TEMPERATURE AND THE SHELL MOVEMENTS OF OYSTERS [1]

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INTRODUCTION

The influence of temperature on the physiology of feeding in the oyster was studied by Galtsoff (1928), who found that the rate at which the gill mechanism pumps food-bearing water depends upon the temperature of the water, and that not only does this rate of pumping become slower with decreasing temperature, but at about 6° C. it actually ceases and the oyster is unable to feed. During this hibernation period induced by low temperature, it may be that cessation of flow of water through the gills is only one of the important changes in behavior. All physico-chemical activities are probably slow at this time.

In the oyster, feeding is limited not only by the rate at which the gill mechanism acts but also by the shell movements. Feeding occurs at temperature conditions favorable to gill activity only if the shells are open, for obviously water can not enter when the valves are pressed tightly together. The question arises as to what environmental factors may influence shell movements. In a work on the effect of sulphite pulp mill waste liquor on oysters by Hopkins (1931), it was shown that the presence of this substance in the water caused the Olympia oyster (*Ostrea lurida*) to remain closed more of the time than specimens in uncontaminated water. The same substance was demonstrated by Galtsoff (1931), to reduce the rate of pumping of water by the gills of both *O. lurida* and *O. gigas*. The mechanisms controlling the activity of both the gill mechanism and the adductor muscle appear to be highly sensitive to environmental factors. Since both of these mechanisms are directly concerned with the feeding habits of the oyster, it is important that they be clearly understood.

In some experiments on the effect of sulphite liquor on the Olympia oyster, the shell movements of the control specimens were recorded by means of kymographs, and thermograph records of water temperature were kept. Several such series, each of from 5 to 30 days' duration, were obtained. These records show a significant correlation between water temperature and shell activity. In the following pages certain of these results are presented and analyzed. That these conclusions are

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probably applicable to the eastern oyster (*O. virginica*) also, is suggested by the similarity between the behavior of this species (recorded without continuous thermograph records) and that of the Olympia oyster.

METHOD

The method of recording shell movements with the kymograph was similar to that of Galtsoff (1928). The specimens were set on a plaster of Paris base and immersed in an aquarium of about 3 liters capacity. Two specimens were in each aquarium. Freshly pumped sea water was running constantly. The recording levers were of celluloid strips, and the weight of the end carried by each oyster was so counterbalanced that there was no noticeable effect on the specimen. A long paper kymograph carrying a paper about 2 meters long was employed.

The bulb of the thermograph was immersed in the water of the aquarium close to the oysters. The large size of the bulb was the source of a certain amount of error in the method. It extended from end to end of the aquarium, and while inflowing water of a changed temperature might strike a specimen and produce a reaction, it would be some time before the temperature throughout the chamber would be different enough to show a change on the record. The temperature chart showed what amounted to an average temperature in the aquarium, and for this reason would be relatively sluggish. In spite of this inaccuracy, however, the results are clear.

EXPERIMENTS WITH OLYMPIA OYSTERS (*OSTREA LURIDA*)

NUMBER OF HOURS OPEN PER DAY

Nelson (1921) found that oysters remained open an average of 20 hours per day, while Galtsoff (1928) obtained an average of 17 hours and 7 minutes. Such a discrepancy is probably due to environmental factors. Galtsoff noted that one specimen remained tightly closed for 67 hours while the temperature was between 0.5° and 1.6° C. If temperature has a marked influence on shell movement, the difference between the results of Galtsoff and Nelson becomes clear.

In Table 1, the data obtained with 18 specimens of *Ostrea lurida* are presented. During most of the tests the temperature was between 14° and 17° C., and these oysters were open a large part of the time. All results together show that, in spite of marked temperature fluctuations in certain cases, the oysters were open an average of 20.45 hours per day. Eliminating those series in which the temperature was very changeable, and one series in which the water was contaminated for a while, the remaining 12 specimens were open an average of 21.9 hours daily. Even when all of the results are considered the oysters were open and presumably feeding over 20 hours per day in spite of unfavorable conditions in certain cases.

In the following section the unfavorable temperature conditions in the above cases are discussed.

TABLE 1.—*Showing length of time which Olympia oysters remain open*

Experiment	Specimen	Hours open	Days recorded	Average number of hours open per day
No. 1	No. 1	90.25	5	18.05
Do	No. 2	103.20	5	20.64
Nos. 2 and 3	No. 3	558.96	34	[1]16.44
Do	No. 4	675.24	34	[1]19.86
Nos. 8 and 9	No. 3	309.23	17	[1]18.19
Do	No. 4	317.56	17	[1]18.68
Nos. 12 and 13	No. 3	188.80	8	23.60
Do	No. 4	186.96	8	23.37
Nos. 16 and 17	No. 3	435.20	20	21.76
Do	No. 4	433.20	20	21.66
Nos. 18 and 19	No. 3	603.00	30	[2]20.10
Do	No. 4	510.00	30	[2]17.00
Nos. 20 and 21	No. 3	695.97	33	21.09
Do	No. 4	702.57	33	21.29
Nos. 22 and 23	No. 3	688.51	31	22.21
Do	No. 4	675.18	31	21.78
Nos. 24 and 25	No. 3	463.20	20	23.16
Do	No. 4	462.00	20	23.10
Total		8,099.03	396	20.45
Totals, after elimination of experiments 2-3, 8-9, and 18-19		5,125.04	234	21.90

[1] Low proportion of time open due to temperature fluctuations.
[2] Low proportion or time open due to contamination.

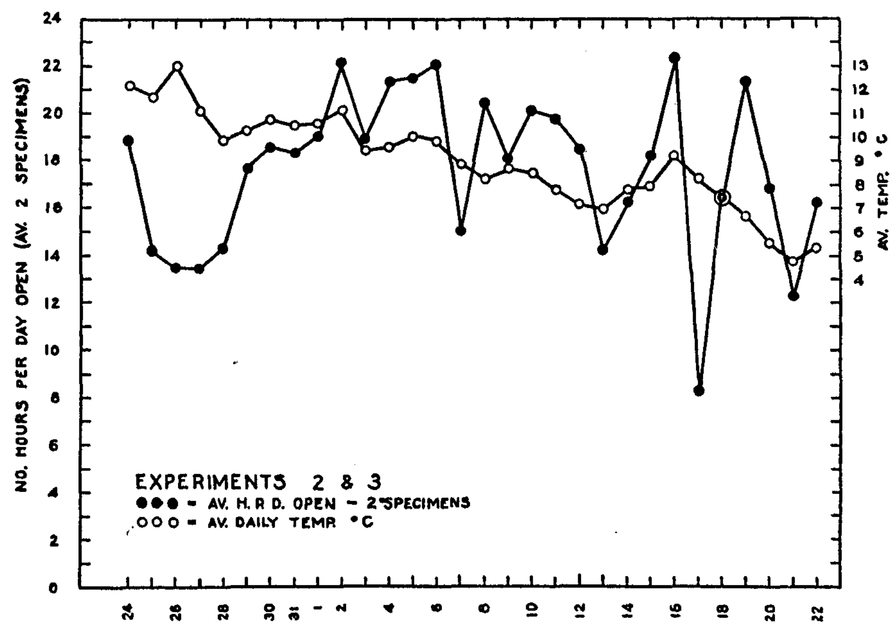

FIGURE 1.—Showing the average number of hours that two specimens of *Ostrea lurida* were open on each of 29 days, and the daily temperature of the water (average of 24 hourly readings)

EFFECT OF TEMPERATURE

That some sort of relationship exists between the temperature of the water and the length of time oysters remain open is indicated in Figure 1, in which the averaged data of the two specimens of experiments Nos. 2 and 3 (Table 1) are presented graphically. On the same graph are given the average number of hours which the two specimens were open on each of the 30 days of the experiment and the average temperature for each day calculated by averaging the 24 hourly temperature readings. The series was begun during the relatively warm weather of October and continued until November 22, when the temperature of the water had fallen to about 5° C., or hibernating temperature, according to Galtsoff.[2] After about the first week when the specimens were not open as much as expected, it will be observed that the curves of shell activity and average temperature are suggestively parallel. Beginning at about November 1, when the temperature was about 10° to 11° C., and the specimens were open something over 20 hours daily, there is a progressive decline until at the end the temperature is only 5° C. and the specimens open only about 15 hours daily. Roughly, then, for with only two specimens considered in this manner a precise statement can not be made, a drop in average daily temperature of 5° C. over about 20 days was accom-

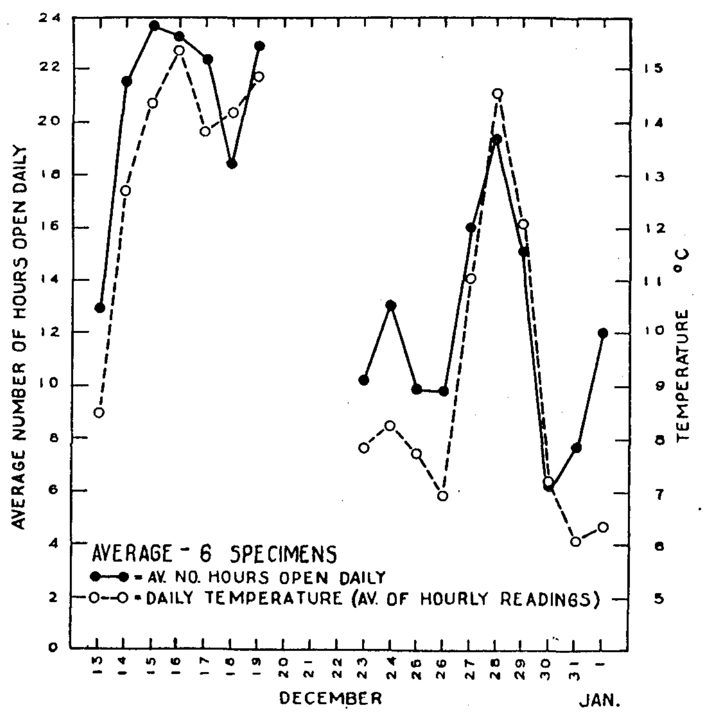

FIGURE 2.—Showing the parallel between the number of hours open daily of six specimens (*O. lurida*) and the average daily temperature. Records for three days were lost

panied by a lowering in hours open daily of about 5, or 25 per cent. These same results are calculated below in a different manner.

At best the above conclusion is only suggestive, but it is important in at least one respect, namely, that at the hibernating temperature (6° C.) during the last three days the oysters were not continually closed.

Another series (8 and 9, Table 1) shows more strikingly this relationship between shell activity and temperature. In this experiment one kymograph sheet was unfortunately lost, and there is a break in the records. (Fig. 2.) During part of the time the inflowing water was slightly heated by passing it through a lead coil which was immersed in heated water. This heating equipment was just being installed and did not work satisfactorily at first, so there are periods during which the water was heated and other periods when the temperature was low. The curves of temperature and

[2] Unpublished manuscript in the files of the Bureau of Fisheries.

amount of time open show clearly parallel fluctuations. These temperature changes are much more rapid than those shown in Figure 1, and the effect on the activity of the specimens much greater. During the first few days a rise of 7° C. was accompanied

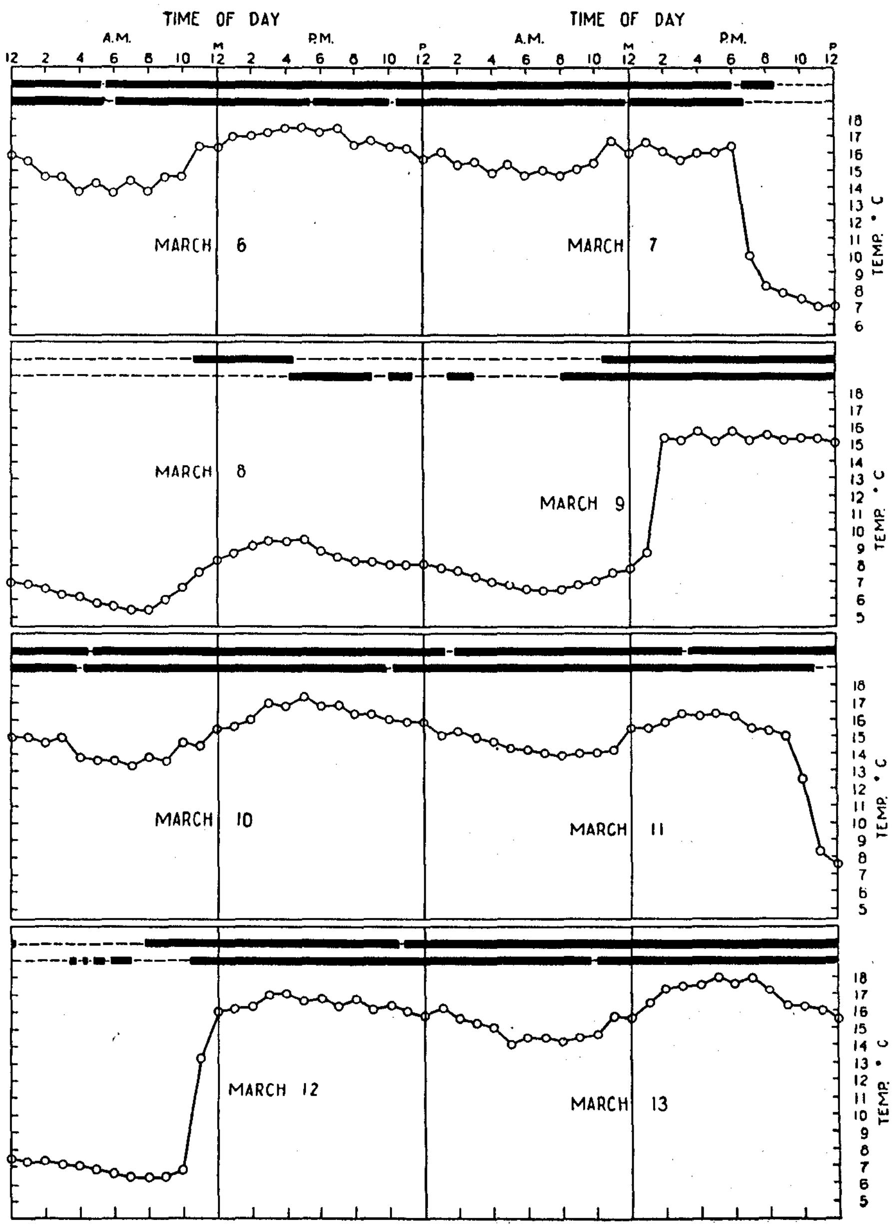

FIGURE 3.—Showing record of shell movements of two specimens of *O. lurida* and hourly temperature readings during eight days. Heavy horizontal lines represent records of oysters when open; broken lines indicate that shell was closed. A sudden drop in temperature caused the specimens to close, while a rise caused them to open

by an increase of 10 hours per day open; near the end of the test a 7.5° rise produced an increase in hours open daily of nearly 10. At the minimum temperature of 6° to 8° C. the oysters were open only about 6 hours, while at the maximum of slightly over 15° C. they were open over 23 hours per day, or nearly four times as long.

From the above two cases it appears that change of temperature is more important in affecting the length of time which Olympia oysters remain open than the degree of temperature itself. In Figure 3 the records of two specimens are reproduced in brief to illustrate the direct effect of changes in temperature of the water.

The figure represents the record of two specimens as heavy, solid lines when the shells were open and light, broken lines when closed. The hours of the day are shown as abscissae and the degrees of temperature as ordinates. During the first day the temperature was fairly high and the specimens were mostly open, but near the end of the second day (Mar. 7) the temperature fell from about 16° C. to 7° or 8° C., due to stopping of the heater, and the specimens closed. On the following day (Mar. 8), the specimens opened for a while following a rise of a few degrees in temperature of the water, but did not remain open. On March 9 they acted similarly, but remained open

FIGURE 4.—Graph showing shell activity of the same two specimens as in Figure 1. The percentage of time open at each hour of the day over the 29-day period is plotted. Average temperature readings for each hour during the same period are plotted to show the regular daily temperature fluctuation

due to the sharp rise in temperature. During the next four days a repetition of this occurred, as shown in the figure.

Many examples such as this are at hand, but their presentation is unnecessary. The closing of the oyster, as a result of lowering of temperature and opening following rise in temperature, both appear to be responses to the stimulation of temperature change, as is discussed further below.

DIURNAL VARIATION IN SHELL BEHAVIOR

It was pointed out by Nelson (1921) that oysters (*O. virginica*) are open less at night than during the day, but he did not consider that this might be due to temperature. Galtsoff (1928) was able to observe no diurnal variation in shell activity, but his temperature records showed no considerable diurnal variation.

In the present investigation not only was there a marked diurnal variation in the amount of time oysters (*O. lurida*) remained open, but also this could be directly correlated with temperature fluctuation.

When the results obtained with the two specimens in experiments Nos. 2 and 3 (Table 1, fig. 1) are plotted according to time of day, a diurnal wave is produced. In Figure 4 the percentage of time that the specimens were open at each of the 24 hours of the day during the entire period (29 days) is plotted. From 4 to 5 p. m., for example, the oysters were open during 95 per cent of the possible 29 hours at this time. Similarly temperature is plotted as the average of the readings at each hour during the period. The resultant graph represents the records of 29 days presented as a single average day. The curves of temperature and percentage of time open are almost identical, although the average daily difference in temperature between trough and crest of the diurnal wave is only 2.1° C. The specimens, however, at the trough of the wave were open only about 50 per cent of the time, and at the crest 95 per cent. Were it not for the fact that the two waves are so closely similar, in spite of individual differences in the behavior of the oysters, it might seem that other factors, such as

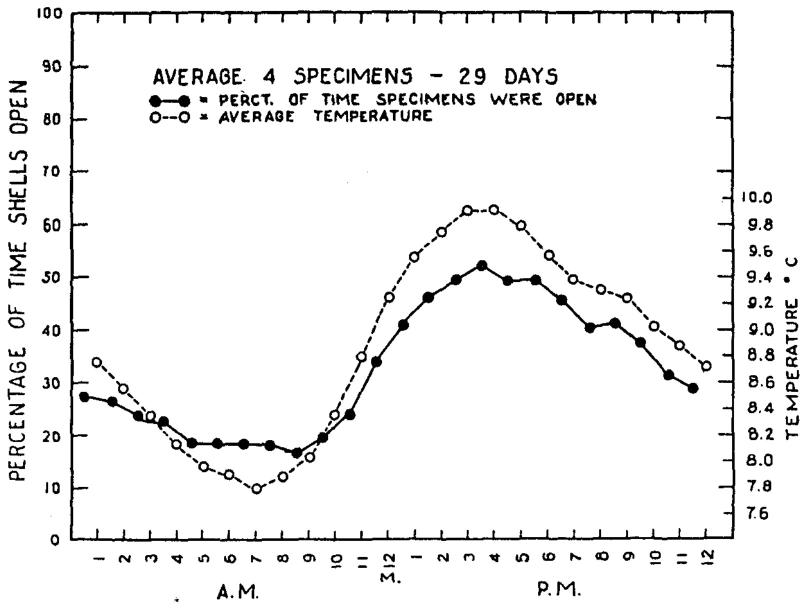

FIGURE 5.—Graph showing diurnal shell activity of four oysters. The percentage of time open during each hour of the day over 29 days is plotted along with the average temperature hourly over the same period. Although the specimens are closed more than those shown in Figure 4, due to presence of sulphite liquor in the water, the parallel between temperature and shell activity is clear

light, might be the cause of the variation. While it is probable that light has such an effect and may have influenced the results to some degree, it is obvious that temperature variation is the primary stimulating agent.

In the same series with the above were four other specimens in dilute solutions of sulphite liquor, and which, because of this, did not remain open as many hours per day as the normal oysters. The results of these four specimens are similarly presented (fig. 5), for their number tends to overcome the variations due to individual differences. Although the curve is lower in percentage of time open, it is definitely of the same character as the accompanying temperature curve. While the maximum temperature difference of the curve was 2.1° C., there was a 32 per cent difference in time the oysters were open.

The relatively great effect of a small average difference in temperature, as in Figure 4, as compared to the lesser effect of the greater change of temperature over a long period, as in Figure 1, indicates that it is the rapidity of the change which determines the oyster's reaction. From all of the foregoing results it may be concluded that a rise in temperature causes oysters to open, while a drop causes them to close. It is of importance to determine how sensitive the oyster is to temperature changes under different conditions, that is, does a certain temperature change at a high temperature produce the same reaction as the same change at lower temperatures?

In an effort to answer this question partially from the existing results, a table (Table 2) was prepared, consisting of data similar to those shown in Figure 4. Several series, or portions of series, were selected to cover the widest available temperature range. The average hourly temperature values and percentages of time open are given in parallel columns for each series. Maxima and minima of the diurnal waves are italicized, except in one case in which the individual variation is too great to be sufficiently eliminated by the few days' duration. The average temperatures of the several series range from about 5° to about 16° C. The maxima and minima are repeated at the bottom of the table, and the difference between them determined in each case. The average temperature difference between trough and crest is close to 2° C. in most cases, so that 2° C. may be considered the standard change in temperature the effect of which it is desired to determine. In order to bring all the results to this basis, the difference between maximum and minimum of the time open wave, or the amount of increase in time open following the given temperature rise, was calculated by simple proportion to conform to a 2° C. difference, that is, in the first column the temperature difference is 2.87 and the time open difference 88.4 per cent. Then to correct the latter to a 2° C. change, $2:2.87=x:88.4$; $x=61.6$ per cent, which may be employed as representing the reaction to a rise of 2°, although this may not be strictly accurate.

In Figure 6 is a graph showing these results (solid points) as the increase in percentage of time open following the 2° C. rise in temperature during the average day (ordinates) plotted against the maximum value of the temperature wave (abscissae). It will be observed that these results fall remarkably well, considering great individual variations, into alignment. At low temperatures a change of 2° C. is accompanied by a great change in the length of time the specimens remain open; at high temperatures (14° to 17° C.) the same temperature change produces scarcely any change in the percentage of time the specimens remain open. In brief, the extent of the oyster's reaction to such a change in temperature of the medium is a function of the existing temperature, and is greater the farther the basic temperature from the optimum. On this curve there are not enough points to permit mathematical analysis. The ideal line may well be actually curved, especially as it approaches the optimum and also near the other end.

In contrast to the above, on the same chart (fig. 6) the results of the same tests are plotted (circles) as the percentage of time the specimens were open during the entire time against the average temperature for the same period. If a direct relationship exists between temperature, as such, and the length of time open, these points should also fall into a definite line. This is not the case, for although the points might be considered as falling about such a line, the variation is tremendous, and also a certain amount of alignment would be expected, due to the difference in sensitivity at different temperatures. The contrast between the two sets of points, representing the same actual data, is striking, and demonstrates that the influence of temperature on shell movement of this type is more a matter of sensitivity to temperature change than of temperature as such.

TABLE 2.—*Effect of temperature on percentage of time oysters remain open* [1]

Time	Series 1 (3 days)		Series 2 (15 days)		Series 3 (4 days)		Series 4 (29 days)		Series 5 (14 days)	
	Average temperature	Average per cent time open	Average temperature	Average per cent time open	Average temperature	Average per cent time open	Average temperature	Average per cent time open	Average temperature	Average per cent time open
	° C.		° C.		° C.		° C.		° C.	
12 p. m.	5.03		7.19		8.15		8.72		10.37	
1 a. m.	5.10	71.7	7.26	71.0	8.16	100.0	8.75	68.5	10.36	64.3
2 a. m.	4.93	50.0	7.09	71.6	8.08	100.0	8.55	69.5	10.13	62.5
3 a. m.	4.67	48.3	6.90	65.0	7.94	100.0	8.34	62.5	9.88	55.7
4 a. m.	4.50	33.3	6.74	62.8	7.82	92.0	8.12	64.5	9.60	58.0
5 a. m.	4.17	20.0	6.55	57.2	7.78	100.0	7.96	57.0	9.51	54.0
6 a. m.	4.07	8.3	6.47	52.6	*7.76*	*96.0*	7.89	57.0	9.42	63.0
7 a. m.	*3.80*	*11.6*	*6.40*	*46.0*	7.79	95.0	*7.80*	*56.3*	*9.31*	*67.8*
8 a. m.	3.80	13.3	6.47	34.5	7.84	94.0	7.88	53.8	9.39	71.0
9 a. m.	3.90	1.7	6.61	37.3	7.98	84.0	8.03	50.5	9.55	65.3
10 a. m.	4.73	13.3	6.94	40.6	8.06	77.0	8.35	53.6	9.86	66.0
11 a. m.	5.50	25.0	7.39	48.5	8.38	85.0	8.80	58.8	10.32	70.2
12 a. m.	6.23	88.3	7.83	63.0	8.64	90.0	9.24	73.2	10.75	82.3
1 p. m.	6.40	100.0	8.14	80.5	8.82	100.0	9.54	84.3	11.05	90.0
2 p. m.	*6.67*	*100.0*	8.37	85.8	8.85	90.0	9.75	91.7	11.24	94.5
3 p. m.	6.50	100.0	*8.48*	*88.5*	8.65	97.5	*9.90*	*91.0*	11.43	93.0
4 p. m.	6.37	95.0	8.36	95.2	8.50	100.0	9.90	95.0	*11.55*	*94.5*
5 p. m.	6.07	98.3	8.18	96.2	8.27	100.0	9.78	95.5	11.50	94.5
6 p. m.	5.60	96.7	7.99	96.0	8.17	100.0	9.57	93.3	11.28	89.3
7 p. m.	5.43	88.3	7.79	93.5	8.22	100.0	9.38	88.0	11.08	81.8
8 p. m.	5.37	96.7	7.70	95.0	8.12	100.0	9.30	85.5	11.02	74.2
9 p. m.	5.33	100.0	7.64	94.6	8.12	100.0	9.24	84.3	10.98	73.0
10 p. m.	5.20	95.0	7.43	86.5	8.17	97.5	9.03	80.7	10.74	75.5
11 p. m.	5.13	80.0	7.29	85.3	8.17	90.0	8.88	80.8	10.59	75.0
12 p. m.	5.03	73.3	7.19	76.8	8.15	100.0	8.72	73.6	10.37	68.5
Average	5.18	62.84	7.38	71.87	8.18	94.50	8.86	73.73	10.46	74.34
Maximum	6.67	100.0	8.48	88.5			9.90	91.0	11.55	94.5
Minimum	3.80	11.6	6.40	46.0			7.80	56.3	9.31	67.8
Difference	2.87	88.4	2.08	42.5			2.10	34.7	2.24	26.7
Difference in per cent time open calculated for temperature difference of 2° C.		61.6		40.9				33.0		23.8

Time	Series 6 (12 days)		Series 7 (12 days)		Series 8 (18 days)		Series 9 (18 days)		Series 10 (7 days)	
	Average temperature	Average per cent time open	Average temperature	Average per cent time open	Average temperature	Average per cent time open	Average temperature	Average per cent time open	Average temperature	Average per cent time open
	° C.		° C.		° C.		° C.		° C.	
12 p. m.	12.44		13.46		14.75		14.76		16.50	
1 a. m.	12.47	92.8	12.52	97.7	14.80	96.7	14.78	98.6	16.17	95.0
2 a. m.	12.28	92.5	12.40	99.5	14.47	92.4	14.47	97.8	16.00	99.2
3 a. m.	12.08	93.3	12.25	100.0	14.38	93.6	14.36	96.4	15.85	100.0
4 a. m.	11.76	93.3	12.19	94.5	14.17	93.6	14.17	91.9	15.83	96.6
5 a. m.	11.43	95.8	11.96	95.5	14.01	92.3	13.94	95.0	15.45	91.6
6 a. m.	11.15	100.0	11.90	98.2	*13.86*	*91.8*	*13.86*	*96.1*	15.35	100.0
7 a. m.	*11.04*	*93.0*	11.65	96.8	13.95	92.2	13.91	95.8	14.87	98.3
8 a. m.	11.05	93.0	*11.21*	*85.5*	13.96	93.2	13.94	96.4	14.02	78.3
9 a. m.	11.38	95.0	11.25	81.8	14.12	94.4	14.03	98.1	*13.98*	*80.0*
10 a. m.	11.82	88.2	11.45	88.2	14.10	94.3	14.08	97.2	14.28	97.5
11 a. m.	12.30	89.0	12.41	93.2	14.54	98.7	14.50	97.5	15.76	100.0
12 a. m.	12.88	88.3	13.07	94.5	15.04	98.3	15.02	99.2	16.77	98.3
1 p. m.	13.51	99.2	13.37	99.5	14.99	100.0	15.56	98.9	17.17	99.2
2 p. m.	13.97	98.7	14.14	93.6	15.77	99.0	15.80	96.6	17.31	95.7
3 p. m.	14.02	96.0	14.21	99.1	15.71	100.0	15.77	99.4	*17.39*	*100.0*
4 p. m.	14.06	100.0	*13.82*	*98.6*	*15.84*	*98.0*	*15.94*	*100.0*	16.86	97.8
5 p. m.	*14.22*	*100.0*	13.00	96.4	15.76	95.6	15.79	99.2	15.70	94.3
6 p. m.	14.12	96.3	13.27	93.2	15.69	94.5	15.71	98.6	16.19	88.6
7 p. m.	13.83	99.5	13.80	97.3	15.52	96.3	15.53	96.7	16.99	95.5
8 p. m.	13.67	100.0	13.79	97.7	15.37	96.7	15.36	95.6	17.03	96.4
9 p. m.	13.22	100.0	13.75	98.6	15.48	89.2	15.47	97.5	16.97	97.8
10 p. m.	12.97	99.5	13.77	98.6	15.09	97.8	15.09	97.5	16.98	98.6
11 p. m.	12.69	96.7	13.64	95.0	15.18	94.7	15.18	97.5	16.77	97.8
12 p. m.	12.44	96.6	13.46	96.8	14.75	94.5	14.76	95.0	16.50	95.0
Average	12.68	95.70	12.84	95.40	14.85	71.40	14.88	97.17	16.09	95.48
Maximum	14.22	100.0	13.82	98.6	15.84	98.0	15.94	100.0	17.30	100.0
Minimum	11.04	93.0	11.21	85.5	13.86	91.8	13.86	96.1	13.98	80.0
Difference	3.18	7.0	2.61	13.1	1.98	6.2	2.08	3.9	3.41	20.0
Difference in per cent time open calculated for temperature difference of 2° C.		4.4		10.0		6.26		3.75		11.73

[1] The table gives records of 10 series of experiments showing the percentage of time which the specimens (two in each case) were open during each of the daily hours, calculated over the entire period concerned, and the average hourly temperature during the same periods. The troughs and crests are given in italicized figures of temperature and of percentage of time open. The summarized data at the end show the results calculated on the basis of a variation of 2° C. between crests and troughs of the temperature waves. The results appear graphically in Figure 6.

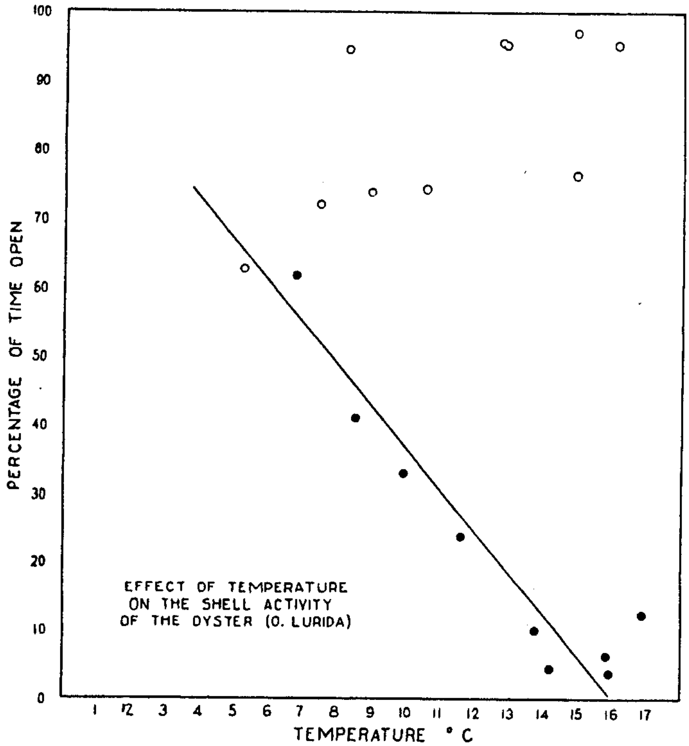

FIGURE 6.—Graphical presentation of the data given in Table 1. The circles represent the average percentage of time the specimens were open during the several series, plotted against the average temperature during the same periods. The solid points represent the increase in percentage of time open following a 2° C. rise in temperature during the average daily cycle, as described in the text

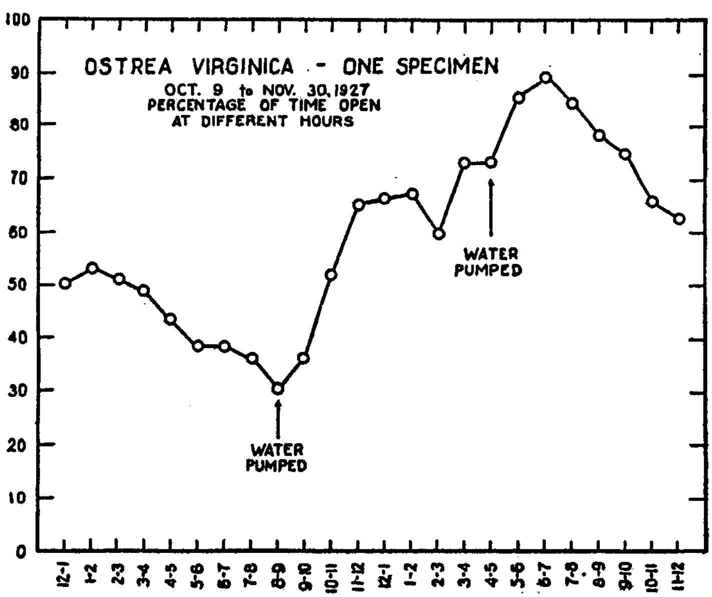

FIGURE 7.—Average day's record of the percentage of time that one specimen of *Ostrea virginica* remained open during each hour of the day during the period from October 9 to November 30, showing the clearly defined diurnal wave of shell activity

EXPERIMENTS WITH EASTERN OYSTERS (*OSTREA VIRGINICA*)

In the foregoing account it was shown that the feeding habits of the Olympia oyster are influenced by temperature changes. It is important to determine whether the eastern oyster also is sensitive in the same manner.

Several series of kymograph records of the shell movements of oysters made at Beaufort, N. C., are available. Thermograph records were not kept of the water temperature in the experimental aquaria, and any conclusion drawn must necessarily be qualified. However, these results bear a close resemblance to those above described and are presented for comparison.

Figure 7 shows the diurnal record of an oyster kept in running water from October 9 to November 30, 1927. Water was pumped twice daily into the storage tank at 8 to 9 a. m. and 4 to 5 p. m. The effect of this pumping appears as two slight

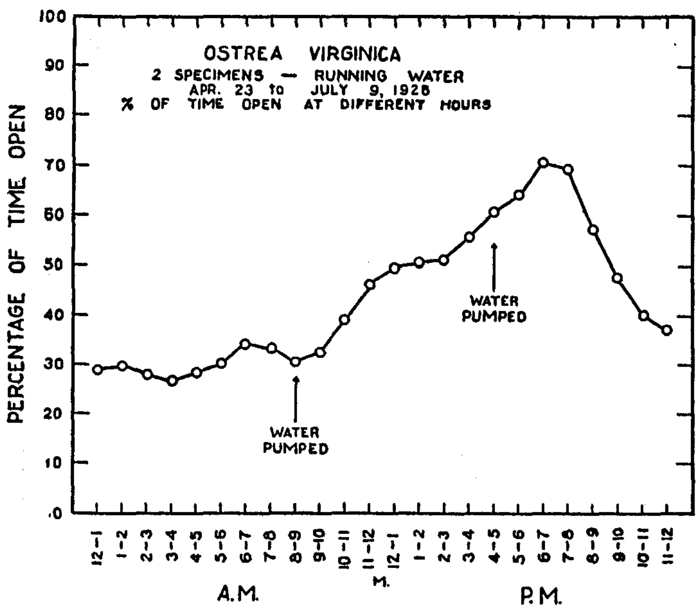

FIGURE 8.—Showing the diurnal wave of percentage of time two specimens of *O. virginica* remained open at different hours during the period of 78 days

irregularities in the record, due perhaps to the different temperature or salinity of the newly pumped water. It is apparent that the character of this curve is not greatly different from those given in Figures 4 and 5 for the Olympia oyster.

A similar and more regular record is that shown in Figure 8 representing the activity of two specimens over a period of 78 days from April 23 to July 9, 1928. In both this case and in Figure 7, the rise in percentage of time open during the day is gradual up until 6 to 7 p. m., after which it falls rapidly. This diurnal behavior is essentially similar to that of the Olympia oysters and leads to the tentative conclusion that temperature variation is at least in some measure responsible. The salt water tank at Beaufort is exposed to the sunshine, and undoubtedly the water warms up during the day and cools after sunset. The temperature of the air in the laboratory also has considerable effect on the water in the experimental tanks.

An entirely different type of curve was obtained from the records of four specimens kept in nonrunning water, closely adjacent to a window. These results are represented in Figure 9. Instead of the crest of the diurnal wave occurring at between 6 and 7 p. m., it occurs at 11 a. m. to 12 m. It was observed that at about 10 a. m. direct sunlight struck the aquaria in which the specimens were immersed and that immediately, or within a few minutes, the oysters opened. It was thought that the bright light was responsible for the reaction; but, although light may have been concerned also, it would appear that rise in temperature was the primary stimulating agent. If it be assumed for convenience that these diurnal waves of shell activity are the effect of temperature fluctuation, as seems justified by comparison with the Olympia oysters, there are two sources of temperature variation which must be considered.

In the first place, those factors in the laboratory, such as room temperature and direct sunlight, produce temperature change in the water in the aquaria. In the case of the specimens in nonrunning water (fig. 9), the most favorable temperature conditions occur at about 12 o'clock noon. On the other hand, the water in the tank

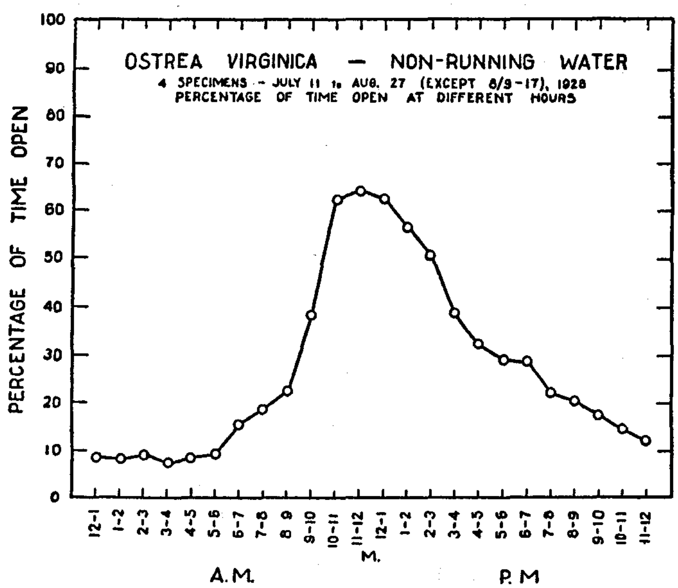

FIGURE 9.—Average day's record of four specimens of *O. virginica* in nonrunning water over a period of 39 days, showing percentage of time open at each hour

reaches optimum temperature (figs. 7 and 8) at around 6 to 7 p. m., because direct sunlight continues to warm the water all day.

In Figures 7 and 8, not only can the effect of the latter be seen, but the former, namely, laboratory temperature, can also be seen. Comparison of the portions of these curves between 9 a. m. and 3 p. m. with Figure 9 shows that the sharp rise in the curves in Figures 7 and 8 at this time, appearing as humps, is strikingly similar to the comparable portion of Figure 9.

It must be admitted that these records do not constitute as conclusive proof of the influence of temperature as the evidence cited for the Olympia oyster. However, by analogy it appears logical to assume that, in view of the similarity of the curves in the two cases, the eastern oyster behaves in a manner very similar to that of the Olympia oyster. The only other probable factor which might influence oysters in this diurnal manner is light, and there is some evidence that this may have been the source of some of the fluctuation in reactions.

That light is not the factor primarily responsible for the diurnal variation in activity is shown by the results of a series of tests made at Galveston, Tex. The shell movements of two specimens in running water were recorded for 25 days. One specimen was in a jar surrounded by a black box which effectively blocked all ordinary light rays while admitting air. The other was exposed in the laboratory. Figure 10 gives the records of the two specimens. The curves are essentially similar, showing that even in constant darkness the diurnal wave of shell activity is clearly marked.

It was pointed out that there was some difference between the results of Nelson (1921) and those of Galtsoff (1928) with regard to the length of time oysters remain open daily. The former found 20 hours to be the average, the latter only 17 hours and 7 minutes, while in the present work it was determined that Olympia oysters remain open well over 20 hours daily. These differences are only proof that the oyster is sensitive to various factors in the environment, such as temperature, as shown above,

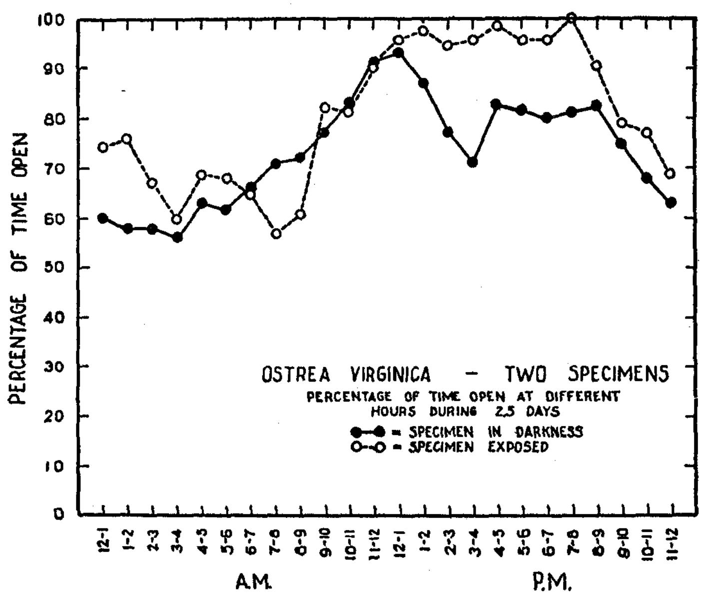

FIGURE 10.—Records of two specimens of *O. virginica*, one in darkness (solid points) and one exposed (circles), in running water at Galveston, Tex., during 25 days. Shows percentage of time each specimen was open during each of the daily hours over this period

and that the number of feeding hours daily depends upon how favorable all such conditions may be.

In contrast to the results stated above are those obtained at Beaufort with presumably normal oysters in running water which so far as known was not contaminated. In the case of one specimen (fig. 7), tested for nearly two months in October and November, the average number of hours open daily was 14.45, which is quite low. However (fig. 8) the two specimens tested under like conditions in summer for 78 days were open an average of only 10.39 hours per day. The four specimens shown in Figure 9 were in still, artificially aerated water, and remained open an average of only 6.57 hours daily. With the exception of the last mentioned, these specimens were apparently living under as favorable conditions as in the case of the tests with Olympia oysters.

In the tests made at Galveston (fig. 10) the specimen in darkness averaged 17.5 hours per day open, while the exposed oyster remained open an average of 19.4 hours daily. It thus appears that under different conditions oysters behave decidedly differently.

Various factors may have been concerned in the low records, such as salinity variations, temperature, hydrogen-ion concentration, or the specific salts comprising the dissolved load of the water. This last will be discussed in a forthcoming paper.

SUMMARY

In the experiments with Olympia oysters it was indicated that it is not so much the existing temperature of the water which determines how long the shells remain open as it is the changes in temperature which occur. Falling temperature causes the shells to close, while opening follows a rise in temperature. The sensitivity of the Olympia oyster to temperature changes varies in an inverse manner with the general water temperature, within the range of 5° to 17° C. The latter temperature appears to be close to the optimum, for at this temperature slight changes (2° C.) produce almost no effect on the proportion of time the shells remain open. At temperatures of 4° to 6° C., when the oyster is hibernating with respect to gill activity, the shells do not remain constantly closed, but the oysters are highly sensitive to temperature change, and at such temperatures consequently remain closed a relatively high percentage of the time.

Because of this type of changing sensitivity and the diurnal temperature wave, with its trough at 6 to 7 a. m. and crest at 3 to 4 p. m., the curve of shell activity is of the same shape as the temperature wave, having trough and crest at the same times.

Similar diurnal curves of the shell activity of eastern oysters are presented, without temperature data, and it is suggested that the conclusions with regard to the Olympia oyster also apply in principle to the eastern variety.

The length of time which oysters remain open depends upon temperature and other factors. The Olympia oysters were open over 20 hours per day, while eastern oysters at Beaufort, N. C., averaged between 10 and 14 hours per day open, as contrasted to Nelson's (1921) figure of 20 hours and Galtsoff's (1928) of 17 hours and 7 minutes for oysters in New Jersey and Massachusetts, respectively.

LITERATURE CITED

Galtsoff, Paul S.

1928. Experimental study of the function of the oyster gills and its bearing on the problems of oyster culture and sanitary control of the oyster industry. Bulletin, United States Bureau of Fisheries, Vol. XLIV, 1928 (1929), pp. 1–39, 13 figs. Washington.

1931. The effect of sulphite waste liquor on the rate of feeding of *Ostrea lurida* and *O. gigas*. *In* Effects of pulp mill pollution on oysters, by A. E. Hopkins, Paul S. Galtsoff, and H. C. McMillin. Bulletin, United States Bureau of Fisheries, Vol. XLVII, 1931. (In press.) Washington.

Hopkins, A. E.

1931. The effect of sulphite waste liquor on the oyster (*Ostrea lurida*). *In* Effects of pulp mill pollution on oysters, by A. E. Hopkins, Paul S. Galtsoff, and H. C. McMillin. Bulletin, United States Bureau of Fisheries, Vol. XLVII, 1931. (In press.) Washington.

Nelson, Thurlow C.

1921. Report Department of Biology, New Jersey Agricultural College Experiment Station for the year ending June 30, 1920 (1921), pp. 317–349, 6 figs,. 5 pls. Trenton.