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Excerpts from "Studies on the larvae of the Canadian oyster."

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EXCERPTS FROM "STUDIES ON THE LARVAE OF THE CANADIAN OYSTER".

(Thesis submitted in partial fulfillment of the requirements for the degree of Doctor Philosophy in Zoology in the Graduate School of the University of Illinois, 1938.)

by

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Critique of Larval Measurements

> "...but, owing to the different convexities of the valves, the greater breadth above and behind, and the different degrees to which it may be tilted in this way or that, the same larva may vary much in apparent size and shape accoringtas to how it is presented to the observer."
>
> Joseph Stafford, 1909

Before attempting a size -frequency study of the collected samples, tests were made to determine, first, the reliability of any single measurement of a larva and, second, which of the two easily measured larval dimensions, height and length, is the more dependable as representative of the actual size. By height, is indicated the distance from the tip of the umbones of the larval shell to the middle of its free margin; by length, the greatest dimension from the anterior to the posterior margins of the shell measured at right angles to the vertical axis.

For testing purposes three larvae were chosen, a small, a middle-sized and a large one. These were mounted in water on glass slides and forty measurements made on each. A length and width reading was made on a larva in one position then the position altered by jarring the slide and the same two measurements made again. This was repeated ten times with the larva lying on the one side, the left, say, with the large umbone facing down. The larva was then turned over to lie on the right side with the larger umbone facing up and the same process repeated. The results of these measurements are presented below in Table 1.

TABLE I. DISTRIBUTION OF TEST MEASUREMENTS

OF 3 LARVAE IN DIFFERENT POSITIONS

Larval Measurement in u.	Description of larva	Position of larva at time of measurement											
		Lying on left side (large umbone down)						Lying on right side (large umbone uppermost)					
		Height			Length			Height			Length		
		S	M	L	S	M	L	S	M	L	S	M	L
120-129	Small												
130-139	Larva				2						3		
140-149	"S"				2			1			3		
150-159		2			3			0			1		
160-169		4.			2	1		5			2		
170-179		4			1	1		4			1	5	
180-189						1						3	
190-199	Medium					2			1			0	
200-209	Sized					0			1			1	
210-219	Larva					4.			1				
220-229	"M"		9.			1			4			1	
230-239			1						3.				
240-249													2
250-259							2						1
260-269	Large						2						5
270-279	Larva						1						1
280-289	"L"						3.						1
290-299				2			2						
300-309				6						3			
310-319				2						7			

. These measurements are included in Table II

From this table it is to be seen that there is a considerable "spread" in the results of measurements of any one larva. The deviations are, no doubt, partly due to a personal error on the part of the writer in marking the limits of the convex surfaces projected by the camera lucida. A more significant irregularity, however, is brought about by the inclination of the larva away from the horizontal plane. This tilting which Stafford (09) found so confusing (See quotation introducing this section, page 29), is due to the convexity of the shell whose nature is such that only very seldom will it settle in a position permitting a truly lateral view.

It should be noted that the convexity of the loggitudinal axis is greater than that of the vertical. As a result there is more likely to a tilting about the vertical axis than about the longitudinal. Thus the spread of the height measurements for any particular larva is less than that of the length values. The former may therefore be considered the better measurements since they are less subject to variation.

The figures further show, but less clearly, that the "spreads" are less when the larvae lie on their left sides with the large umbones down than when resting on the right. This may be partly due to the fact that when a larger umbone is uppermost the centre of gravity of the larva is raised higher above the surface on which it rests. This position is the less stable and the larva is more likely to be tilted than when it rests with the heavier umbone down. Fortunately, when a sample is poured onto a counting slide nearly all the larvae settle with the larger heavier umbone resting against the glass. It is therefore possible in most cases to make the more reliable measurement, the height, when the larva is in the more favourable position, lying on the left side.

Before the writer could feel justified in making only a single measurement as representative of each larva, a series of length-width readings was made on a number of larvae found in a plankton sample taken July 22, 1936. The results of this study appear below in Table II.

TABLE II. SIZE FREQUENCY DISTRIBUTION OF HEIGHT MEASUREMENTS OF 37 LARVAE TAKEN A TOW MADE JULY 29, 1936.

Larval height in u. \ Larval length in u	110-119	120-129	130-139	140-149	150-159	160-169	170-179	180-189	190-199	200-209	210-219	220-229	230-239	240-249	250-259	260-269	270-279	280-289	290-299	300-309	310-319	320-329	330-339
110-119	1																						
120-129			1																				
130-139	1		1	1																			
140-149				1	1																		
150-159																							
160-169							11																
170-179					1	1	2																
180-189							1																
190-199							1	1	1														
200-209								1		1													
210-219																							
220-229										• 1	1	1											
230-239											1	1	1										
240-249													1										
250-259										1													
260-269														2		1							
270-279														2	1		1						
280-289														1				1					
290-299																	•						
300-309																							
310-319																							
320-329																							
330-339																							
340-349																							
350-359																							
360-369																							*

. Position of modes from Table I

* Position of modes from Table III.

From Table II it is clear that the size-proportions of developing larvae are fairly constant. Considering the reliability of the present method, it seems justifiable, therefore, to accept height measurements of larvae as a reasonable index to size in the size-frequency distributional studies.

Table I suggests that a single height measurement usually falls within 10 µ of the mode of a series of such values for the same larva. A single hgight measurement for each larva encountered, therefore, should yield results that have an error tolerable in the present analysis.

Nelson (1917) states that with ocular micrometer measurements of larvae mounted in water he could get dependable accuracy only to the nearest 0.01 mm. The writer's figures clearly support his statement.

There is some difficulty in distinguishing very young oyster larvae from those of other species. On the fifth or sixth day after fertilization they take on a race colour which is of great assistance in identifying fresh animals. The larvae are about ten days old and measure 100-120 µ in height when they assume the typically asymmetric appearance which identifies the later stages. Since the colours fade in formalin preservation and most of the counts were made in Illinois during the winter seasons, there was no ready means of detecting the presence of oysters measuring less than 100-120 µ in the catches studied. For this reason there is a considerable interval between the spawning date of any one brood and the date of its first appearance in the records of the size-frequency distribution studies.

Treatment of Settlement Data

The methods employed in the collection of settlement data have already been described in the section "Outline of study and sources of materials and data". A short explanation is necessary, however, of their present interpretation.

With very few exceptions the 1937 daily counts of spat on the 10 shells were made at 9.00 A.M., as the morning's first task. Only the average sets per shell are listed in Appendix I and were obtained by dividing the totals of each day's catch by 10. The 1936 counts were less regular and sometimes a day's counting was skipped. These omissions are indicated in the Appendix. In such cases two or even three days' settlement is lumped in the one observation. Where blanks occur it is to be understood that no spat were found during the examination of the corresponding date.

The settlement curves appearing on Graphs II and IV are developed from the figures appearing in this appendix but in plotting, the observations are all set back one day. This is because the fresh spat observed on any particular morning appeared during the previous 24 hours and therefore belong, properly, to the date previous. The 1937 results are plotted quantitatively but the 1936 observations are qualitative and are suggested by "humps" whose heights are only roughly proportional to the extent of settlement that took place.

Because some larvae of a brood develop more quickly than others they will mature and settle earlier. It may be assumed that the amount of settlement likely to occur on any one day will be proportional to the number of mature larvae in the water at that time. In like manner, it is to be expected that the peaks of settlement will occur when those larvae which have all along occupied the modal positions in broods attain a height of 360 - 370 μ. That is to say, settlement data can be combined with the results of larval size-frequency distributional studies in plotting the growth rate of the larval age groups.

Summary

From a combined study of temperature fluctuations, changes in gonads of adult oysters, larval life histories and settlement data, the writer has been able to demonstrate the practicability of predicting the time of set in the Bideford river. The dependability of the proposed method has been proven already, in part, by the results of certain predictions made during the past summer of 1937.

ON THE SIZE OF THE MATURE OYSTER LARVA

In order to determine the size of the larva at the time of settlement a series of measurements was made of the prodissoconchs of 32 freshly settled Bideford river spat during the summer of 1936. Unfortunately only the two diameter measurements were listed at that time without stating which wax length and which was height. Accordingly, only the average diameters are reported here. The distribution of these measurements is illustrated below.

Average diameter in µ.	Frequency of measurement.
280 - 290	1
290 - 300	0
300 - 310	1
310 - 320	7
320 - 330	5
330 - 340	9 mode
340 - 350	8
350 - 360	0
360 - 370	1
Total	32

Prytherch ('34) has shown that metamorphosis of the larva to the "spat" condition begins immediately after settlement. As a result, growth of the prodissoconch ceases at this time. Since the character of the dissoconch is distinct from that of the earlier deposit, it is a simple matter to judge the mature size of the original larva from the examinations of fresh spat.

In 1937 more careful and more extensive measurements were made on Bideford river spat, the results of which appear in Table III.

Although the length of the prodissoconch of an oyster larva is actually greater than the height (Stafford '12c) the mode of the 1937 measurements suggests that it is smaller. This apparent contradiction might be explained on the basis of a greater tilting of the longitudinal axis than of the vertical similar to that described for the larvae in the section on the critique of larval measurements. Such an explanation seems logical, since the orientation of spat depends on the position of the mature larval at the time it cements itself to any surface.

From Table III, it seems the best average diameter of freshly settled spat would be 350 µ. This approximates closely the value derived from the 1936 studies. These two years showed some consistent differences in the lengths of the larval periods and in the average temperatures during those periods. The logical inference is, that insofar as the hydrographic conditions varied during these two years, they did not alter the maturation size of larvae to any appreciable extent. In other words, within the limits encountered here the ultimate size of the larva is constant.

Sherwood ('30) states in his report that the largest larvae he ever found in his tows measured 360 µ. In view of the present study this is not to be wondered at. Commenting on this observation and comparing it with the reports of Nelson ('17) who claimed that the Canadian oyster larvae grew to a size one fourth larger than that of the New Jersey strain, Sherwood suggested that there might be some marked variation in the mature size from year to year. The present study would seem to discount this hypothesis and to support the belief that a height of 300 - 370 µ for the mature larva is characteristic of the Bideford river area.

TABLE V SHOWING SIZE-FREQUENCY DISTRIBUTION OF LENGTH - HEIGHT MEASUREMENTS OF PRODISSOCONCHS OF 194 YOUNG 1937 SPAT OYSTERS FROM BIDEFORD RIVER.

	250-259	260-269	270-279	280-289	290-299	300-309	310-319	320-329	330-339	340-349	350-359	360-369	370-379	380-389	390-399	400-409	410-419	420-429	430-439	Larval length in µ
250-259																				
260-269																				
270-279										1										
280-289								1	1											
290-299								1												
300-309			1		2	1	2	1	1		3									
310-319		1		1	1	3	1	1												
320-329				2	2	1	1	1												
330-339			2		1	1	1	3	4	2	2									
340-349				2	1	2	6	3	6	2		1								15
350-359			2	3	3	3	9	6	6	1		1								22
360-369			1				7	7	7	13	3		1							34
379-379							1	7	11	8	2	2								26
380-389				1			1	3	1	4	4	1							1	Totals within polygon
390-399									3		1	1								
409-409											1	1								
410-419								1												
420-429																				
430-439																				
Larval height in µ.							22	23	30	21										

Totals within polygon

Most representative values:

Height 360-379 µ

In 1938 a series of measurements of 52 spat oysters taken from the Bras d'Or Lakes of Nova Scotia where hydrographic conditions are considerably different from those of Bideford river, showed a modal value of height 365 μ, length 345 μ. This is identical with that obtained for the Bideford river in 1937 and suggests that throughout its range the Acadian oyster has a characteristic size for the mature larva. Of nearly 3000 measurements of larvae reported here in Tables V and VIII only one exceeded 370 μ. The prodissoconch measurements show also that the number of larvae exceeding a height of 370 μ at the time of settlement is much smaller than those which settle at a smaller size. Judging from the present studies the values, height 369 μ, length 384 μ are the best of the several figures, offered by Stafford (See page 18).

In the present consideration 365 μ will be taken as a reliable value for the height of mature oyster larvae.

Brood Studies of 1936

A size-frequency distributional analysis was made of larvae taken in tows on the following dates:

June 27	August 4
July 15	" 7
" 20	" 12
" 24	" 20
" 29	

The numerical results are reported in Table V and are represented in Graph III. This latter will be analyzed following the well-known "Petersen method" in which the maturation of age groups as illustrated by the progressive shifting of the modes along the abscissa is studied. Each age group will be dealt with separately.

TABLE V RESULTS OF SIZE-FREQUENCY DISTRIBUTIONAL STUDY OF SAMPLES OF 1936 OYSTER LARVAE.

Height of larva in u.	Date of Sampling										
	June	July				August					
	27	15	20	24	29	1	4	7	12	17	20
	Frequencies										
80-89					11	6	1				
90-99											
100-109		5	1		26	18	2				
110-119		4	2	2	7	16	8			1	
120-129		8	13	4	3	15	16		4	1	1
130-139		6	26	3	7	11	23	2	9	3	
140-149		0	32	7	4	8	22	5	12	3	
150-159	1	2	43	16	9	3	26	9	13	4	3
160-169	4	2	16	15	12	1	15	6	20	7	5
170-179	3	1	8	14	18	3	7	27	12	11	5
1809189			4	21	18		2	27	9	9	2
190-199	1	1	2	18	19		5	35	2	16	8
200-209	1	3		4	19	1	2	37	6	17	11
210-219		3		1	19	2	2	27	3	15	10
220-229		1		2	15		1	25	5	16	12
230-239			1		22		3	18	2	9	8
240-249					13			20	1	14	17
250-259					18			8	2	7	14
260-269					16		1	3	1	5	19
270-279					19		1	1		3	17
280-289					15	3		3	3	2	9
290-299					4	1			2	8	14
300-309					1		1			7	4
310-319						1			1	5	6
320-329					1				1		4
330-339									1	3	1
340-349								1	1	1	
350-359							1	1	0		1
360-369											
Total number measured in the sample	10	36	148	107	296	89	139	255	110	167	171

Grand total 1528

determined from only ten measurements that they are not accurately placed.

In criticism of the curves developed in the present study it should be stated that their accuracy can be only approximate because of the method of their construction. The location of each additional segment beyond the first, during the "piecing-together" process depends on extrapolution of the preceding segment and the placing of the middle point of the segment to be added on this extended line. The error in the construction is therefore cumulative--a fact which must be borne in mind in the use of the curves. However, the results check very well with those of the study described in the section, "Temperature as a regulator of the larval period." The close agreement suggests that the curves are not far wrong.

To develop a really reliable curve, larvae should be cultured under conditions of constant temperature, a feat not easily performed.

The Taxonomic Status of the Canadian Oyster

The size of the mature Bideford river larvae seems to be the same from year to year and to be identical with that determined for the Bras d'Or lake, Nova Scotia, for 1936. This is true in spite of the fact that the salinity conditions in the latter area are so different from those in the river. Some differences might have been expected if that factor were of great importance in regulating maturation. Unfortunately the length of the larval period has never been worked out for the Bras d'Or lakes.

The similarity in size of larvae growing under these diverse conditions suggests that this character may be either fundamental to the Canadian strain of O. virginica or that environmental factors other than salinity combine to produce the same results in the animal.

The ultimate larval height in Barnegat bay, New Jersey, is 300-320 μ, according to Nelson ('21). Comparing this with the northern strain where the height is 365 μ it will be seen that the latter is greater by about 18%. Similarly, the larval period in New Jersey is less, 13-15 days. Using Nelson's date ('23) it may be shown that at an average temperature of 22°C. the growth rate of larvae ranging in size from 130-170 μ is about 16 μ per day. A similar part of the 22°C curve--over the range 150-230μ--of Graph VII suggests that the daily growth rate of Bideford river larvae is apparently 14 μ.

Although the evidence is not too clear, the comparison suggests that at similar temperatures the larval growth rate in the two regions is approximately the same. Salinities in those two areas are very different for, while in the Bideford river they range from 26 to 28 parts per mille, they stand at about 16 in Barnegat bay. If this environmental difference, which might be important, is disregarded, it may be said that the growth procedes at the same rate in both districts being influenced only by temperature. On the whole, the Barnegat bay is warmer than Bideford river.

It has been noted for various cold-blooded animals that with lower temperatures growth to any particular size proceeds more slowly. This has been demonstrated here for the Bideford river. Further, the life span and ultimate size are increased by low temperatures. (For a discussion of this relationship for invertebrates the work of McArthur and Baillie ('29) may be cited.) All these generalizations seem to hold true in the case of oyster larvae because in Bideford river they live longer and grow larger than in New Jersey. After he compared the German form of the European oyster, O. edulis, with that of Italy, Kändler ('28) pointed out the same peculiarity as has just been described for O. virginica.

The above comparisons might be considered as having a bearing on the taxonomic status of the Canadian oyster. It seems possible that regional differences in the growth characteristics can be attributed merely to variations in environmental factors. Unless this simple difference is to be regarded as sufficient, then, a taxonomic separation of northern and southern strains would seem unnecessary. Certainly, if a separation of the American forms is made, it would seem only logical to split up the European species as well.

A more careful analysis of this problem would be interesting, From the present study one might expect to find an intergradation of growth characteristics from north to south. The peculiar isolation of the Canadian oyster colonies from those of the United States makes such a comparison difficult. Perhaps, in the end, results of a detailed study of the European species will help to establish one or other of our two present views relating to the North American species.

Criticism of the Method

The method of prediction developed from the present studies has the disadvantage that it can be practised only by a worker skilled in the use of a microscope. Further, it requires the keeping of temperature records for the district concerned but beyond this it requires only the use of a boat, a plankton net and a few other pieces of simple laboratory equipment such as pipettes watch glasses, formalin, jars, etc.

From another point of view it has short-comings. So little is known, as yet, of the behaviour of larvae in these waters and of the ravages their enemies make on them, that the method is almost purely qualitative. It is the writer's hope to pursue the study further and by elaboration make it quantitative. This will be possible only after a great deal of careful study of larval behaviour, if we may judge from the investigations Nelson and Perkins ('31) have carried out in New Jersey.

In defense, it may be stated that the method permits a more accurate prediction of the time of settlement than that of gonadial examination now practised in Canada. Besides this, it involves less laborious work, avoiding tonging and opening of adult oysters. A prediction made in this way is also better founded since it is based on observations made at a time much closer to the date of settlement. There is a shorter interval between the date of prediction and actual settlement, therefore, during which an upset of the natural coubse of a brood's history might come about.

Comparing the method with those practised elsewhere, it may be said that is is essentially like that practised by T. C. Nelson in Barnegat bay, except that it is considerably modified to suit the particular conditions found in Bideford river and the Canadian strain of O. virginica.

Such a method as Prytherch's could not be applied in this area for, as was pointed out above, there is no clear relationship between lunar cycles and spawning season.

With the present limited knowledge of larvae this seems to be a sound practical attempt at a solution of the Canadian prediction problem.

The life history and distribution of the Atlantic oyster has been described with comments on the importance of its various peculiarities in the practises of oyster culture.

A survey of that special knowledge of the Acadian strain of O. vriginica which bears on the present study has been made.

The methods of the study have been described and the data on which it is based have been presented in tabular and graphic form.

A combined study of (a) temperature conditions in Bideford river (b) spawning reactions of adult oysters (c) size-frequency distribution of larvae found in plankton tows taken on different dates and (d) records of daily settlements of larvae, throughout the summers of 1936 and 1937 has been carried on partly at the Prince Edward Island Marine Station in Canada and partly in the zoological laboratories at the University of Illinois in the United States.

A reliable basis for size-frequency distributional studies of samples of the larval oyster population has been developed. On this basis was laid a seasonal statistical study in which age groups in the larval population were followed after the Petersen method.

Average growth curves for larvae at different temperatures have been developed.

The ultimate size of the free-swimming larva has been carefully determined from a longer series of measurements than has been previously reported.

The length of the free-swimming period of the Canadian oyster has been determined more accurately than ever before. Its variation has been related directly to differences in the average daily water temperatures to which the larvae were subjected. The effect of temperature on larval growth has been studied. The taxonomic position of the Canadian form of O. virginica has been discussed in relation to environmental factors.

Besides adding to the previously accumulated knowledge of the Acadian oyster, the study has led to the development of a method for accurately predicting the time of larval settlement in Bideford river.

Several methods of prediction practised elsewhere have been outlined and the peculiar conditions obtaining in the waters of Bideford river which predetermined the details of the method applicable there, have been described. The new method has been criticised and compared with that already practised in Canada and with those applied in various ports of the United States.

The accuracy and practicability of the method has been demonstrated by successful predictions made during the summer of 1937.

The literature which the writer has found of particular value in this study has been cited.

CONCLUSIONS FROM THE STUDY

1. The stability of other factors in the waters of Bideford river suggests that there it would be convenient to study the effects of temperature on the life history of the oyster.
2. Spawning reactions of the Bideford river oysters are so obscurely related, if at all, to lunar cycles that the latter may be disregarded in the present study.
3. The "latent period" succeeding a temperature rise to the spawning threshold and preceeding spawning, seems to be much shorter in Bideford river than that reported by Nelson ('28) for oysters in Barnegat bay, New Jersey.
4. Spawning seems to come in "bursts" in Bideford river, just as it does in Barnegat bay and Milford harbour, resulting in the establishment of distinct age groups in the larval population.
5. Due to peculiar shell convexities it is difficult to make accurate measurements of larvae under ordinary conditions. A difference of 10-20 μ in successive measurements of the same larva is common.
6. In making series of measurements for size-frequency distributional studies a shell-height is more reliable than a shell-length measurement as an index to the true size of any larva.
7. The length-height proportions of larvae seem to be constant for all larvae throughout their free-swimming period.
8. The larvae of each age group develop and mature together, all settling at the same time within a day or two.
9. In 1936 and 1937 the lengths of the larval periods have been shown to vary from 23 to 31 days depending on the average temperature during the period.

10. Judging from the results of the analysis the periods would be 24, 26½ and 32 days with a continual average surface temperatures of 22, 21 and 19°C. respectively.

11. The ultimate size of the larva in Bideford river seems to be relatively constant from year to year and the average height of the mature prodissoconch to be 365 u.

12. The oyster larvae living in the brackish waters of the Bras d'Or lakes have the same size at maturity as those of Bideford river.

13. There is a definite need in Canada for a dependable method for predicting the date of larval settlement because cultch begins to foul rapidly soon after it is placed in the water.

14. With the results of the present study as a basis, it is possible to predict accurately the time of larval settlement in Bideford river, from an examination of the year's temperature curves and the study of the planktonic larvae of the oyster.

15. This method, besides involving less laborious work than that now in practice has been shown to be more accurate by results of the 1937 tests.

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