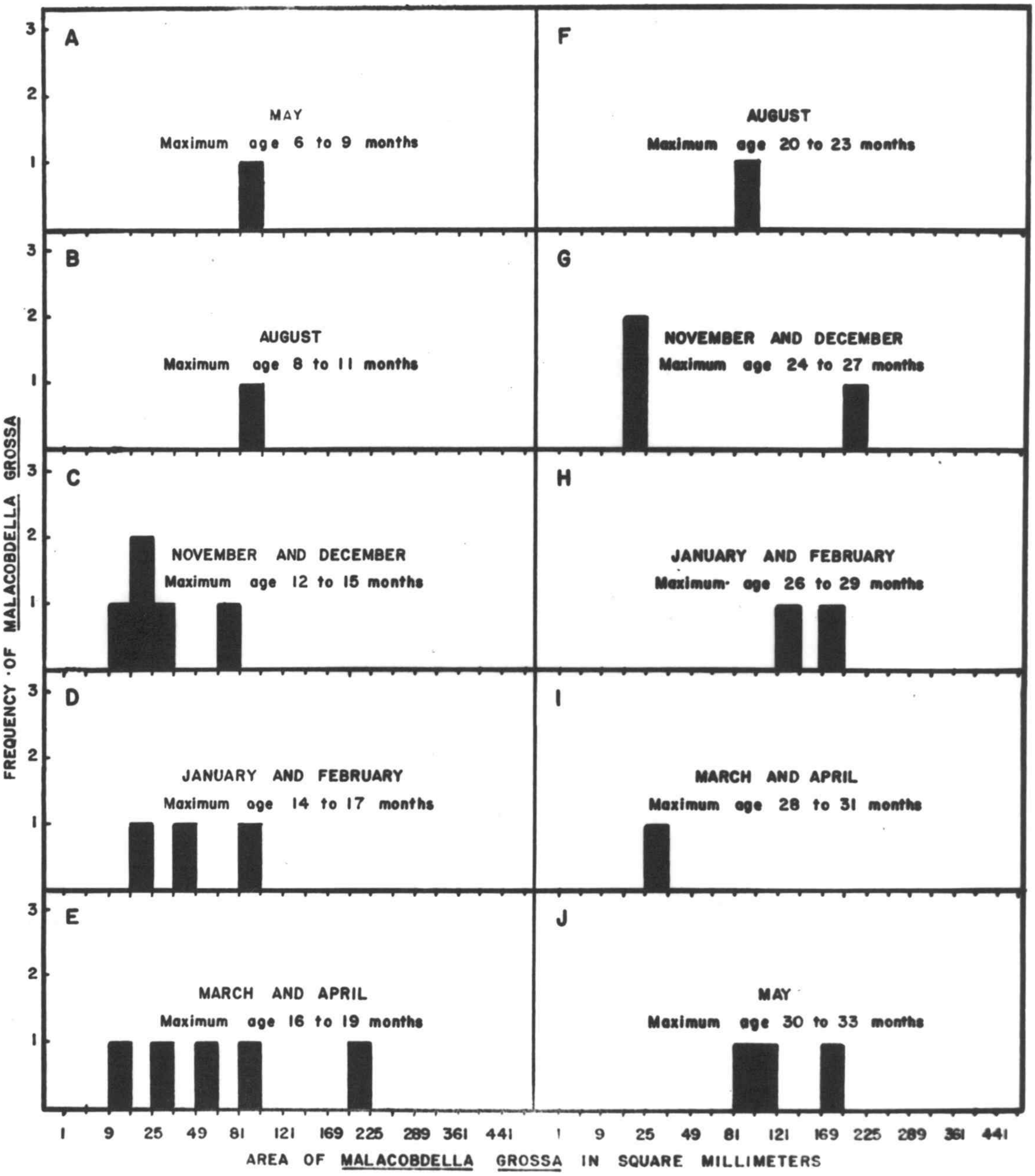
Size-frequency relationship of female *Malacobdella grossa* for designated months from March 1950 to February 1951. A and B are from razor clams in the first year class, C to G are from razor clams in the second year class, and H to L are from razor clams in the third year class. Continued on the following page.

GRAPH 3 (CONTINUED)



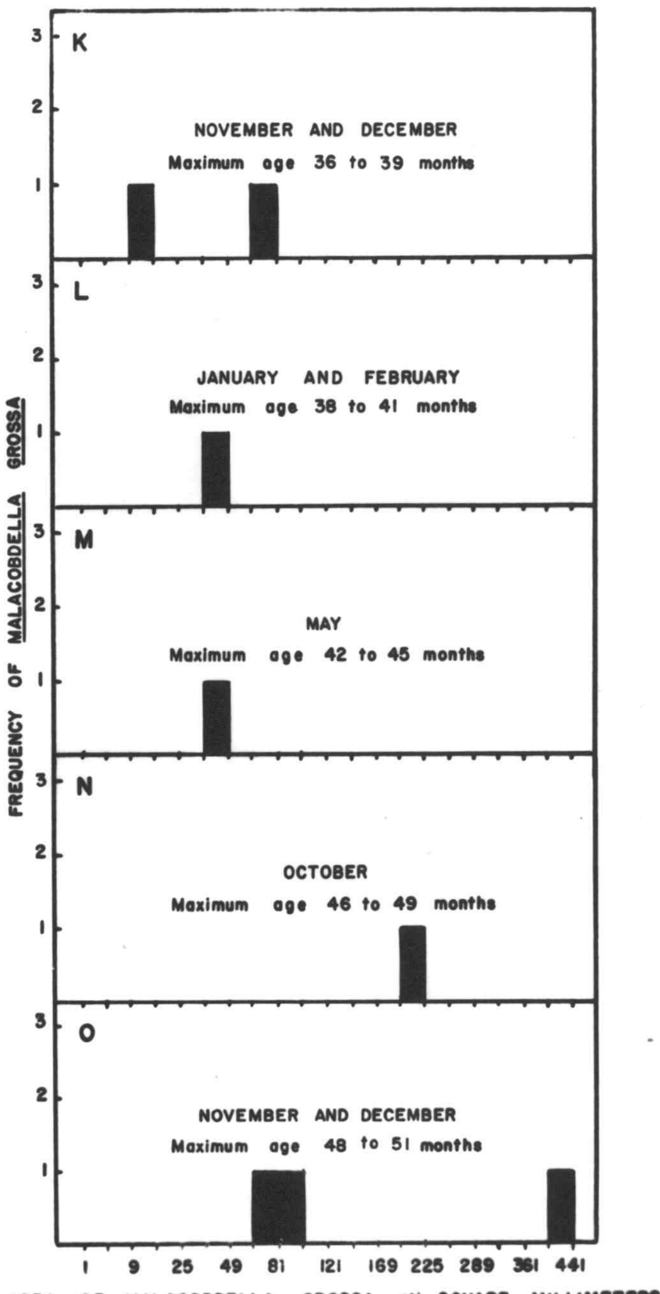
Size-frequency relationship of female *Malacobdella grossa* for designated months from March 1950 to February 1951. M and N are from razor clams in the fourth year class.

GRAPH 4



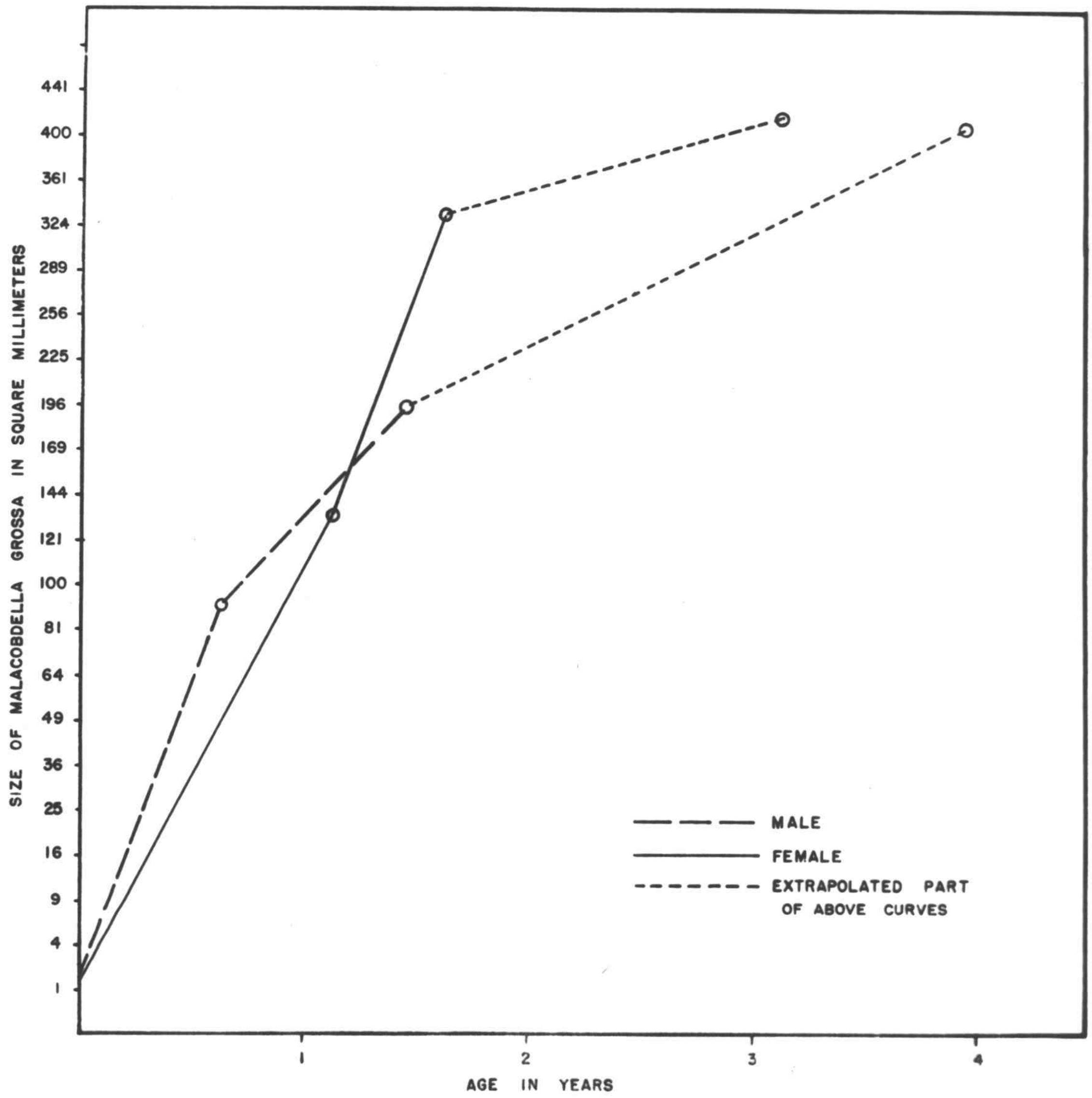
Size–frequency relationship of male *Malacobdella grossa* for designated months from March 1950 to February 1951. A to D are from razor clams in the first year class, E to H are from razor clams in the second year class, and I to L are from razor clams in the third year class. Continued on the following page.

GRAPH 4 (CONTINUED)



Size-frequency relationship of male *Malacobdella grossa* for designated months from March 1950 to February 1951. M to O are from razor clams in the fourth year clams.

GRAPH 5



Maximum size to age relationship of <u>Malacobdella grossa</u> for each sex.

Table 1

	Month	February	March April	May June	August	October	November December	January February	Total
1st year class	Clams examined		6	15	29*	0	44	22	116
	Clams infected		1	1	4*	0	20	11*	37
	Percent infection		16.7	6.7	13.8	0	45.5	50.0	31.7
2nd year class	Clams examined		37	25	9	1	28	9	109
	Clams infected		11	7	5	0	9*	5	37
	Percent infection		29.7	28.0	55.6	0	32.1	55.6	33.9
3rd year class	Clams examined		6	11	1	1	8	5	32
	Clams infected		3	5	1	0	5	3	17
	Percent infection		50.0	45.5	100.0	0	62.5	60.0	53.1
4th year class	Clams examined		1	1	1	1	6	3	13
	Clams infected		0	1	0	1	5*	2*	9
	Percent infection		0	100.0	0	100.0	83.4	66.7	69.2
Total	Clams examined	42	50	52	40	3	86	39	312
	Clams infected	6	15	14	10	1	39	21	106
	Percent infection	14.3	30.0	26.9	25.0	33.0	45.3	52.3	34.0

Monthly incidence of infection of Malacobdella grossa in designated year classes of razor clams from February 1950 to February 1951.

* One clam of the sample infected with two Malacobdella

Table 2

	Month	February	March April	May June	August	October	November December	January February	Total	Percent
1st year class	Immature		0	0	4	0	8	9	21	48.9
	Females		1	0	0	0	9	2	12	27.9
	Males		0	1	1	0	5	3	10	23.3
2nd year class	Immature		2	0	2	0	3	0	7	19.4
	Females		3	6	2	0	4	3	18	50.0
	Males		5	0	1	0	3	2	11	27.8
3rd year class	Immature		0	0	0	0	1	1	2	11.8
	Females		2	2	1	0	2	1	8	47.1
	Males		1	3	0	0	2	1	7	41.2
4th year class	Immature		0	0	0	0	2	2	4	36.4
	Females		0	0	0	0	1	1	2	18.2
	Males		0	1	0	1	3	0	5	45.4
Total	Immature	0	2	0	6	0	14	12	34	30.1
	Females	3	6	8	3	0	16	7	43	38.1
	Males	3	6	5	2	1	13	6	36	31.9

The number of immature, female, and male *Malacobdella grossa* found by month from February 1950 to February 1951 in designated age classes of razor clams.

Plate 1

Fig. 1 Ovary containing mature eggs. 200X

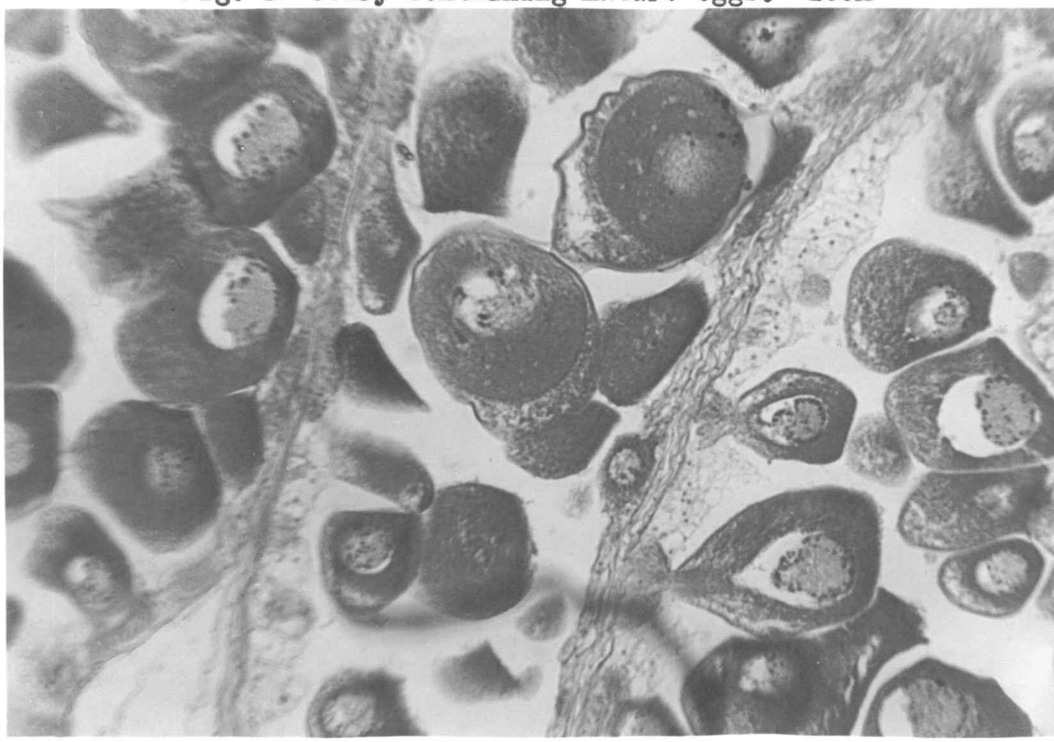


Fig. 2 Ovary showing stages of oögenesis. 200X

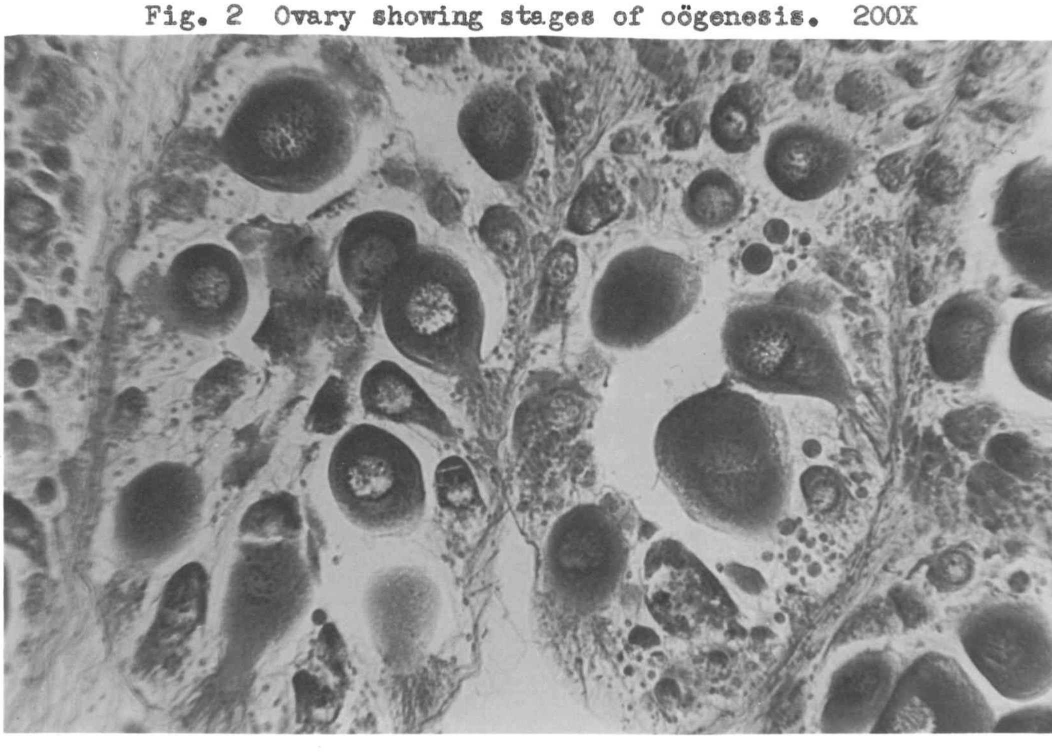


Plate 2

Fig. 3 A testicular follicle of a small Malacobdella. 450X

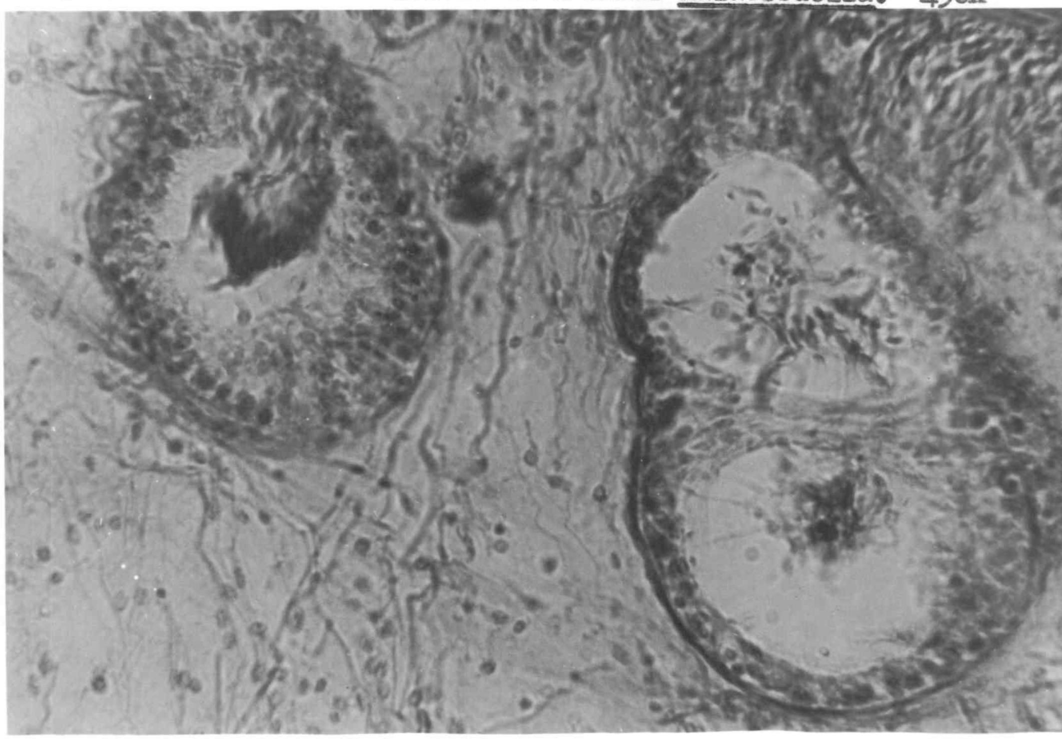
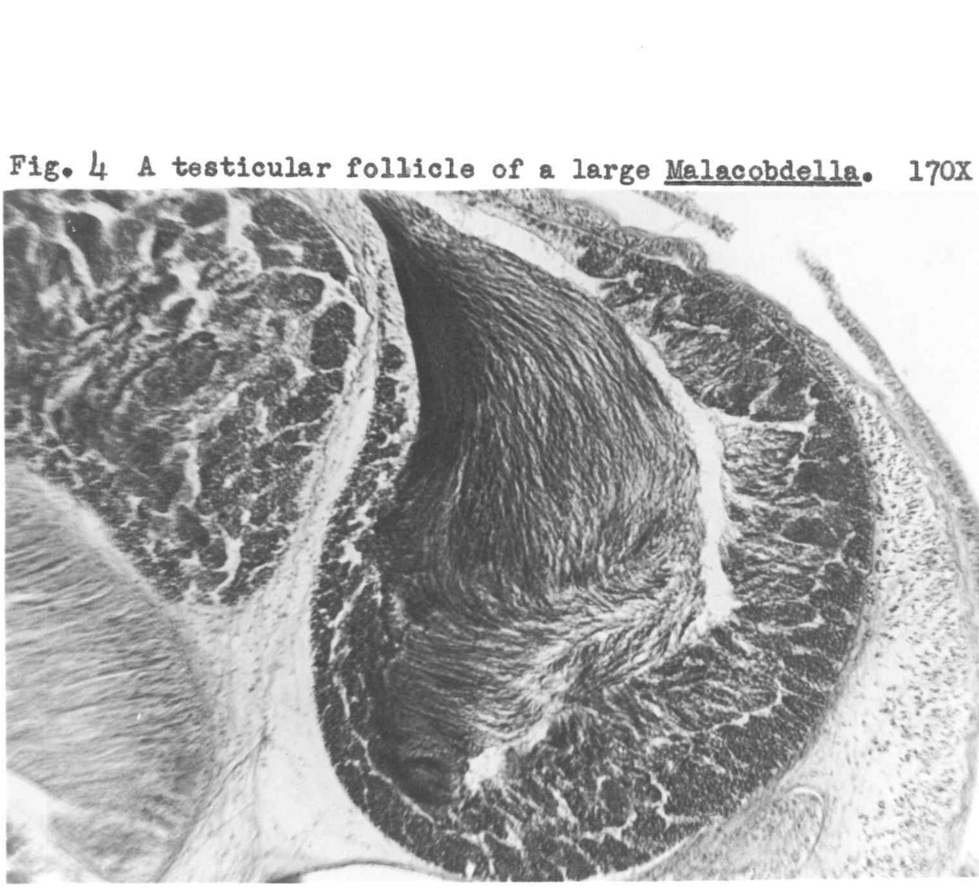


Fig. 4 A testicular follicle of a large Malacobdella. 170X



BIBLIOGRAPHY

1. Gering, Gustaf. Beiträge zur Kenntnis von Malacobdella grossa (Müll.). Zeitschrift fur wissenschaftliche Zoologie 97: 673-720. 1911.

2. Guberlet, John E. Malacobdella grossa from the Pacific Coast of North America. Publications of the Puget Sound biological station 5:1-14. 1925.

3. Hammarsten, Olof D. Beitrag zur Embryonalentwicklung der Malacobdella grossa (Müll.). Arbeten från Zootomiska Institutet vid Stokholms Högskola 1:1-95. 1918.

4. Hoffmann, C. K. Zur Anatomie und Ontogenie von Malacobdella. Niederländisches Archiv für Zoologie 4:1-30. 1877-78.

5. Kennel, von J. Beiträge zur Kenntnis der Nermertinen. Arbeiten aus dem Zoologie-Zootom Institutet zu Würzburg 4:305-381. 1877-78.

6. McMillin, Harvey C. The life history and growth of the razor clam. State of Washington, Department of fisheries. Annual report to the Superintendent of fisheries no. 34. 1925. 52p.

7. __________. Condition of the razor clam fishery of Washington. United States bureau of fisheries economic circular 64:1-7. 1928.

8. Riches, T. H. A list of the nemertines of Plymouth Sound. Journal of the marine biological association of the United Kingdom 3:1-29. September 1893.

9. Riepen, Otto. Anatomie und Histologie von Malacobdella grossa (Müll.). Zeitschrift fur wissenschaftliche Zoologie 143: 323-496. 1933.

10. Weymouth, Frank W. and Harvey C. McMillin. Relative growth and mortality of the Pacific razor clam, Siliqua patula (Dixon) and their bearing on the commerical fishery. Bulletin of the United States bureau of fisheries 46:543-567. 1931.

11. __________, Harvey C. McMillin and Harlan B. Holmes. Growth and age at maturity of the Pacific razor clam, Siliqua patula (Dixon). Bulletin of the United States bureau of fisheries 41:201-236. 1925.