ANNUAL GROWTH OF FRESH-WATER MUSSELS[1]

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CONTENTS

INTRODUCTION

In view of the progressive depletion of the natural beds of commercial fresh-water mussels used in the manufacture of pearl buttons, it has become desirable to determine the action of various factors bearing on future supplies of these shells. At present no adequate data exist on the age and growth of commercial mussels; and, consequently, little is known concerning the age at which these mussels could best be taken from the streams, considering both the economic value of the shells to the manufacturers and the interests of conservation. Accordingly a detailed study of the growth of fresh-water mussels representing four commercial North American species has been made, using the "annual ring" method as applied to mollusks by Weymouth (1923) in his work on the Pismo clam.

The determinations of the length-age relations of the upper Mississippi shells used in these studies were begun in the laboratories of physiology at Stanford University in 1926. Subsequently, additional material was measured at the United States Bureau of Fisheries Biological Station, at Fairport, Iowa. The length-age and weight-age studies of the Arkansas and Texas shells, and all of the thickness-age studies, were made in the laboratories of physiology of the University of Missouri. The writer is greatly indebted to Dr. F. W. Weymouth, of Stanford University, and to Dr. M. M. Ellis, of the University of Missouri, for their advice and suggestions in connection with this work.

METHOD

In many organisms the variations in growth rate, occurring at intervals and associated with such factors as temperature or drought, produce rings or other marks in the hard structures. The use of these records in the determination of the age of trees, where the rapid growth of summer, the slow growth of winter, and sometimes intermediate stages caused by drought or other unfavorable conditions, leave distinct rings in the cross section of the trunk, which can be recognized as belonging to

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known seasons of the year, first established the ring method of age determination. The accuracy of this method for trees has been demonstrated recently by the remarkable researches in the Southwest by Douglass (1929).

Certain ridges, lines, or other marks appearing on or in the scales, otoliths, vertebræ, and other hard parts of fish have been determined by investigators to be of annual occurrence. Because of resemblances to the rings of growth of trees, these marks of growth in animals also have been called rings.

Gilbert (1913), Frazer (1917), Rich (1920), Creaser (1926), and others have used the rings in scales in determining the rate of growth of fish. Crozier (1914, 1918) showed that the growth lines in the shells of chiton were significant in determining age. Weymouth (1923) established the association of the rings occurring in the Pismo clam with the retardation of growth during the winter period, and McMillin (1924) made use of the rings occurring in the razor clam in determining the normal course of growth in that animal.

Hessing (1859), working with European species, was perhaps the first scientific writer to call attention to the possible correlation of certain rings in the shells of fresh-water mussels with the annual growth of these animals, although he was unable to decide definitely that these rings were of annual occurrence. Hazay (1881), following the growth of individual Hungarian mussels, found that no growth occurred during the late winter months, resulting in the formation of a definite ring in the periostracum of the shells. As there was but a single major growth period each year, Hazay's work established these rings as annual marks. Lefevre and Curtis (1912), from their studies of specimens of the North American mussel, the pocketbook, *Lampsilis ventricosa* (Barnes), which they kept under observation for three years, conclude that the rings mark the boundaries of growth periods; but since various factors may cause cessation of growth, these writers were not entirely certain that a single growth period always corresponds to a single year.

Rubbel (1913), after measuring over 300 specimens of a European fresh-water mussel, *Margaritana margaritifera* (Linnæus), which he then planted, and remeasured two years later, also felt uncertain as to the significance of these rings as marks of annual growth. Isley (1914), from his study of some 900 specimens of North American species of fresh-water mussels which he tagged and subsequently recovered, states that the winter rings, or arrested growth rings, as he recommends calling them, are usually sufficiently regular and definite to be used as indicators of age. He did not, however, make use of these rings in his own studies of the normal course of growth.

Coker, Shira, Clark, and Howard (1921) held a number of fresh-water mussels at the United States Fisheries Biological Station at Fairport, Iowa, for periods of years and measured them annually. These authors made a very careful study of the growth rings by using sections of the shell. They pointed out that the growth of the shell in length and breadth is accomplished by the secretion by the mantle of the three layers of shell substance at or near the margin of the mantle. A period of cold or any disturbance, such as handling, causes the mantle to withdraw from the margin of the shell to such an extent as to break its continuity with the thin and flexible edge of the shell. When the deposition of shell is resumed, the new layers of prismatic substance and periostracum are not continuous with the old. The amount of overlapping of layers in the region of interrupted growth appears to depend on the extent to which the mantle has been withdrawn, which in turn appears to depend on the degree of the disturbance. The duplication of layers of periostracum and prismatic substance, but particularly the former, gives the appearance of a dark band on the shell, which is the so-called growth ring. These authors suggest that this ring might be better termed duplication ring, or interruption ring. They also found that the annual rings which are associated with the cessation of growth in the winter season are actually formed by repeated startings and stoppings of growth, in both the late fall and early spring, due to the passing warm and cold spells, so that the annual rings thus produced are usually broad, compound rings, quite different from the single narrower interruption rings resulting from more temporary disturbances of growth. Grier (1922) used the rings of certain Ohio species to check the age of his specimens in a study of relative rates of growth of various lake species.

It is evident then that the various writers agree that the rings in the shells of fresh-water mussels are caused by cessation in growth and that the rings formed during the winter period are, in the main, heavier and better marked. It remains, therefore, in the application of these rings to a study of annual growth, to devise a method by means of which the annual rings—that is, those rings formed by the cessation of the major period of annual growth—may be differentiated from the lesser lines produced by temporary cessation of growth due to temporary unfavorable conditions.

In the case of many species of fresh-water mussels, particularly many members of the *Lampsilinæ* and other comparatively thin-shelled species, the growth interruption rings developed from all causes are partially apparent to the unaided eye. Illumination of the shells, obtained by placing an incandescent bulb immediately behind one valve of the shell, was used with considerable success in the earlier work on the light-colored yellow sand shells and Lake Pepin muckets. Such illumination brings out the full extent of each ring and was of great aid in separating the more conspicuous annual rings.

An improvement was made later by using monochromatic yellow light, in the place of ordinary light, for the illumination of the shells. The single valve was placed on a plate of monochromatic yellow glass (Corning glass, No. G38–H) through which the light from an incandescent bulb was passed. This yellow light was found to be particularly effective in bringing out the rings in the thinner-shelled species. Some of the shells were placed in front of a powerful ultra-violet light. The ultra-violet rays caused the calcium in the shell to floresce with a yellow-green light which caused the thicker annual rings to stand out sharply in contrast. The use of ultra-violet rays was found quite effective in differentiating the annual rings in even thick shells of the *Quadrula* group (results to be given in another paper), but for the shells used in the present studies, the monochromatic yellow light was found amply satisfactory.

In addition to the measurement of length—that is, the greatest antero-posterior distance measured as a chord and bounded by the ring under consideration—weight was taken and thickness determined in several series. When weights were to be taken, the shells were first heated in an electric oven to a temperature of 95° to 105° C. for an hour before the actual weighings were made. The readings were taken to the nearest 0.1 gram. In the case of weight determinations, only left valves were used for the sake of uniformity, as the two valves are not quite the same weight, owing to the differences in the teeth along the hinge margin. Thickness determinations were made by means of steel bow calipers, operated with a milled screw. As the females are readily distinguishable in the species of *Lampsilis* by the greater convexity of the shell in front of the posterior ridge and by the more or less inflated character of the posterior outline of the shell, the females and males have been considered separately. Owing to the small number of specimens of *Unio popei* Lea and *Tritogonia verrucosa* (Rafinesque) used, no separation of the sexes was made in these species.

MATERIAL

In the present studies two species—the yellow sand shell, *Lampsilis anodontoides* (Lea), and the Lake Pepin mucket, *Lampsilis siliquoidea pepinensis* Baker (*Lampsilis luteola* of authors)—have been given particular consideration because of their commercial importance. In addition, the buckhorn, *Tritogonia verrucosa* (Rafinesque) or *Tritogonia tuberculata* of authors, and Pope's purple, *Unio popei* Lea, were used for certain comparisons. In all, 1,107 specimens were examined. Of these, 600 were Lake Pepin muckets, 484 yellow sand shells, 16 buckhorns, and 7 Pope's purple.

INDIVIDUAL SPECIES

YELLOW SAND SHELL

The yellow sand shell, *Lampsilis anodontoides* (Lea), perhaps the most valuable single species of fresh-water mussel in North American waters, is found throughout the Mississippi River drainage system, with the possible exception of the upper Missouri. Simpson (1914) also records the species as occurring in the entire Gulfwise drainage area from Withlacoochee River, Fla., to the Rio Grande, and south into old Mexico. It is usually found on sandy bottoms in the larger rivers of its range but may also occur in the quieter portions of these streams on mud bottoms.

In the present studies, shells from three localities—the Mississippi River, at Fairport, Iowa; the White River, at Newport, Ark.; and the lower Rio Grande, near Mercedes, Tex.—representing the northern, middle, and southern portions of the range of this species, have been examined. In all three localities the shells are commonly taken in sufficient quantities for commercial use.

Fertilization of the eggs in the northern waters takes place during the later half of summer. The glochidia are developed by fall and are held in the marsupia until the following spring or early summer. Breeding seasons occasionally overlap. (See Lefevre and Curtis, 1912; and Coker, Shira, Clark, and Howard, 1921.) The ripe glochidia are extruded, and their parasitic stage begins some time in May or June. As their parasitic stage is usually completed in three weeks or less in northern waters, the free existence of the juvenile mussel probably begins about the first of July. This cycle gives a period of three or four months before the onset of cold weather and the formation of the first large interruption or growth ring. This period of growth for the first season is probably of 5 months' duration in Arkansas and possibly 7½ months in southern Texas. The respective durations of the growing season after the first year are estimated at 5 months in Iowa, 7 in Arkansas, and 9 in southern Texas.

The shells from the Mississippi River, at Fairport, Iowa, represented two independent collections. The first of these consisted of 100 valves from female mussels and 100 from males, as obtained from local shellers in the summer of 1926. These valves were not paired. This collection was used for growth in length determinations. The second Mississippi collection was obtained by local shellers in 1927, 1928, and 1929 and consisted of 50 left valves from female mussels and 50 from males. These shells were used for growth in weight determinations.

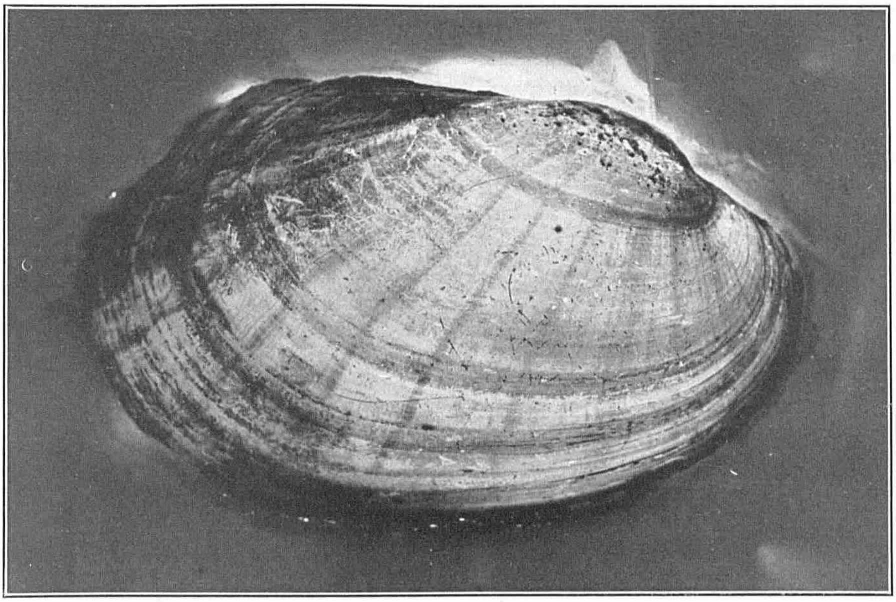

FIGURE 1.—Right valve, 7.73 centimeters in length, of a 7-year-old Lake Pepin mucket, *Lampsilis silquoidea pepinensis* Baker (*Lampsilis luteola*, of authors), illuminated to show major interruption rings, *i. e.*, annual growth rings

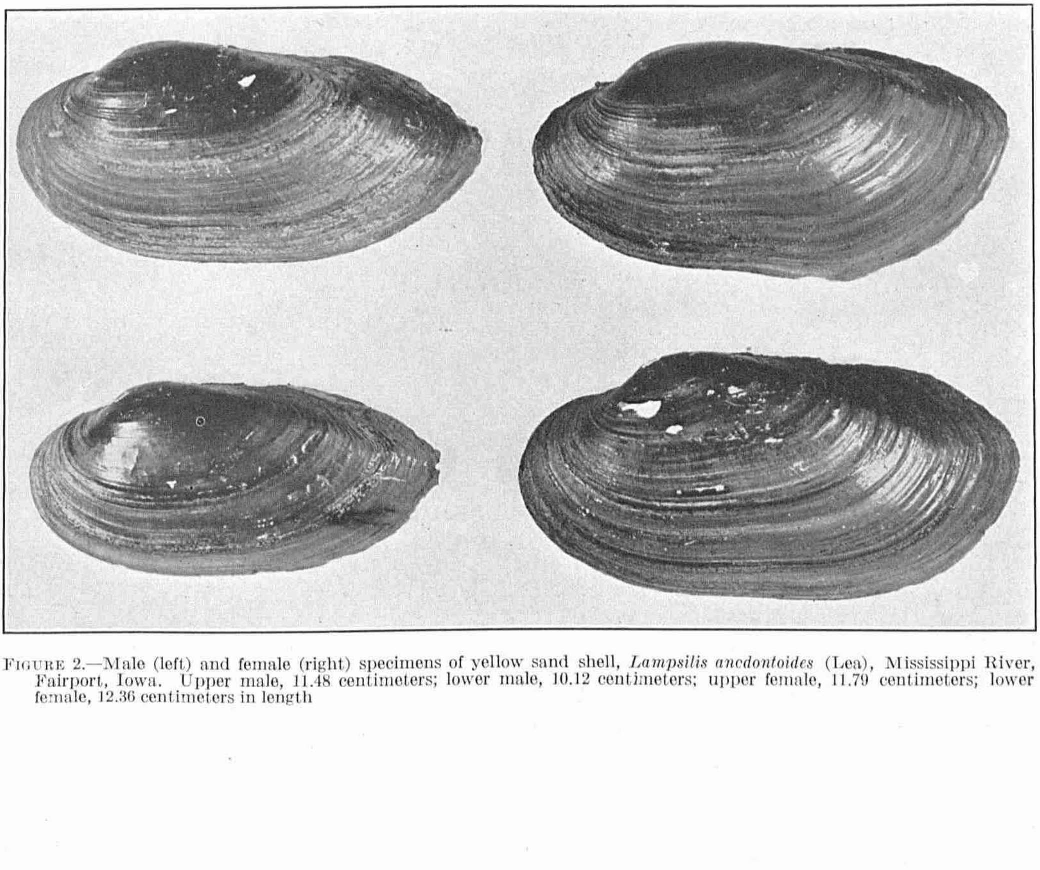

FIGURE 2.—Male (left) and female (right) specimens of yellow sand shell, *Lampsilis anodontoides* (Lea), Mississippi River, Fairport, Iowa. Upper male, 11.48 centimeters; lower male, 10.12 centimeters; upper female, 11.79 centimeters; lower female, 12.36 centimeters in length

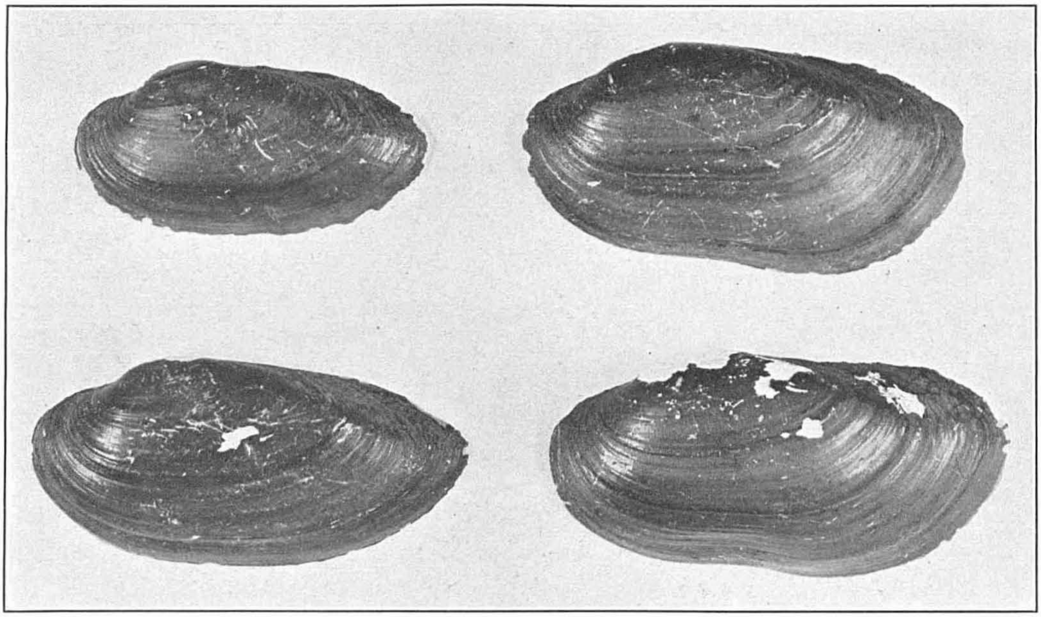

FIGURE 3.—Male (left) and female (right) specimens of yellow sand shell, *Lampsilis anodontoides* (Lea), White River, Ark. Upper male, 8.69 centimeters; lower male, 10.72 centimeters; upper female, 11 centimeters; lower female, 11.33 centimeters in length

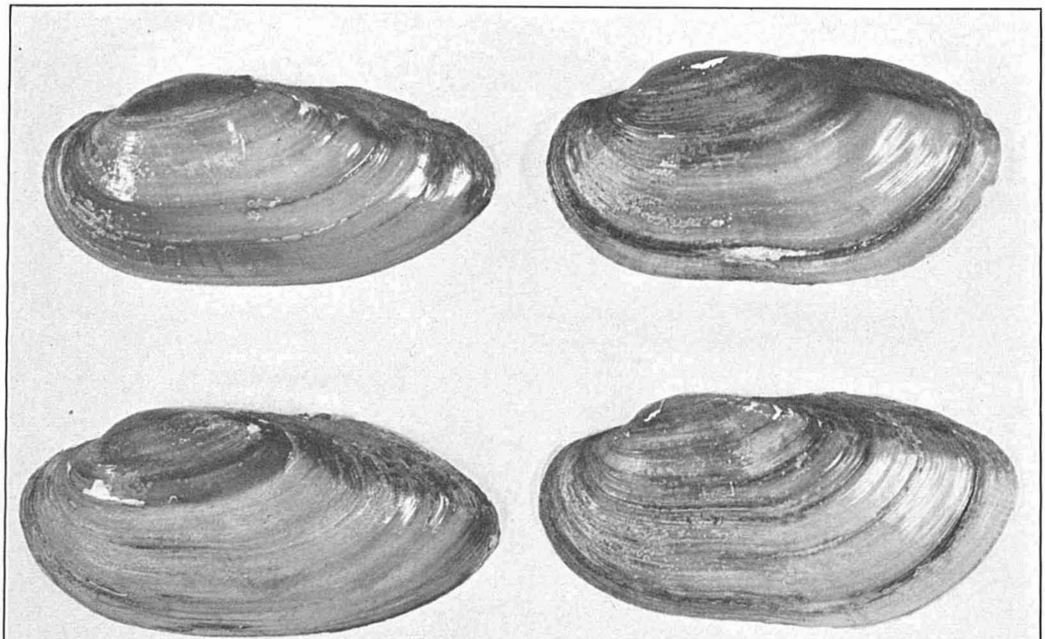

FIGURE 4.—Male (left) and female (right) specimens of yellow sand shell, *Lampsilis anodontoides* (Lea), Rio Grande Valley near Mercedes, Tex. Upper male, 11.22 centimeters; lower male, 11.89 centimeters; upper female, 11.30 centimeters; lower female, 11.93 centimeters in length

The shells from the White River of Arkansas were collected by shell buyers during the summer of 1927. The collection consisted of 50 mixed left and right valves from males and the same number from females.

The lower Rio Grande Valley shell collection was obtained from canals, settling basins, and "resacas" tributary to the Rio Grande during the winters of 1928–29 and 1929–30. This Rio Grande collection consisted of 56 shells from males and 26 from females.

LENGTH IN RELATION TO AGE

The maximum shell lengths included within each of the major interruption rings—that is, within the annual rings—having been obtained, the data were analyzed by the percentile method of Galton (1875). By inspection the 10 per cent groups seemed satisfactory for the various comparisons desired, consequently the first, fifth, and ninth decils were computed for each set of measurements. The following formula has been used throughout this work:

$$\text{Decil} = \frac{(d-F)\, i}{f} + v$$

in which d equals coefficient of decil, that is, the number of cases considered times the numerical percentage determining the decil; F, the sum of the frequencies below the class in which the coefficient of the decil is located; i, the class interval; f, the frequency of the cases within the class in which the coefficient of the decil is located; and v, the value of the lower boundary of the class in which the coefficient of the decil is located. The probable errors for the first and ninth decils were computed by the formula:

$$\text{Probable error} = \frac{0.6745\, i\sqrt{.09\, N}}{f}$$

and for the fifth decil by the formula:

$$\text{Probable error} = \frac{0.6745\, i\sqrt{N}}{2f}$$

These formulæ for the probable error can, of course, be evolved from the formulæ for standard deviation and mean probable error as currently used in statistical studies. (See Davenport, 1914.)

Using the fifth decil values from the above data, curves were drawn showing trends of growth for the yellow sand shell from the Mississippi River in Iowa, the White River in Arkansas, and the lower Rio Grande in Texas. First and ninth decils, bounding as they do the 80 per cent of the population which conformed most closely to the normal growth of the group, were also plotted. It was felt that the 10 per cent on either side of the first and ninth decils included most of the abnormal cases and errors in age determinations. At the same time it was realized that each of these two groups of extreme cases would quite likely contain true maximum and minimum deviations from the normal. As individuals of extremely rapid growth are likely to be of interest in connection with any genetic work which may be done with fresh-water mussels, in the figure showing all decils for each locality, the maximum and minimum cases for each year class have been added. These are indicated by the symbol for the locality in question, with a line drawn through it.

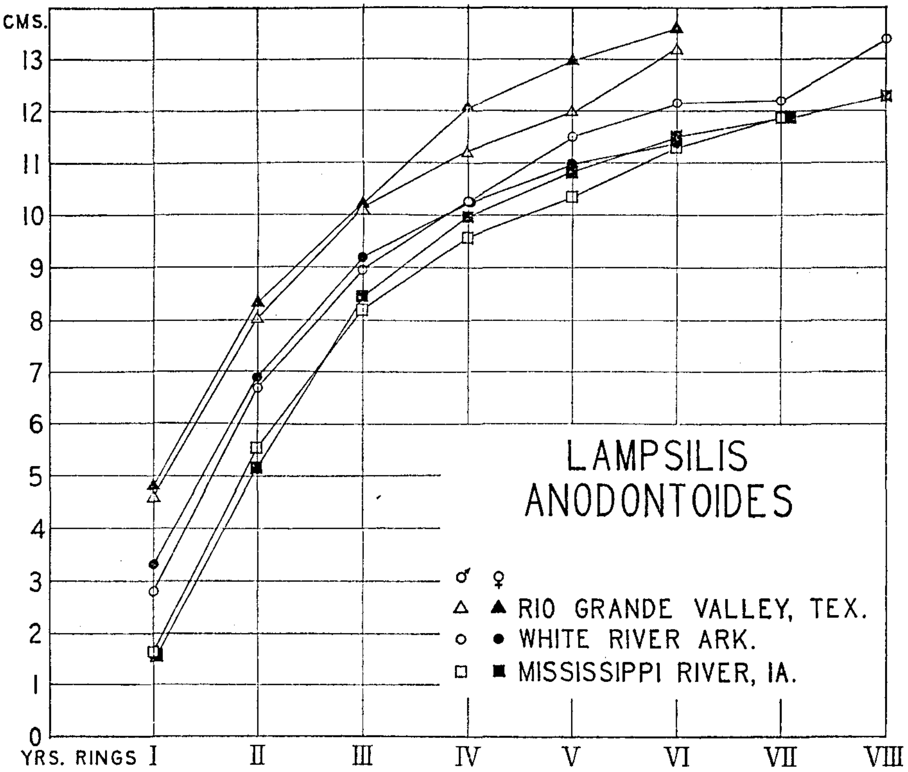

FIGURE 5.—Median curves of growth in length for both sexes of yellow sand shell, *Lampsilis anodontoides* (Lea) from the Mississippi River, Fairport, Iowa; the White River, Newport, Ark.; and the Rio Grande Valley near Mercedes, Tex. Curves obtained by plotting median values for annual length against age; that is, first year's growth precedes formation of Ring I

TABLE 1.—*Median values of length in relation to age of the yellow sand shell, Lampsilis anodontoides (Lea)*

MALES

Ring No.	Mississippi River, Iowa		White River, Ark.		Rio Grande Valley, Tex.	
	Number of specimens	Length	Number of specimens	Length	Number of specimens	Length
		Centimeters		*Centimeters*		*Centimeters*
I	100	1.61±0.055	50	2.80±0.2012	56	4.61±0.1079
II	100	5.54± .067	50	6.69± .1255	56	8.02± .1052
III	100	8.22± .089	40	8.93± .0767	49	10.11± .1072
IV	97	9.57± .085	24	10.26± .0970	35	11.21± .0832
V	57	10.38± .091	7	11.50± .1489	6	12.00± .3932
VI	20	11.30± .101	4	12.10± .1686	2	13.26
VII	9	11.90± .145	4	12.2 ± .4497		
VIII			2	13.3		

FEMALE

I	100	1.58±0.059	50	3.35±0.1703	26	4.80±0.1428
II	100	5.17± .094	50	6.93± .1135	26	8.33± .1320
III	100	8.47± .073	49	9.13± .1389	18	10.20± .1832
IV	100	9.96± .055	33	10.43± .0878	5	12.10± .1130
V	92	10.83± .054	29	10.97± .1067	1	13.00
VI	33	11.50± .108	4	11.40± .3373	1	13.63
VII	10	11.90± .178				
VIII	3	12.30± .117				

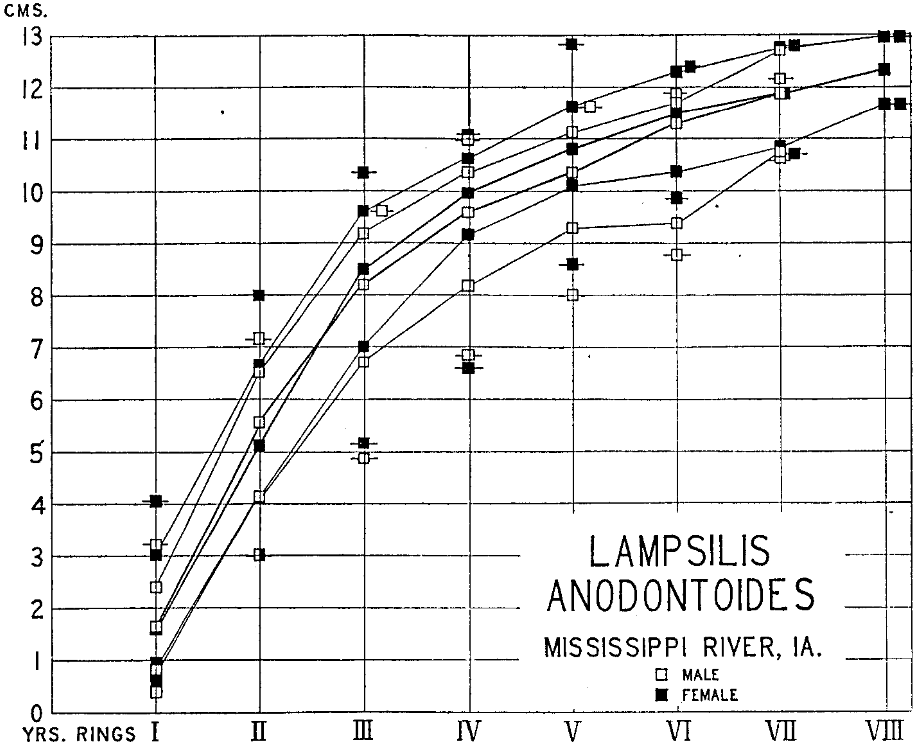

FIGURE 6.—Median curve, together with first and ninth decil curves of growth in length for both sexes of yellow sand shell, *Lampsilis anodontoides* (Lea), Mississippi River, Fairport, Iowa. Maximum and minimum cases for the various year classes are represented by the locality symbol, transfixed by a horizontal line

TABLE 2.—*Length in relation to age of yellow sand shell, Lampsilis anodontoides (Lea), Mississippi River, Iowa*

[All values in centimeters]

MALE

Ring No.	Minimum	First decil	Median	Ninth decil	Maximum
I	0.4	0.88±0.058	1.61±0.055	2.43±0.092	3.4
II	3.0	4.12± .184	5.54± .067	6.50± .081	7.2
III	4.8	6.72± .135	8.22± .089	9.20± .070	9.6
IV	6.8	8.32± .090	9.57± .085	10.36± .055	11.0
V	8.0	9.27± .152	10.38± .091	11.13± .085	11.6
VI	8.8	9.40± .452	11.30± .101	11.70± .070	11.8
VII	10.6	10.78± .304	11.90± .145	12.22± .121	12.2
FEMALE					
I	0.6	0.94±0.052	1.58±0.059	3.00±0.337	4.6
II	.3	4.10± .107	5.17± .094	6.70± .135	8.0
III	5.2	7.00± .253	8.47± .073	9.60± .081	10.4
IV	6.6	9.20± .088	9.96± .055	10.64± .061	11.2
V	8.6	10.11± .084	10.83± .054	11.62± .149	12.8
VI	9.8	10.33± .193	11.50± .108	12.27± .097	12.4
VII	10.6	10.80± .641	11.90± .178	12.80± .160	12.8
VIII	11.6	11.66± .070	12.30± .117	12.94± .070	12.8

Figure 5 shows the median curves of growth in terms of length for the yellow sand shell as found in all three localities; and Figure 6 the growth curves for each sex of this species from the Mississippi River. It will be noted from Figure 6 that length of the individuals from the Mississippi increases very rapidly through the second year, after which a decrease in the growth rate sets in, becoming pronounced the fourth year. This rapid growth appears associated with the mussel's juvenile period, and with the coming of maturity, in the third season, the rate of increase in length steadily decreases. There is some difference in the rate of increase in length between the sexes. After the formation of the second annual ring the females take the lead in growth over the males, which up to this time have grown faster. This lead remains definite until the seventh year, when there is an indication of a mutual drawing together of the curves of growth in length of the two sexes. The males increase in rate, while the females decrease. The fact that the females do not grow quite as rapidly as the males the second year but more rapidly the third year suggests that the females do not reach maturity the second year, in as great a proportion at least, as the males. All, or a greater proportion, of the females appear to mature a year later than the males.

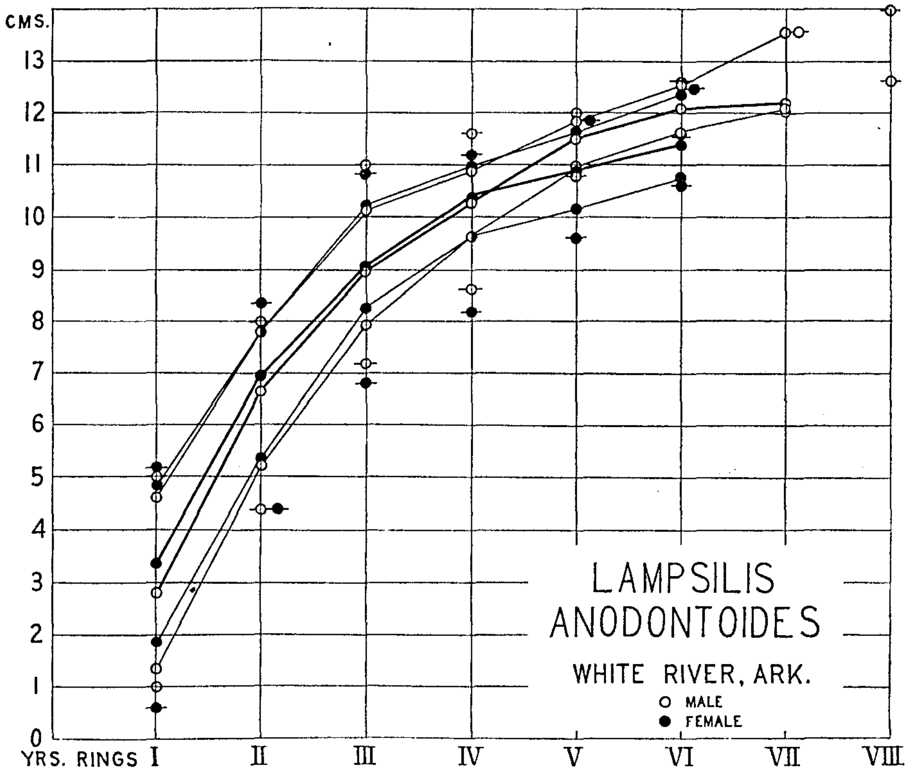

FIGURE 7.—Median curve, together with first and ninth decil curves, of growth in length for both sexes of yellow sand shell, *Lampsilis anodontoides* (Lea), White River, Newport, Ark. Maximum and minimum cases for various year classes are represented by locality symbol transfixed by a horizontal line

Figure 7 gives the curves of growth in length for the individuals found in the White River of Arkansas. As with the Mississippi shells, length increases most rapidly during the first and second years, after which a steady decrease in rate of growth sets in. The rates of increase in length for the two sexes remain close together until the fourth year. Thereafter, a marked divergence appears for the fifth and sixth years. Unlike the Mississippi River shells, the Arkansas males have the greater rate of growth in length. No specimens of females of more than 6 years of age were available in the Arkansas collection, which was unfortunate, as the marked drop in length increase for the males in the seventh year suggests that the trend of the two sexes might be toward each other, as in the case of the Mississippi shells, although the location of the 8-year class suggests a new trend for the males in extreme age.

TABLE 3.—*Length in relation to age of yellow sand shell, Lampilis anodontoides (Lea), White River, Ark.*

[All values in centimeters]

MALE

Ring No.	Minimum	First decil	Median	Ninth decil	Maximum
I	1.0	1.27±0.1192	2.80±0.2012	4.60±0.1589	5.0
II	4.4	5.20± .1589	6.69± .1255	7.80± .1192	8.0
III	7.2	7.90± .1275	8.93± .0767	10.10± .1594	11.0
IV	8.6	9.64± .1102	10.26± .0970	10.88± .1983	11.6
V	10.8	10.94± .1776	11.50± .1489	11.86± .1332	11.8
VI	11.6	11.68± .1349	12.10± .1686	12.52± .1349	12.4
VII	12.0	12.08± .1398	12.2 ± .4497	13.52± .4195	13.4
VIII	------------	[1] 12.6	------------	[1] 14.0	------------

FEMALE

Ring No.	Minimum	First decil	Median	Ninth decil	Maximum
I	0.6	1.88±0.1589	3.35±0.1703	4.85±0.1430	5.2
II	4.4	5.27± .1787	6.93± .1135	7.78± .0670	8.4
III	6.8	8.26± .1342	9.13± .1389	10.27± .1175	10.8
IV	8.2	9.66± .0726	10.43± .0878	10.99± .0715	11.2
V	9.6	10.13± .0987	10.97± .1067	11.61± .1207	12.0
VI	10.6	10.22± .4047	11.40± .3373	12.32± .4047	12.2

[1] One individual.

Coker, Shira, Clark, and Howard (1921), give some figures on the lengths of 40 specimens of yellow sand shell from the St. Francis River, Ark., which they studied. Ages were determined from the growth rings. Their figures are of interest in comparison with those obtained in these studies. They state that they found 3-year-old specimens about 4 inches (10.16 centimeters) long. This compares with the median length for the White River shells, averaging males and females, obtained in these studies of 9.03 centimeters. Four-year-old specimens, they state, were 4 to 4½ inches (10.16 to 11.43 centimeters). The corresponding figure in these studies is 10.35 centimeters. For 5-year shells they give no figure, but 5-inch (12.7 centimeters) shells, they state, are 6 or more years of age. The median length of the 6-year-old shells from the White River is 11.75 centimeters.

In Figure 8 the curves of growth in length for the specimens from the lower Rio Grande Valley may be seen.

In the lower Rio Grande Valley the growth in length during the first year is very great, but thereafter there is a decline in the growth rate. The sexes diverge in rate after the third year, with a marked separation the following year. There is a suggestion that the curves for the sexes tend to approach each other after the fifth year, but since only one female over 4 years old was available, this can not be established definitely with the material at hand.

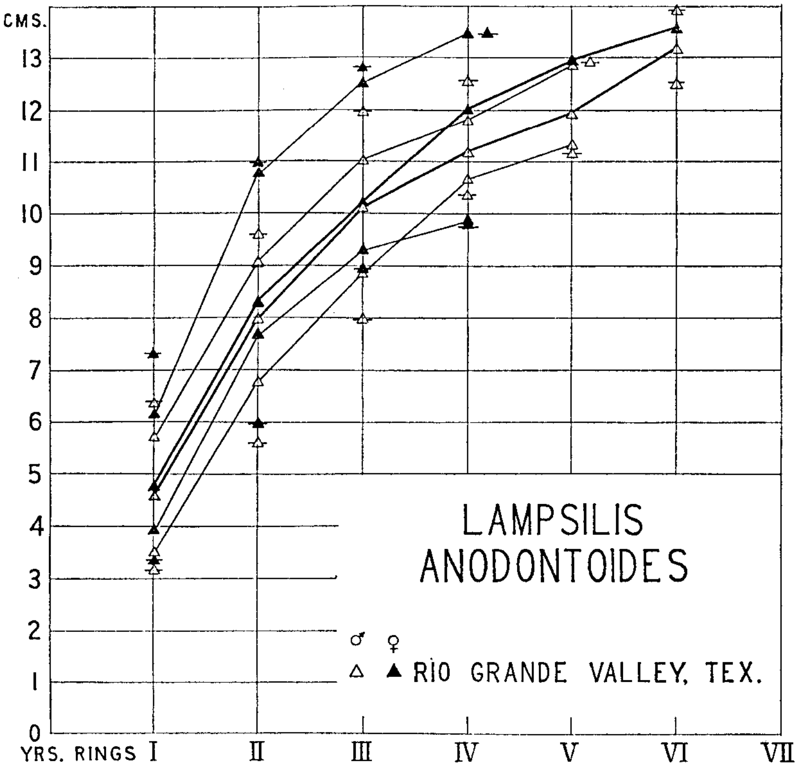

FIGURE 8.—Median curve, together with first and ninth decil curves, of growth in length for both sexes of the yellow sand shell, Rio Grande Valley, near Mercedes, Tex. Maximum and minimum cases for the various year classes are represented by the locality symbol transfixed with a horizontal line

TABLE 4.—*Length in relation to age of yellow sand shell, Lampsilis anodontoides (Lea), Rio Grande Valley, Tex.*

[All values in centimeters]

MALE

Ring No.	Minimum	First decil	Median	Ninth decil	Maximum
I	3.2	3.52±0.0944	4.61±0.1079	5.69±0.0944	6.4
II	5.6	6.76± .2496	8.02± .1052	9.09± .0944	9.6
III	8.0	8.99± .0951	10.11± .1072	11.03± .0405	12.0
IV	10.4	10.67± .1103	11.21± .0832	11.85± .8863	12.6
V	11.2	11.32± .2496	12.00± .3932	12.88± .1568	12.8
VI		[1] 12.54		[1] 13.97	

FEMALE

Ring No.	Minimum	First decil	Median	Ninth decil	Maximum
I	3.4	3.91±0.1710	4.80±0.1428	6.14±0.1710	7.4
II	6.0	7.72± .1001	8.33± .1320	10.84± .1710	11.0
III	9.0	9.36± .1685	10.20± .1832	12.60± .2964	12.8
IV	9.8	9.90± .4519	12.10± .1130	13.50± .4519	13.4
V			[1] 13.00		
VI			[1] 13.63		

[1] One individual.

Returning to Figure 5, which contains the median curves for increase in length for the species as found in all three localities, the differences in rate of increase in length become apparent. The actual values are given in Table 4. The essential difference lies in the fact that in the most southern of the three localities, the Rio

Grande Valley, growth in length is very much the greatest for any year class. Following as second in growth rate are the shells from the mid range of the species—the White River, Ark.—while those from the Mississippi in Iowa, made the slowest gains. This is true not only of the length gains but also to a large extent of the gains in weight and thickness.

A study of the extent of growth in length for the different years brings out some interesting characteristics of the different localities. In both the Mississippi and White River shells, the amount of increase in length the second year is as great, or even greater, than that shown in the first year. A decline begins the third year, which is apparently associated with sexual maturity. In the case of the Rio Grande shells on the other hand, not only is there very much greater growth the first year than in other years, but the decline in rate begins the second year. It is suggested that these Texas mussels mature a year earlier than the northern forms, but no definite data are on hand regarding this point. It is common knowledge that the growth rate of many organisms declines on reaching sexual maturity. Since the Texas mussels may possibly reach maturity a year earlier than the northern forms, the slump in growth rate begins that much sooner; but apparently the advantages gained by the greater juvenile growth, in part at least, are maintained throughout life. Figure 9 shows the relative annual growth for the species in the three localities; not only for each year, but also for periods of the year during which growth takes place in each locality. The point at which decline in growth rate begins is clearly brought out. The growing season increases progressively in length from the northern to the southern limits of the range. To this fact must be added the statement that the first season of growth for fresh-water mussels is also their shortest. In Iowa and northward the close of the parasitic period—that is, the beginning of free existence when actual growth starts—may come as late as July for the yellow sand shell. The cooling of the water with the approach of winter, may stop shell growth in September. In other words, an estimated average period of growth for this species in this locality during the first year is only 3 months. In Arkansas, the corresponding period may be 5 months; and in southern Texas, possibly 7½ months. The greater length of the growing season during the first year gives the shells from the more southern localities a pronounced gain in linear growth; but the earlier approach of maturity, which is also apparently correlated with the southern habitat, may, however, partially discount this advantage.

The variations in rate of growth in length between the sexes for the species in the different localities may be compared. In all three localities, males and females remain at about the same corresponding length until after the formation of the third ring. At this time, the shells are beginning to take on pronounced secondary sexual characteristics, which are brought out by the measurements. It is noticed that at the time of the formation of the third ring, the females of all three localities are slightly longer. This excess in length of the females also holds in the first and second years in the case of the shells from the White River and the Rio Grande. In the case of the Mississippi shells, the males exceed the females during these first two years. After the third year, and apparently associated with the species period of maximum sexual activity, pronounced and characteristic differences in growth between the sexes appear. With the approach of old age and lessened sex activity, these differences in increase in length tend to diminish, and a tendency in both sexes toward an equal length for a given age seems to be discernable.

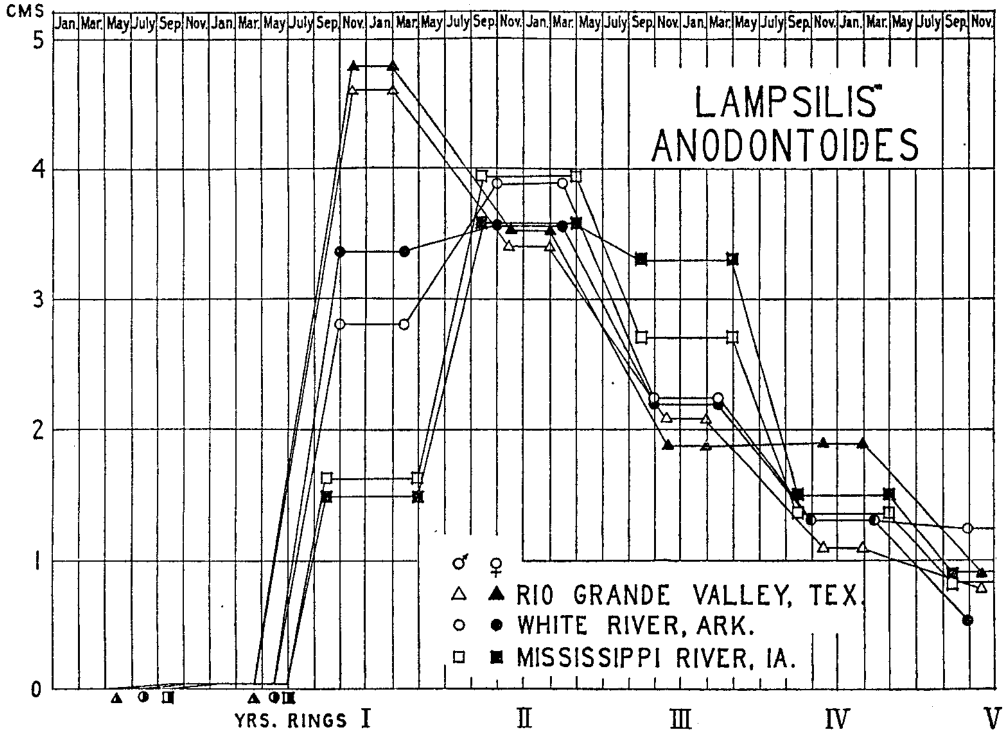

FIGURE 9.—Curves of annual growth in length, showing seasons of growth and rest of yellow sand shell at Mississippi River, Fairport, Iowa; White River, Newport, Ark.; and Rio Grande Valley near Mercedes, Tex. Increase in size; that is, growth values are actual; resting periods estimated on basis of geographic location and length of cold season as shown by Weather Bureau

TABLE 5.—*Increase in length per month of growth for each year of yellow sand shell, Lampsilis anodontoides (Lea)*

[Growing periods estimated]

Year	Mississippi River, Iowa			White River, Ark.			Rio Grande Valley, Tex.		
	Length of growing season	Male	Female	Length of growing season	Male	Female	Length of growing season	Male	Female
	Months	*Cm.*	*Cm.*	*Months*	*Cm.*	*Cm.*	*Months*	*Cm.*	*Cm.*
Glochidial year [1]	2	0.01	0.01	2	0.01	0.01	2	0.01	0.01
I	3	.53	.52	5	.56	.67	7½	.61	.64
II	5	.79	.72	7	.56	.51	9	.38	.39
III	5	.54	.66	7	.32	.31	9	.23	.21
IV	5	.27	.30	7	.19	.19	9	.12	.21
V	5	.16	.17	7	.18	.08	9	.09	.10
VI	5	.18	.13	7	.09	.06	9	.14	.07
VII	5	.12	.08	7	.01				
VIII	5		.08	7	.16				

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[1] See Merrick, 1930.

TABLE 6.—*Annual increase in length of yellow sand shell*

Locality and increase	Year ring							
	I	II	III	IV	V	VI	VII	VIII
MISSISSIPPI RIVER, IOWA	*Cms.*	*Cms.*	*Cms.*	*Cms.*	*Cms.*	*Cms.*	*Cms.*	*Cms.*
Male, annual increase	1.61	3.93	2.68	1.35	0.81	0.92	0.60	--------
Female, annual increase	1.58	3.59	3.30	1.49	.87	.67	.40	0.40
Male, cumulative increase from first year	--------	3.93	6.61	7.86	8.77	9.69	10.29	--------
Female, cumulative increase from first year	--------	3.59	6.89	8.38	9.25	9.92	10.32	10.72
WHITE RIVER, ARK.								
Male, annual increase	2.80	3.89	2.24	1.33	1.24	.60	.10	1.10
Female, annual increase	3.35	3.58	2.20	1.30	.54	.43	--------	--------
Male, cumulative increase from first year	--------	3.89	6.13	7.46	8.70	9.30	9.40	10.50
Female, cumulative increase from first year	--------	3.58	5.78	7.08	7.62	8.05	--------	--------
RIO GRANDE VALLEY, TEX.								
Male, annual increase	4.61	3.41	2.09	1.10	.79	1.26	--------	--------
Female, annual increase	4.80	3.53	1.87	1.90	.90	.63	--------	--------
Male, cumulative increase from first year	--------	3.41	5.50	6.60	7.39	8.65	--------	--------
Female, cumulative increase from first year	--------	3.53	5.40	7.30	8.20	8.82	--------	--------

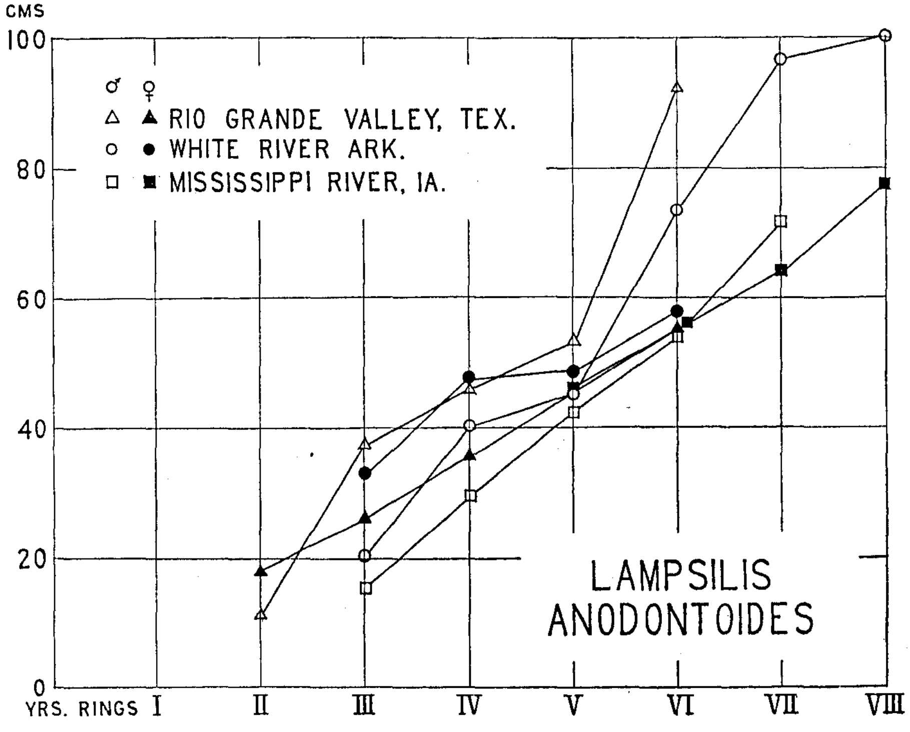

FIGURE 10.—Mean weight of left valves for year classes of yellow sand shell, Mississippi River, Fairport, Iowa; White River, Newport, Ark.; and the Rio Grande Valley near Mercedes, Tex. Weight plotted against age

WEIGHT IN RELATION TO AGE

Figure 10 shows the mean weights for the different year classes of the left valves of both sexes of the yellow sand shell from the three localities. Actual values are given in Table 7. Since only a single weight was taken from each valve, while several length values may be taken, there is a much more limited range to the weight values than to the length values. However the weight values obtained seem sufficient to indicate the essential differences in annual weight gains made by this species in the three localities.

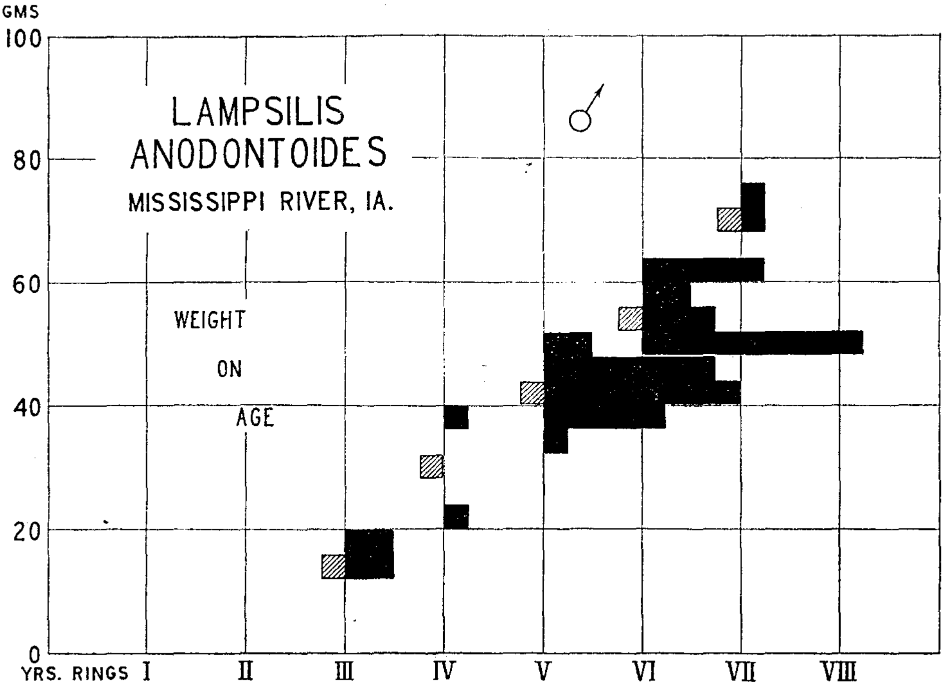

FIGURE 11.—Bar graph showing weight plotted against age for individual left valves of shells of male yellow sand shells, Fairport, Iowa. Weight values of individual left valves indicated by black squares at right of year classes. Mean weight valves shown by striated squares to left of respective year classes

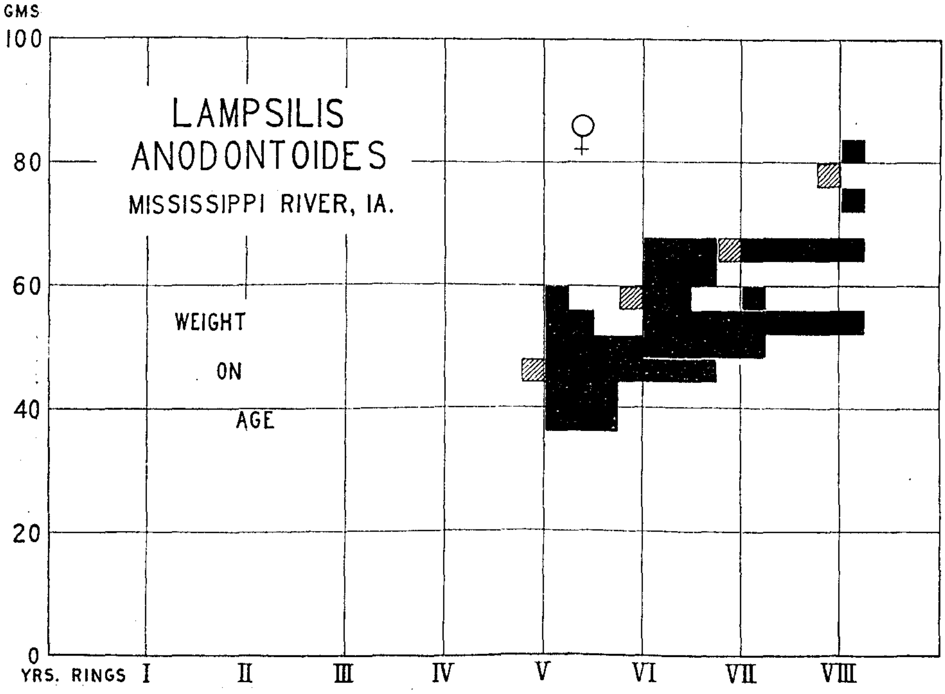

FIGURE 12.—Bar graph showing weight plotted against age for individual left valves of shells of female yellow sand shells at Fairport, Iowa. Weight values of individual left valves indicated by black squares at right of year classes. Mean weight values shown by striated squares to left of respective year classes

Before comparing the weights of the shells for the three localities, attention is called to Figures 11 and 12, which give the mean weights for males and females, respectively. The weights of individual valves are shown by the black squares on the right hand side of their respective year classes, while the mean weight for each class is shown by a square with diagonal lines to the left of the year class.

TABLE 7.—*Mean weight of left valves of yellow sand shell, Lampsilis anodontoides (Lea)*

MALE

Ring No.	Mississippi River, Iowa		White River, Ark.		Rio Grande Valley, Tex.	
	Number of specimens	Weight	Number of specimens	Weight	Number of specimens	Weight
		Grams		*Grams*		*Grams*
II	-----	-----	-----	-----	6	11.04
III	4	15.3	3	20.7	14	38.64
IV	2	29.7	8	40.5	28	43.62
V	23	42.5	5	45.1	2	53.35
VI	19	54.0	2	73.0	1	92.20
VII	2	71.5	2	96.7	-----	-----
VIII	-----	-----	1	100.1	-----	-----
FEMALE						
II	-----	-----	-----	-----	8	18.08
III	-----	-----	1	33.9	9	26.19
IV	-----	-----	6	48.0	4	38.00
V	20	46.9	15	49.0	-----	-----
VI	22	56.0	2	58.2	1	57.10
VII	6	64.6	-----	-----	-----	-----
VIII	2	77.9	-----	-----	-----	-----

Returning to the consideration of the weight values (as shown in fig. 10 for all three localities), there seems to be a tendency toward greater weight for the males than for the females of the same age in spite of the fact that the graphs of increase in weight are much more irregular than those of increase in length, presumably as the result of the smaller number of observations made on weight. This trend toward greater weight for the males is more evident in the older shells, becoming apparent after the fifth year for the shells from the Rio Grande Valley, and after the sixth year for the shells from the Mississippi River, with the shells from the White River as intermediate between the two. It is probable that the lighter weight of the female shells may be corollated with the reproductive activities of the female; that is, the calcium and other metabolic demands of the glochidia while developing from the eggs.

If the weight and length of the shells be considered together, the shells from the Rio Grande Valley are found to be definitely lighter for any given length than the shells from either the Mississippi in Iowa, or the White River in Arkansas. This is particularly true of the females from the Rio Grande which have weight values in the different year classes markedly lower than those of either sex from either of the other two localities. Commercially, the button manufacturers reject the smaller yellow sand shells from the Rio Grande Valley as being too thin for use, but accept those of the same linear dimensions from the White and Mississippi Rivers. This fact is readily understood when it is remembered that the 2, 3, and 4 year old shells from the Rio Grande district are definitely longer than shells of the same ages from either the White or Mississippi Rivers. The rapid growth in length made by the Rio Grande shells seems to be made in part, at least, at the expense of gains in shell weight.

The manufacturers agree that shells which have just reached a "fair commercial size" are the most satisfactory for use in the production of buttons. The smaller shells, if they be large enough to justify handling and the general overhead of production, are more valuable than the larger shells, which are likely to be more difficult to cut without chipping, and which yield blanks so thick that considerable grinding down is required. As the term "fair commercial size" is relative, an effort has been made to define this size for purposes of comparison. In view of various observations made by the manufacturers themselves, the fair commercial size for the yellow sand shell seems to be a shell about 10.5 centimeters (approximately 4 inches) in length, with a thickness at a point on the pallial line (v. i.) of 0.30 centimeters (0.12 inches, or about 5 lignes), and weighing 42 grams (about 1½ ounces). With this somewhat arbitrarily defined size as a standard, Table 9 has been prepared to determine the time required in each of the three localities for the yellow sand shell to reach a fair commercial size. At Fairport, Iowa, both males and females required 5 years or more; at Newport, Ark., only 4; while in the Rio Grande Valley, the males attained this size in 3 years, while the females required 4 because of their greater thinness of shell. Figure 13 shows the weight values with sex for the various year classes of the Mississippi specimens of the species for which weight values were taken, imposed on length. Actual values are given in Table 8.

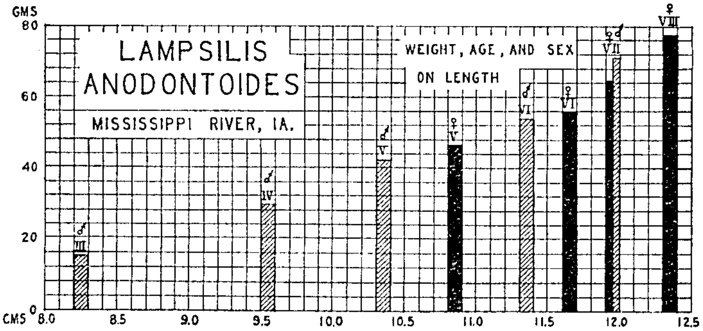

FIGURE 13.—Bar graph showing weight, sex, and age plotted against length, for yellow sand shell at Fairport, Iowa

THICKNESS IN RELATION TO AGE

The thickness of the shells of the various year classes from each locality was measured. For the sake of uniformity, this measurement was taken at a corresponding point on each specimen; namely, immediately dorsal to the pallial line on a line at right angles to the long axis of the shell, passing from the umbo across the shell. Thickness was measured with a pair of steel bow calipers with screw adjustment.

TABLE 8.—*Weight, age, and sex in relation to length of yellow sand shell, Lampsilis anodontoides (Lea), in Mississippi River, Iowa*

Ring	Length	Weight	Sex	Ring	Length	Weight	Sex
	Centimeters	*Grams*			*Centimeters*	*Grams*	
III	8.22	15.3	Male.	VI	11.50	56.0	Female.
IV	9.57	29.7	Do.	VII	11.90	71.5	Male.
V	10.38	42.5	Do.	VII	11.90	64.6	Female.
V	10.83	46.9	Female.	VIII	12.30	77.9	Do.
VI	11.30	54.0	Male.				

TABLE 9.—*Increase in length, weight, and thickness of yellow sand shell, Lampsilis anodontoides (Lea)*

Annual ring	Male						Female					
	Length		Weight		Thickness		Length		Weight		Thickness	
	Centimeters	*Per cent*	*Grams*	*Per cent*	*Centimeters*	*Per cent*	*Centimeters*	*Per cent*	*Grams*	*Per cent*	*Centimeters*	*Per cent*
MISSISSIPPI RIVER, IOWA												
I	1.61	15					1.58	15				
II	3.93	53					3.59	49				
III	2.68	78	15.3	36	0.25	83	3.30	81				
IV	1.35	91	29.7	71	.35	117	1.49	95				
V	.81	99	42.5	101	.40	133	.87	103	46.9	112	0.45	150
Total	10.38						10.83					
WHITE RIVER, ARK.												
I	2.80	27					3.35	32				
II	3.89	64					3.58	66				
III	2.24	85	20.7	49	0.30	100	2.20	87	33.9	81	0.35	117
IV	1.33	98	40.5	96	.40	133	1.30	99	48.0	114	.40	133
V	1.24	110	45.1	107	.45	150	.54	104	49.0	117	.45	150
Total	11.50						10.97					
RIO GRANDE VALLEY, TEX.												
I	4.61	44					4.80	46				
II	3.41	76	11.04	26			3.53	79	18.08	43		
III	2.09	96	38.64	92	0.30	100	1.87	97	26.19	62	0.25	83
IV	1.10	107	43.62	102	.35	117	1.90	115	38.00	90	.30	100
V	.79	114	53.55	127	.40		.90	124				
Total	12.00						13.00					

As might be expected, after the consideration of the relative weights of the shells from the three localities since thickness is in a way a function of weight, the measurements of shell thickness obtained (see Table 9) show the shells from the Mississippi River in Iowa and the White River in Arkansas to be definitely thicker than those from the lower Rio Grande Valley in Texas. The shells of the females from the Rio Grande were found to be thinner than the males of the same year class, again paralleling the weight-age data from this locality, although the females equalled or exceeded in thickness the males of the same year classes in both the White River and Mississippi River collections. It is obvious that from a commercial standpoint, the shells must not only be of a good texture and size, but must be of suitable thickness; that is, neither too thin nor excessively thick. As has been pointed out in a previous section, shells having a thickness of 0.30 centimeters or a little more, are of a desirable thickness. This thickness is attained by the females in the Rio Grande Valley and by the males and females in the White River in northern Arkansas by the end of the third year, but not until the end of the fourth year in the Mississippi at Fairport, Iowa. The annual increase in thickness in all year classes averaged about 0.05 centimeter suggesting that the rate of increase in thickness is a relatively constant factor. As, however, these measurements were taken in the region of the pallial line, these observations concerning the thickness of the shell and the annual increment of thickness can not be extended to other parts of the shell until additional data have been collected.

LAKE PEPIN MUCKET

The species, *Lampsilis siliquoidea,* (*Lampsilis siliquoidea pepinensis* Baker, *Lampsilis luteola* of authors) including all varieties, occurs, according to Baker (1928), from the Mohawk River, N. Y., west to Iowa, Kansas, and Missouri; north to Ontario, Michigan, and Minnesota; and south to Kentucky, Oklahoma, and West Virginia. It varies greatly in commercial value, the variety, *pepinensis,* as found in Lake Pepin—a widened portion of the Mississippi River between Minnesota and Wisconsin—being probably its most valuable form. Practically the same form, or a very close relative, is found in the small lakes including Cross Lake, which is connected with the Snake River, Minn., about 150 miles north of Lake Pepin.

The fish on which the Pepin mucket can pass its parasitic period include several species of spiny-rayed fishes. In other respects, the life history of the Pepin mucket is essentially the same as that of the yellow sand shell. The Pepin mucket is, however, less abundant than this last species of fresh-water mussel and ordinarily brings only about two-thirds of the market price of the yellow sand shell.

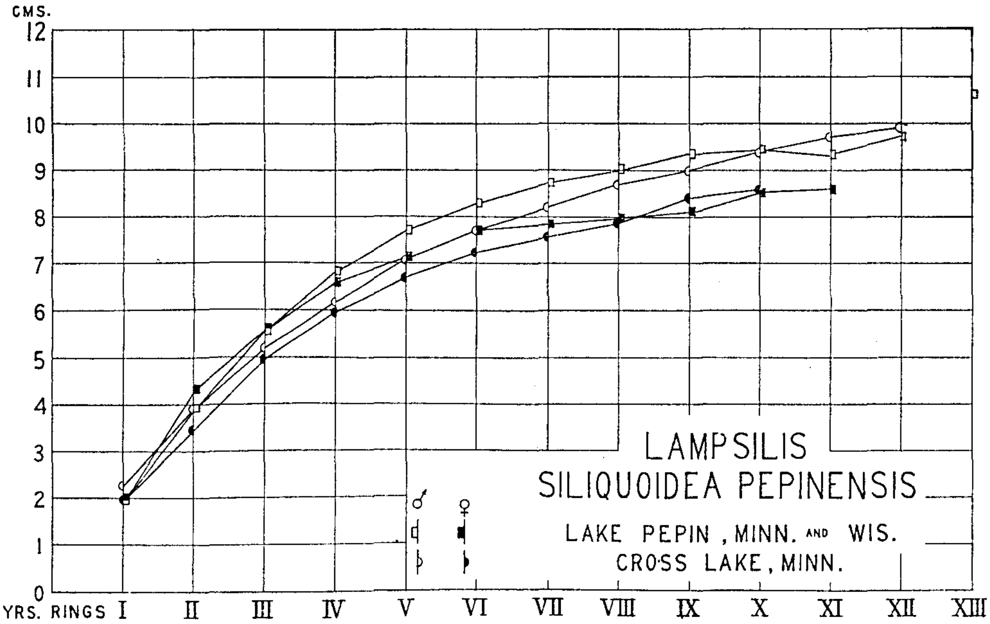

FIGURE 15.—Median curves of growth in length for both sexes of the Lake Pepin mucket. Curves obtained by plotting median valves for annual length against age; that is, first year's growth precedes formation of Ring I

Two series of Lake Pepin muckets were used in the study of growth in this species. One lot was taken from Lake Pepin in the summer of 1926, and the other from Cross Lake, Minn., in 1927. Figure 15 shows the median curves for growth in length for both sexes of this species as found in each locality, and Table 10 gives the actual values. All curves are given in Figure 16, together with the location of maximum and minimum cases for each year class as found in Cross Lake. The actual values are given in Table 11.

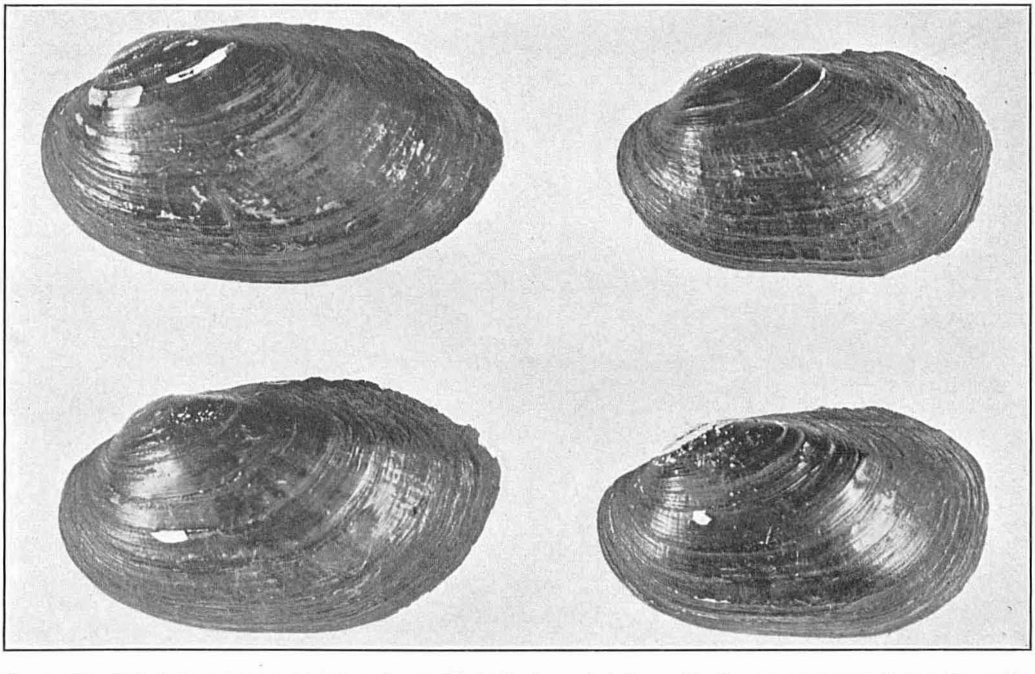

FIGURE 14.—Male (left) and female (right) specimens of Lake Pepin mucket, *Lampsilis siliquoides pepinensis* Baker (*Lampsilis luteola* of authors), Cross Lake, Minn. Upper male, 9.22 centimeters; lower male, 8.82 centimeters; upper female, 8.82 centimeters; lower female, 7.93 centimeters in length

TABLE 10.—*Median length in relation to age of the Lake Pepin mucket, Lampsilis siliquoidea pepinensis, Baker*

MALE

Ring No.	Lake Pepin		Cross Lake	
	Number of specimens	Length	Number of specimens	Length
		Centimeters		*Centimeters*
I	200	1.98 ± 0.048	100	2.25 ± 0.0548
II	200	3.95 ± .050	100	3.88 ± .0609
III	200	5.57 ± .054	100	5.11 ± .0527
IV	200	6.77 ± .052	100	6.17 ± .0581
V	196	7.65 ± .054	100	7.09 ± .0489
VI	185	8.31 ± .053	97	7.69 ± .0500
VII	132	8.70 ± .057	85	8.21 ± .0525
VIII	85	9.05 ± .071	60	8.72 ± .1221
IX	46	9.32 ± .091	33	9.01 ± .0742
X	25	9.43 ± .130	10	9.32 ± .1180
XI	8	9.33 ± .191	4	9.70 ± .1686
XII	3	9.70 ± .292	1	9.81 ±
XIII	1	10.60		

FEMALE

Ring No.	Lake Pepin		Cross Lake	
	Number of specimens	Length	Number of specimens	Length
I	200	1.96 ± 0.049	100	1.98 ± 0.0511
II	200	4.27 ± .042	100	3.42 ± .0535
III	200	5.66 ± .037	100	4.93 ± .0535
IV	200	6.59 ± .040	100	5.96 ± .0486
V	192	7.15 ± .034	100	6.67 ± .0456
VI	139	7.59 ± .042	100	7.24 ± .0475
VII	86	7.86 ± .050	73	7.56 ± .0564
VIII	30	7.97 ± .092	32	7.87 ± .0723
IX	17	8.10 ± .116	12	8.40 ± .1938
X	7	8.50 ± .228	2	8.55 ±
XI	1	8.60		

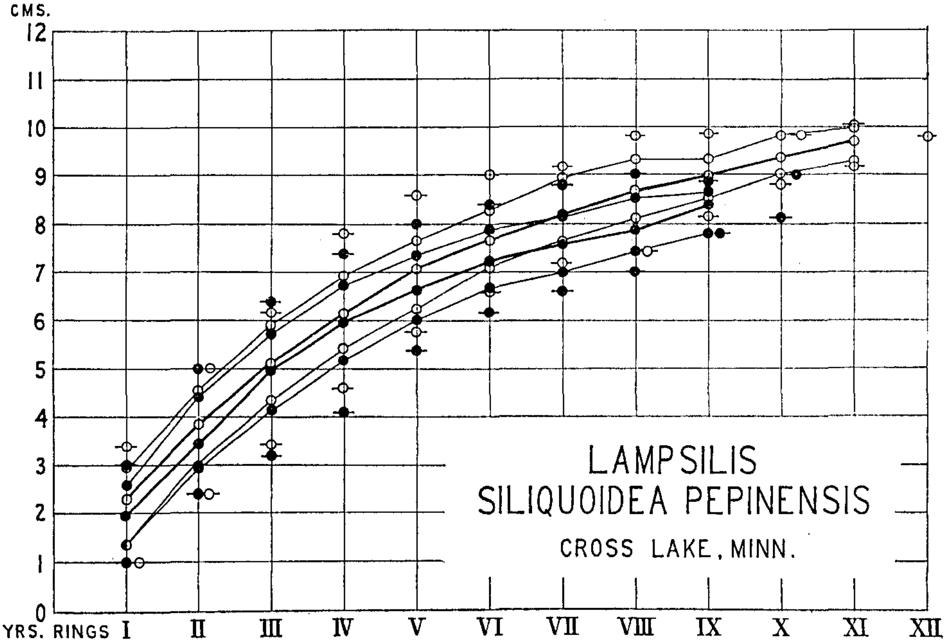

FIGURE 16.—Median curve, together with first and ninth decil curves, of growth in length for both sexes of the Lake Pepin mucket. Maximum and minimum cases for the various year classes are represented by the locality symbol transfixed by a horizontal line.

TABLE 11.—*Length in relation to age of Lake Pepin mucket, Lampsilis siliquoidea pepinensis, Baker, Cross Lake, Minn.*

[All values in centimeters]

MALE

Ring No.	Number of specimens	Minimum	First decil	Median	Ninth decil	Maximum
I	100	1.0	1.42 ± 0.0519	2.25 ± 0.0648	2.96 ± 0.0506	3.4
II	100	2.4	3.02 ± .0613	3.88 ± .0609	4.54 ± .0533	5.0
III	100	3.4	4.36 ± .0843	5.11 ± .0527	5.90 ± .0675	6.2
IV	100	4.6	5.47 ± .0749	6.17 ± .0581	6.90 ± .0636	7.8
V	100	5.8	6.25 ± .0613	7.09 ± .0489	7.65 ± .0519	8.4
VI	97	6.6	7.12 ± .0452	7.69 ± .0500	8.38 ± .0497	9.0
VII	85	7.2	7.68 ± .0443	8.21 ± .0525	8.94 ± .0601	9.2
VIII	60	7.4	8.09 ± .0742	8.72 ± .1221	9.35 ± .0616	9.8
IX	33	8.2	8.46 ± .0725	9.01 ± .0742	9.39 ± .0609	9.8
X	10	8.8	9.00 ± .0713	9.32 ± .1180	9.80 ± .0624	9.8
XI	4	9.2	9.28 ± .1349	9.70 ± .1686	9.92 ± .1349	9.8
XII	1	----------	----------	9.81	----------	----------

FEMALE

Ring No.	Number of specimens	Minimum	First decil	Median	Ninth decil	Maximum
I	100	1.0	1.34 ± 0.0637	1.98 ± 0.0511	2.60 ± 0.0431	3.0
II	100	2.4	2.90 ± .0413	3.42 ± .0535	4.42 ± .1920	5.0
III	100	3.2	4.22 ± .0637	4.93 ± .0535	5.71 ± .0749	6.4
IV	100	4.2	5.23 ± .0612	5.96 ± .0508	6.72 ± .0685	7.4
V	100	5.4	6.03 ± .0595	6.67 ± .0456	7.31 ± .0505	8.0
VI	100	6.0	6.68 ± .0460	7.24 ± .0475	7.89 ± .0723	8.4
VII	73	6.6	7.01 ± .0443	7.56 ± .0564	8.16 ± .0523	8.8
VIII	32	7.0	7.44 ± .0637	7.87 ± .0723	8.56 ± .0882	9.0
IX	12	7.8	7.85 ± .1123	8.40 ± .1938	8.65 ± .0843	8.8
X	2	----------	8.11	8.55	8.98	----------

The growth curves of the Pepin mucket are of the same general type as those of the yellow sand shell, of the buckhorn, and of Pope's purple, the major differences between these several curves being those of rate—the Pepin mucket having an appreciably slower rate of growth than its congener, the yellow sand shell. The year classes in the curves of the Pepin mucket, however, are quite suggestive in comparison with the curves of the yellow sand shell. Although no selection of individuals was made when the original collections were obtained, the year classes in the yellow sand shell groups include only the VIII-year class, with most of the individuals dropping out at the VI-year class, while the year classes of the Pepin mucket groups include the XIII-year class, with a good representation in the X and XI year classes. Shellers along the river regularly report that they do not find "mossbacks" and "old-timers" among the yellow sand shells as they do among the Pepin muckets, and examinations of various heaps of unsorted shells as collected from the river verify these statements in that yellow sand shells more than 6 years old are hard to find. No explanation of these differences in the apparent lengths of the life spans of the Pepin mucket and yellow sand shells is offered; but of the four species studied, the two slow-growing species, the Pepin mucket and the buckhorn, are both well represented in the higher year classes—that is, those above the VI-year class.

Within the species, the Pepin muckets from Lake Pepin show a slightly greater rate of growth in length than the Pepin muckets from Cross Lake. Several factors may combine to produce this difference, but it may be pointed out that Cross Lake is farther north, and that the ice is known to remain in this lake much later in the spring than in the Mississippi at Lake Pepin.

Figure 17 shows the distribution of the left valves of the Cross Lake shells in the different year classes according to weight, males in the upper portion of the chart, and females in the lower portion. Each black square represents one left valve. The mean weight for each class is indicated by the squares with diagonal lines. Actual values for the mean weights are given in Table 12. It will be noticed that not only were the males longer for each year class than the females, but they also exceed the females in weight in those year classes for which data are available.

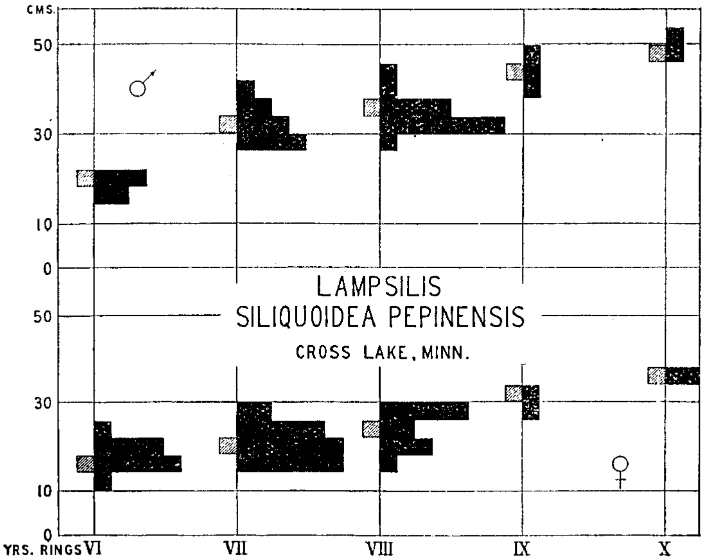

FIGURE 17.—Bar graph showing weight plotted against age for individual left valves of shells of male (above) and female (below) Lake Pepin mucket. Weight values of individual left valves indicated by black squares at right of year classes. Mean weight values shown by striated squares to left of respective year classes

TABLE 12.—*Mean weight of left valves of Lake Pepin mucket, Lampsilis siliquoidea pepinensis, Baker, Cross Lake, Minn.*

Ring No.	Male		Female	
	Number of specimens	Weight	Number of specimens	Weight
		Grams		*Grams*
VI	5	21.2	11	19.8
VII	9	25.4	19	24.3
VIII	14	28.1	11	25.9
IX	3	39.6	2	32.3
X	2	49.8	2	38.9

Coker, Shira, Clark, and Howard (1921), held six specimens of this species at the United States Bureau of Fisheries Biological Station at Fairport, Iowa, for six years. The specimens were held in ponds freshly made at the start of the investigations and kept filled with water pumped from the Mississippi River. The Fairport station is over 250 miles south of Lake Pepin which would give an appreciably longer and warmer growing season. The average length of these six specimens for each year compare very well with the lengths obtained for the Lake Pepin and Cross Lake specimens. After averaging the lengths for the two sexes for these last named localities, and comparing the lengths for each age in the following order: Fairport, Lake Pepin, and Cross Lake, the figures for the second year are 4.34, 4.11, and 3.65 centimeters respectively; for the third year, 6.88, 5.62, and 5.02; for the fourth year, 7.70, 6.68, and 6.07; for the fifth year, 8.06, 7.40, and 6.88; for the sixth year, 8.49, 7.95, and 7.47. Aside from the fact that so few specimens were available in the Fairport tests, it is believed that they check up very well with what might be expected in relation to Lake Pepin and Cross Lake individuals.

BUCKHORN AND POPE'S PURPLE

To test the applicability of the ring method to studies of growth in species belonging to other genera, 16 specimens of the buckhorn, *Tritogonia verrucosa* (Rafinesque), *Tritogonia tuberculata* of authors, from the Mississippi River at Fairport, Iowa, and 7 specimens of Pope's purple, *Unio popei* Lea, from the lower Rio Grande Valley in Texas, were weighed and measured.

The buckhorn is a heavy, comparatively slow-growing shell, ranging (Simpson, 1914) throughout the Mississippi drainage system generally, and streams tributary to the Gulf from Alabama to central Texas. This shell has some commercial value.

Pope's purple is a moderately thin, rapidly growing shell, ranging (Simpson, 1914) through southern Texas and northeastern Mexico. This species, although purple in color, has considerable commercial importance, as the shells can be bleached quite readily to a good, usable white color.

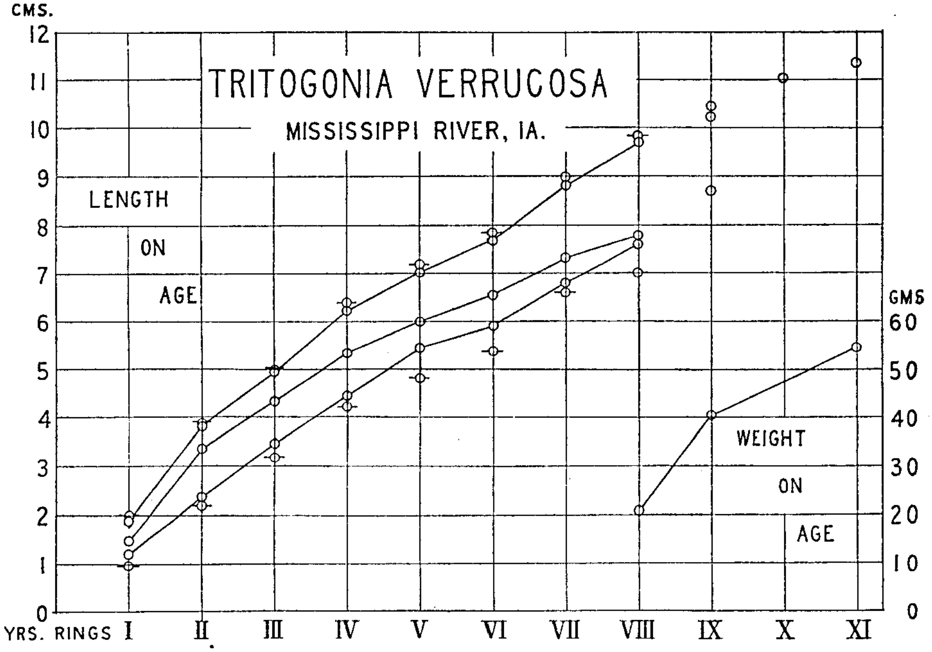

FIGURE 19.—Median curve, together with first and ninth decil curves of growth in length for the buckhorn from Fairport, Iowa. Maximum and minimum cases for various year classes are represented by the locality symbol transfixed by a horizontal line. Also curve showing mean weight on age for the eighth, ninth, and eleventh year classes

TABLE 13.—*Length in relation to age of male and female buckhorns, Tritogonia verrucosa (Rafinesque), Mississippi River, Iowa*

[All values in centimeters]

Ring No.	Number of specimens	Minimum	First decil	Median	Ninth decil	Maximum
I	16	1.0	1.23	1.49	1.88	2.0
II	16	2.2	2.32	3.35	3.77	3.8
III	16	3.2	3.48	4.35	4.94	5.0
IV	16	4.2	4.48	5.36	6.24	6.4
V	16	4.8	5.46	6.00	7.08	7.2
VI	16	5.4	5.92	6.56	7.68	7.8
VII	16	6.6	6.76	7.30	8.88	9.0
VIII	16	7.0	7.60	7.80	9.68	9.8
IX	2	----------	8.69	9.59	10.49	----------
X	1	----------	----------	11.01	----------	----------
XI	1	----------	----------	11.39	----------	----------

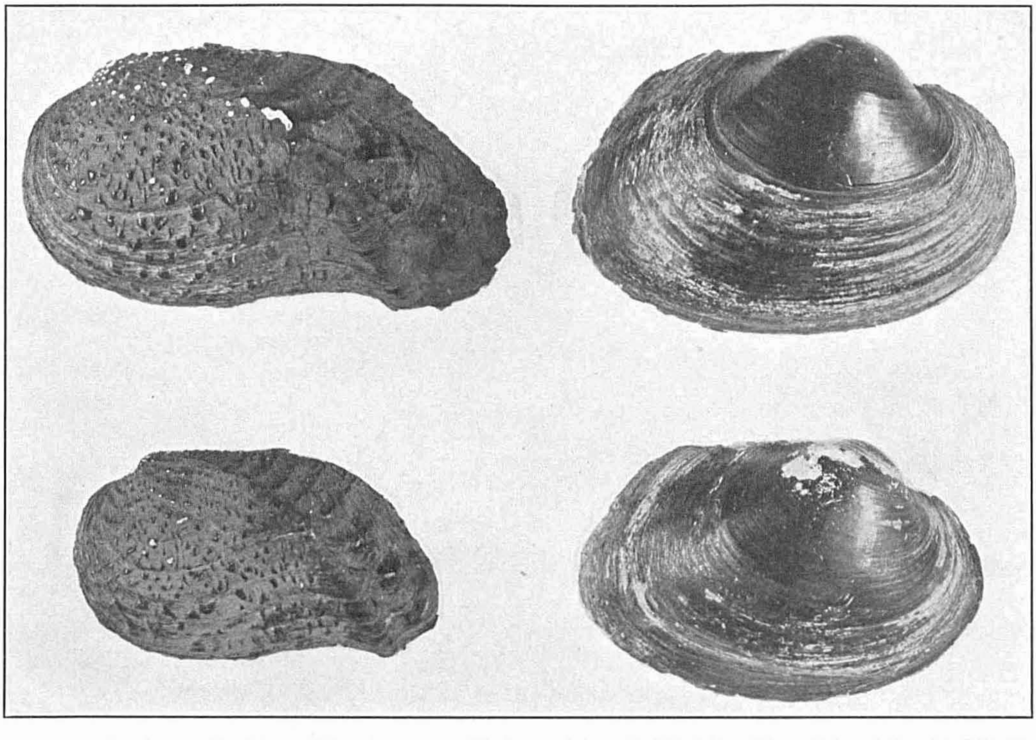

FIGURE 18.—Specimens of buckhorn, *Tritogonia verrucosa* (Rafinesque) (on left), Mississippi River, Fairport, Iowa; and Pope's purple, *Unio popei* Lea (on right), Rio Grande Valley near Mercedes, Tex. Upper buckhorn, 10.22 centimeters; lower buckhorn, 7.69 centimeters; upper purple, 9.26 centimeters; lower purple, 8.36 centimeters in length

The values obtained for these two species have been incorporated in Figure 19 and Tables 13 and 14 for the buckhorn; and Figure 20 and Table 15, for Pope's purple.

TABLE 14.—*Weight in relation to age of buckhorn, Tritogonia verrucosa (Rafinesque), Mississippi River, Iowa.*

Ring	Weight
	Grams
VIII	20.1
IX	40.3
X	------
XI	54.8

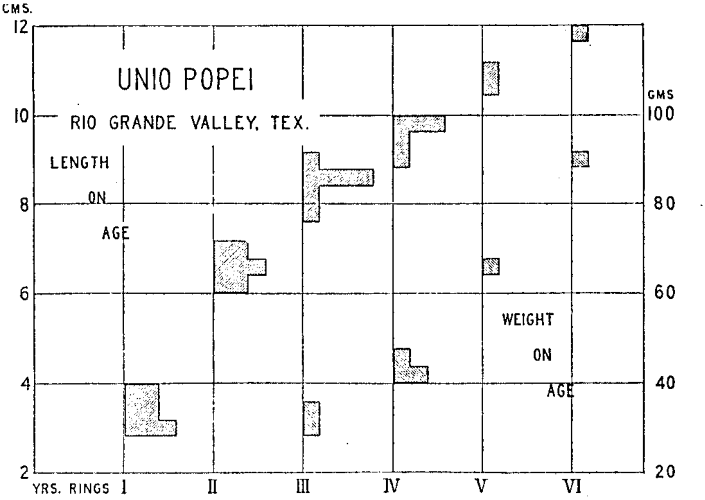

FIGURE 20.—Bar graph showing length (left) plotted against age, and weight (right) plotted against age of seven individual right valves of Pope's purple from Rio Grande near Mercedes, Tex.

TABLE 15.—*Males and females, Pope's purple, Unio popei, Lea, Rio Grande Valley, Tex.*

Age in years	Weights			Length	Height	One-half ventricosity[1]	Annual rings					
	Left valve	Right valve	Mean				I	II	III	IV	V	VI
	Grams	*Grams*		*Centimeters*	*Centimeters*	*Centimeters*						
3	31.4	29.9	32.4	8.41	5.50	1.91	3.29	6.71	8.41	-------	-------	-------
	-------	34.9	-------	8.55	5.65	1.94	3.66	6.51	8.55	-------	-------	-------
4	-------	41.3	42.6	9.13	6.02	2.01	3.08	6.08	7.85	9.13	-------	-------
	44.9	45.0	-------	9.32	6.35	2.19	3.13	6.20	8.16	9.32	-------	-------
	-------	41.6	-------	9.92	6.95	2.13	3.78	6.92	8.62	9.92	-------	-------
5	64.5	64.0	64.0	10.82	7.38	2.45	3.05	6.63	8.61	9.92	10.82	-------
6	88.7	89.3	89.3	11.79	8.17	2.86	3.52	6.80	8.81	9.91	10.70	11.79

[1] By ventricosity is understood the greatest thickness of the two valves when closed, measurement usually falling in the umbonal region.

As it is not intended to give a detailed study of these species here, they are reviewed together. It was found that the ring method was quite as satisfactory for the study of these species as for *Lampsilis anodontoides* and *Lampsilis siliquoidea pepinensis,* and that the same type of growth curves were obtained in all cases.

Comparisons within the species show that the rate of growth of the yellow sand shell was greater in the southern and middle portions of its range than in the northern portion. If the same type of variation of growth rate holds for the buckhorn in its northern and southern ranges, the buckhorn may be listed as having the slowest growth rate of any of the four species studied, as its actual growth rate at Fairport, Iowa, was about the same as that of the Lake Pepin mucket at Cross Lake, Minn.

AREA OF SHELL

Although length, weight, and thickness furnish indices of growth from which growth curves giving the physiological aspects of the problem may be constructed, from a practical commercial standpoint the growth of the shell is measured largely by the area of the shell from which button blanks may be cut.

Since even the shells of the very flat species, as the pink heelsplitter, *Proptera alata*, are actually curved plates presenting both concave and convex surfaces, it is rather difficult to measure exactly the surface area of a mussel shell. For purposes of comparison, however, a projection was chosen, as in the cutting of blanks the shell is handled to a large extent as if it were a plane surface. Placing the valve on a piece of white paper, and tracing around its margin with a pencil, a projection of the shell was readily obtained. The area of this figure was then measured in square centimeters by tracing the outline of the projection with a planimeter.

The average values for the areas of the projections of shells from the various year classes are listed in Table 16. It is evident from this table that the surface of the yellow sand shell is greater for each year class in specimens from the southern portion of the range of this species than from the northern part. There is also a noticeable difference in area of the shell correlated with the sex of the individual.

Considering shell area alone in terms of year classes, the comparisons of the four species examined favor the rapidly growing species and the southern habitats.

TABLE 16.—*Average areas (in square centimeters) of valves by year classes*

Species	Sex	Year classes							Locality
		II	III	IV	V	VI	VIII	XI	
Yellow sand shell, Lampsilis anodontoides.	Male		23.0	28.8	40.8				Mississippi River, Fairport, Iowa.
Do	Female				41.3				Do.
Do	Male		20.7	38.0	39.1				White River, Newport, Ark.
Do	Female			40.8	46.6				Do.
Do	Male	23.9	42.3	44.8		64.2			Rio Grande, near Mercedes, Tex.
Do	Female		35.9	59.8					Do.
Lake Pepin mucket, Lampsilis siliquoidia pepinensis.	Male				19.9	24.5		38.3	Cross Lake, Minn.
Buckhorn, Tritogonia verrucosa							26.5		Mississippi River, Fairport, Iowa.
Pope's purple, Unio popei			37.4			67.2			Rio Grande, near Mercedes, Tex.

DISCUSSION

Considering all of the data obtained from over 1,100 specimens, the application of the annual-ring method to growth studies of fresh-water mussels seems both reliable and practical, judging from the uniformity of the growth curves developed from these data and the ease with which these measurements may be made on the great majority of shells.

That the shell rings are the result of an interruption of growth has been established experimentally (Lefevre and Curtis, 1912; Coker, Shira, Clark, and Howard, 1921); and that the changes in environmental conditions during the winter months provoke a major interruption of growth has been observed by various writers (Hazay, 1881; Isley, 1914). Weinland (1918) working with the European fresh-water mussel, *Anodonta cygnea,* found that the daily oxygen consumption fell from 5.3 milligrams in November to 1.7 milligrams during December, January, and February; rising again to 5.3 milligrams in March, 9.6 milligrams in April and May, and 17.0 milligrams in June. This fall in oxygen consumption during the winter months to a level only one-tenth of that maintained by the same animal during the month of June, implies metabolic changes which might readily provide a physiological basis for the winter growth interruption and account for the extent of this interruption.

Eliminating the few problematic individuals which are always found in any large series of animals, this major annual ring was rather easily differentiated from the other narrower interruption rings.

During the analysis of the data, the length was plotted against age on semilogarithmic paper to ascertain whether the growth in length in fresh-water mussels represents a logarithmic function comparable to many other biological corollaries of growth. (See Brody, 1927; Brody, Comfort, and Matthews, 1928.) In the main, up to the VI-year class, the length values from mussel shells were reducible to a straight line by this treatment. After passing the VI-year class, the gains in length were less than the logarithmic values required to maintain a straight line, indicating a more abrupt decline in growth rate than that represented by a simple logarithmic progression; that is, there was a distinct slowing of linear growth, suggesting a senile stage. (See Minot, 1908.)

Since the commercial value of the fresh-water shells decreases very rapidly beyond the VI-year class, this period of senile decline is not discussed in detail here.

As several factors, such as increase in the weight of the shell and changes in the metabolism of the older animals, may be correlated with this change in the linear growth rate of the older mussels, additional data are being collected on this phase of the problem.

SUMMARY

By means of the annual ring method, the year classes of over 1,100 fresh-water mussel shells have been determined. Studies of length, weight, and thickness were made on the shells of these groups.

Four commercial species, the yellow sand shell, *Lampsilis anodontoides;* the Lake Pepin mucket, *Lampsilis siliquoidea pepinensis;* the buckhorn, *Tritogonia verrucosa;* and Pope's purple, *Unio popei,* were used. Growth curves were developed for each of these species.

Yellow sand shells from three localities—the Mississippi River at Fairport, Iowa; the White River at Newport, Ark.; and the Rio Grande Valley, near Mercedes, Tex.—were studied. These localities represented the northern, middle, and southern portions of the range of this species.

The growth curves for length of the yellow sand shell show that the Mississippi shells made their greatest gain in length during the second year; that the White River shells made about equal gains during the first and second years; and that the Rio Grande shells made their greatest gain during the first year. After passing the maximum rate gain, the rate of gain in length declines very rapidly to the VI-year class, beyond which the gains in length are small.

By comparing the weights of the yellow sand shells from the three localities, it may be seen that the Texas shells were conspicuously lighter in proportion to their length than the shells from Arkansas and Iowa. Thickness studies emphasize this difference.

Combining the data on length, weight, and thickness, it was found that the yellow sand shell requires about 5 years to reach a fair commercial size in the Mississippi at Fairport, Iowa; 4 years in the White River, in Arkansas; and but 3 or 4 years in the lower Rio Grande.

Differences in the rates of growth of the two sexes of yellow sand shell, apparently correlated with the changes in the contour of the shell accompanying sexual maturity, were noted in each of the three localities.

Considering the commercial aspect of length, weight, and thickness, together with the age of the year class, the yellow sand shells from the White River in Arkansas made the most satisfactory growth.

Growth curves for the Pepin mucket, the buckhorn, and Pope's purple were of the same general types as those described for the yellow sand shell.

The Pepin mucket and the buckhorn grow more slowly and have longer life spans under the existing conditions in the upper Mississippi than the yellow sand shell in any part of its range as studied.

Comparisons of valve areas—that is, the surface available for the cutting of blanks from the shells of the four species studied—made on the basis of year classes, favored both the rapidly growing species and the southern habitats.

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