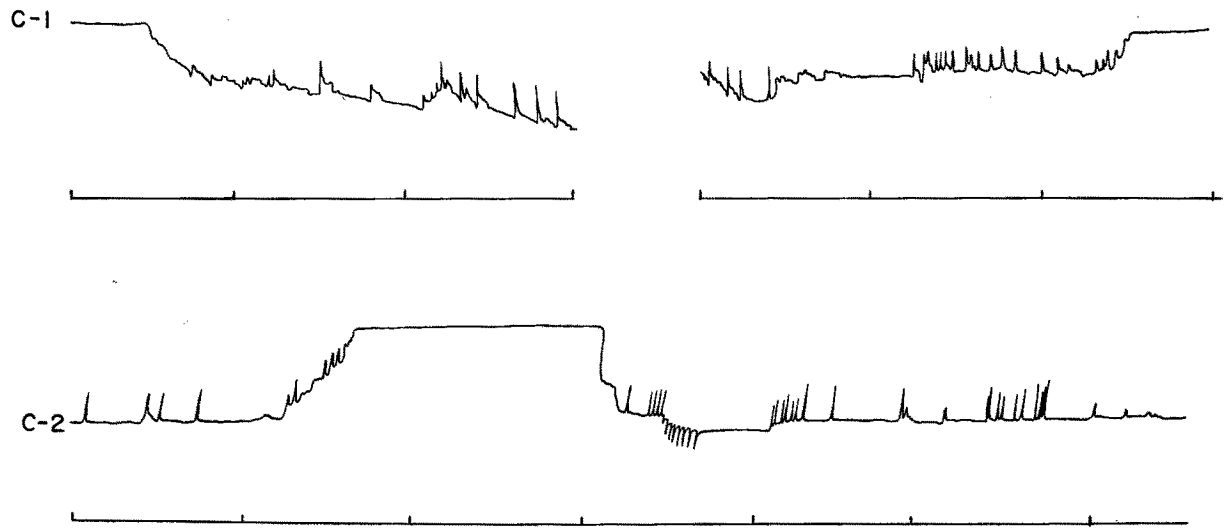

FIGURE 155.—Shell movements of type C, preceding the closing of valves (left side) and following their opening (right side). Note staircase movement in C–2. Time interval: C–1 and C–2, 1 hour each.

to the water. A "staircase" in reverse direction sometimes takes place during the opening of the valves (C–2, right half). This behavior was provoked by small doses of oyster sperm, vitamins, and sugars injected between the valves into the pallial cavity. The "reversed staircase" may be interpreted as a testing reaction of the oyster, which adjusts the opening of the valves to a needed rate of ventilation.

Type D

Shell movement of type D (fig. 156) was observed in oysters affected by various poisons which caused increased excitability of the adductor muscle (D–1). In case of a prolonged action of poison the periods of greater excitability (D–2 and D–3) are interrupted by gradually increasing durations of periodical closure (D–4 and D–5). This type of shell movement is a symptom of a highly advanced pathological condition resulting from poisoning, disease, or exposure to adverse physical conditions. It is typical for dying mollusks (D–5).

Type E

The E type of shell movement associated with the spawning of the female oyster is characterized by great regularity, rapidity, and rhythmic up and down strokes (fig. 157). At the beginning of the reaction the time needed to reach the maximum relaxation level is very brief, almost equal to the time of the contraction (see: E–2). During the relaxation phase (downward stroke) there is a brief period of slowing down in the decrease of muscular tension. On the curve this period is represented by a small plateau. This moment coincides with the passage of eggs through the gills into the pallial cavity. The eggs in the pallial cavity are dispersed into the surrounding water by rapid contractions of the adductor.

Shell movements that take place during the spawning of a female do not occur at any other time and cannot be induced by drugs. They cease with the cessation of spawning. The factor that induces female spawning (temperature or chemical stimulation by sperm) has no effect on the type of shell movement of a male and is ineffective on nonspawning females. It is probable that this type of muscular activity is associated with the discharge of eggs from the gonads.

DURATION OF PERIODS OF OPENING AND CLOSING

The length of time the shells remain open or closed and the conditions that affect this behavior are of importance to oyster biology. Obviously the normal functions of the organism, such as respiration, feeding, and elimination of waste products, can be performed only when the valves of the mollusk are open. It does not follow, however, that the opening of the shell indicates that the mollusk is feeding or is ventilating its gills. Under certain conditions water may be shut off from the pallial cavity by the pallial curtain or by the cessation of ciliary motion while the valves remain open. However, in the majority of laboratory observations of the behavior of oysters in unadulterated sea water the opening of the valves coin-

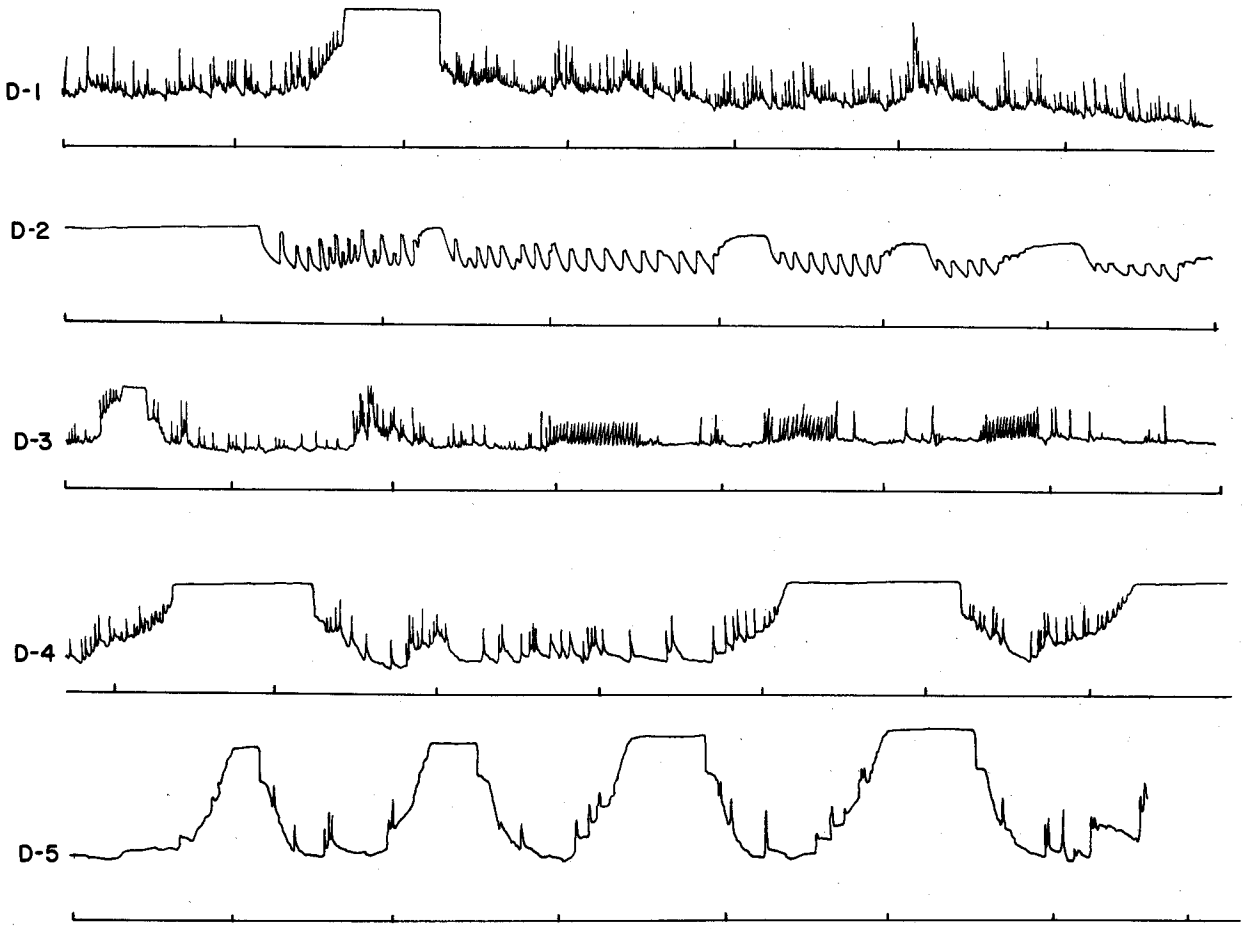

FIGURE 156.—Shell movements of type D are observed in the oysters poisoned by toxic substances or weakened by adverse environment. D–5 shell movements of a dying oyster. Vertical excursions of the writing pen are magnified three times in all tracings. Uppermost level of the curves corresponds to closed shells. Time interval: D–1, D–2, D–3, D–4, D–5, 1 hour each.

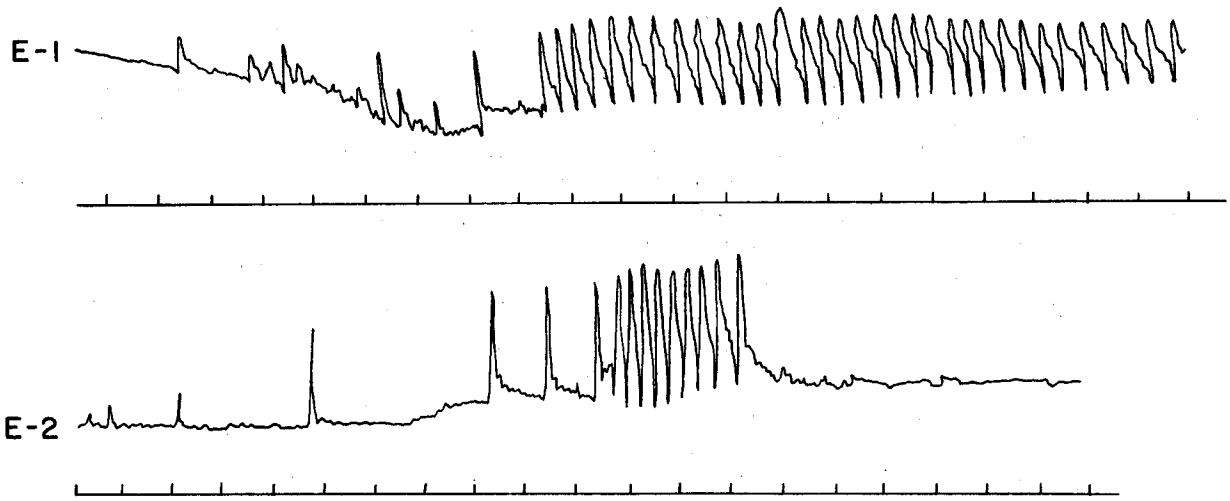

FIGURE 157.—Shell movements of a spawning female. Note the frequencies of up and down movements, brevity of the relaxation periods and slowing down at the middle of the downward strokes; this brief period coincides with the penetration of eggs through the gills. Time interval: E–1 and E–2, 1 minute each.

733-851 O—64——12

cided with the maintenance of a steady cloacal current.

The determination of the number of hours the oyster remains open under average normal conditions is of significance in studies of reactions of the mollusk to changes in its environment. Certain industrial wastes discharged in sufficient concentrations into natural waters reduce the time the oysters stay open. It was found, for instance, that the red liquor which is the waste product of pulp mills using acid digestion of wood and the black liquor of pulp mills which employ a sulfate process exert this effect on the Olympia oyster (Hopkins, 1931) and on *C. virginica* (Galtsoff, Chipman, Engle, and Calderwood, 1947). Any condition that forces oysters to remain closed for an abnormally long time deprives them from taking in food and eventually may harm them.

The percentage of time during each 24-hour period that the oysters are open can be used as an index of normal behavior, provided the shell movements of the mollusk do not indicate pathological conditions of the type shown in curves D–1 to D–5. Failure to recognize the significance of this type of shell movement while recording the time the oyster remains open may lead to serious misunderstandings and errors. Unfortunately there are many published data in which the "time open" was recorded without observing the character of shell movements.

The length of time *C. virginica* remains open is also influenced by temperature and by the state of the oyster itself. Since the shell movement is influenced by several external and internal factors, it is not surprising that there is a great discrepancy in the estimates of the average duration of "open shells" reported by various investigators.

In the Bureau's shellfish laboratory at Woods Hole from June 15 to October 15, 1926, 132 daily records of 34 oysters observed gave an average of 17 hours 7 minutes for open shells. The temperature of the water during this period ranged from 13° to 22° C., but daily fluctuations of temperature were insignificant, never exceeding 1.5° C. (Galtsoff, 1928). Records of the three oysters kept by Nelson under observation for 21 days in New Jersey water indicated that the shells remained open on the average of 20 hours per day at temperatures varying between 22° and 25° C. (Nelson, 1921). For oysters kept in running sea water at a Beaufort, N.C., laboratory, average time open in October to November varied between 10 and 14 hours (Hopkins, 1931). The temperature of water was not recorded. Two hundred and one daily records of 49 York River (Virginia) oysters kept under observation in the laboratory at Yorktown showed that the periods of opening varied from 19.2 to 24.0 hours a day (Galtsoff, Chipman, Engle, and Calderwood, 1947). Within the temperature range of 17.0° to 28.0° C. Long Island Sound oysters were found to remain open for an average period of 22.5 hours. The latter data are based on 64 records of 18 oysters (Loosanoff and Nomejko, 1946). *O. lurida* of the Pacific Coast remained open for an average of 20 hours a day at the temperature range of 5° to 17° C. (Hopkins, 1931).

A sample of oysters always includes several individuals that may remain closed for 24 hours or longer. One or two of them will reduce unduly the average figure based on a small number of observations. Furthermore, under identical conditions of the normal environment (i.e., not affected by pollution, dredging, or other disturbances) an oyster may keep its shell open or closed for varying periods of time depending on the requirements of the organism for food and oxygen. I found that immediately after spawning the female oysters have a tendency to keep their shells closed for several days. On the other hand, oysters left overnight out of water open almost immediately upon being returned to sea water. It is reasonable to assume that they accumulated an oxygen debt during the period of closure. In view of these observations the differences in the duration of periods of opening or closing described for oysters of different localities have no particular significance. The average value may be useful, however, in determining the adverse effects of the changes in the population of oysters in a given locality and in making a comparison between the behavior of these individuals in clean and polluted waters.

EFFECT OF TEMPERATURE

Temperature as such has no direct influence on the duration of shell opening. There was no significant difference in the length of time the Woods Hole oysters remained open when kept at temperatures varying from 15° to 30° C. (Galtsoff, 1928). It is rapid change in temperature, often occurring in those laboratories where sea water is subject to wide diurnal fluctuations, that has a pronounced effect on shell movements. *O. lurida*,

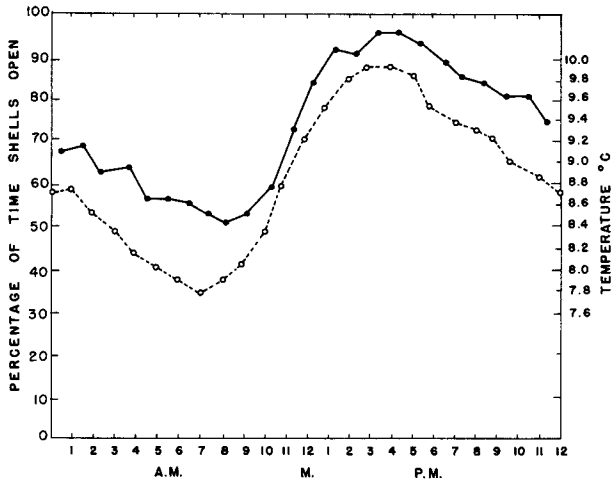

FIGURE 158.—The average percentage of time open of two specimens of *O. lurida* at each hour of the day observed over the 29-day period (solid circles). Average temperature readings for each hour during the same period (open circles). From Hopkins (1931), fig. 4, p. 6.

for instance, has a tendency to close with the falling of temperature and open with a rise of temperature (Hopkins, 1931). The sensitivity of this oyster to temperature changes was reported to be greater at the lower range. At 4° to 6° C. the oysters remained closed a relatively high percentage of the time; at 6° to 8° C. they were open only about 6 hours, while at the maximum of about 15° C. they remained open over 23 hours per day. In both cases the diurnal curve of shell activity was parallel to the curve of temperature fluctuation observed by Hopkins (1931) although the percentage of time open in warmer water was consistently higher (fig. 158). It would be of interest to repeat these observations and compare them with controls kept at a constant temperature since Hopkins' temporary laboratory near Olympia, Wash. lacked adequate equipment for regulation of temperature. He concluded that "change of temperature is more important in affecting the length of time Olympia oysters remain open than the degree of temperature itself." The results of his observations on *C. virginica* at Beaufort, N.C., bear close resemblance to those described above but, unfortunately, they were not accompanied by thermograph records and so are not entirely convincing. His conclusions need clarification.

EFFECT OF LIGHT AND DARKNESS

Periods of light and darkness have no apparent effect on the closing or opening of the valves. Analysis of 103 daily records of shell movements of oysters kept in the Bureau's Woods Hole laboratory in running sea water at nearly constant temperature (daily fluctuations ±0.5° C.) and constant salinity shows that of the total number of 831 hours of inactivity (shell closures), 266 hours or 32 percent occurred during the 8-hour period of darkness and the balance of 565 hours, or two-thirds of the total, took place during the remaining two-thirds of daylight (Galtsoff, 1928). During the summer, from June to August inclusive, the Long Island Sound oysters kept their shells open for 94.4 percent of the total time during daylight and 93.8 percent during the hours of darkness (Loosanoff and Nomejko, 1946). These observations repudiate Nelson's conclusion that the periods of inactivity (or closings) occur during darkness (Nelson, 1921, 1923c).

EFFECT OF TIDE

There is no evidence that the opening and closing of oyster valves is related to the stages of tide. The idea that oysters living below the low-water mark are relatively inactive during the outgoing tide and that the times of cessation and commencement of feeding are correlated to stages of the tide, was several times expressed by Nelson (1922, 1923a, 1923c, 1938) and without verification was accepted by Orton in his article in Encyclopedia Britannica (Orton, 1929). Loosanoff and Nomejko (1946) analyzed the kymograph tracings of shell movements of oysters kept under virtually natural conditions on a platform installed on a small oyster bed on the bottom of Milford Harbor in Long Island Sound. They found that the shells remained open on an average of 93.4 percent of the time during the flood periods and 95.2 percent of the time during the ebb periods. The tidal changes in Long Island Sound are not accompanied by the excessive changes in the temperature, salinity, pH, and turbidity of water which frequently take place in the tidal streams of the southern Atlantic states and may influence the shell movements of oysters.

POWER OF THE ADDUCTOR MUSCLE

Anyone who attempts to open a live oyster by inserting and twisting a knife between the two valves becomes aware of the considerable resistance exerted by the mollusk. As a rule the valves of healthy oysters just taken out of sea water are difficult to pry apart. The power of the adductor muscle, which is solely responsible for keeping

the valves tightly closed, varies greatly in oysters of the same size and environment. Prolonged exposure to air so weakens the adductor that oysters left out of water for several days can be easily opened.

In attempts to measure the power of the adductor of various bivalves Plateau (1884), Marceau (1905a, 1905b), and Tamura (1929, 1931) drilled holes near the edge of the shells and inserted rods or hooks to which they attached weights. The opposite valve was immobilized. Assuming that the adductor muscle is an elastic body, the amount of work (W) done by the adductor against the loaded weight (G) was calculated by using a simple formula $W=\frac{ac}{ad}G$ where ac is a distance in centimeters from the ligament to the attachment of the weights; ad is the distance in centimeters from the ligament to the center of the adductor muscle; and G is the weight in grams applied to the valve. Under a known pulling force the shell movements were traced on a kymograph and a record was made of the time and load under which the muscle fibers were torn off. Continuous irritation of the adductor by the foreign body (hook or rod) inside the shell near the mantle makes this technique objectionable. Furthermore, the end point of the experiment, the tearing off of the muscle, is of no biological significance compared to a determination of the tensile force of the muscle fibers.

The method used in the Bureau's shellfish laboratory eliminates these objections. The left valve of the oyster is mounted on a heavy cement block, using a very strong mixture of portland cement and sand to which a small amount of plaster of paris is added (fig. 159). The base is bolted to the frame D which may be placed in the aquarium tank B supplied with running sea water. A galvanized iron screw (a) about 1 inch in length is inserted into the valve at the center of the attachment of the adductor muscle. Its tip should not penetrate the valve. Enough portland cement or other highly adhesive mixture is applied to the shell surface around the screw to make a cone of about 1 inch in diameter; the top of the screw (a) should protrude above the cement. A metal stirrup (E) consisting of a pair of iron bars (b) with pronged arms at the lower end and a hook (d) mounted at the upper end connect the valve and the pan (e) of the laboratory balance

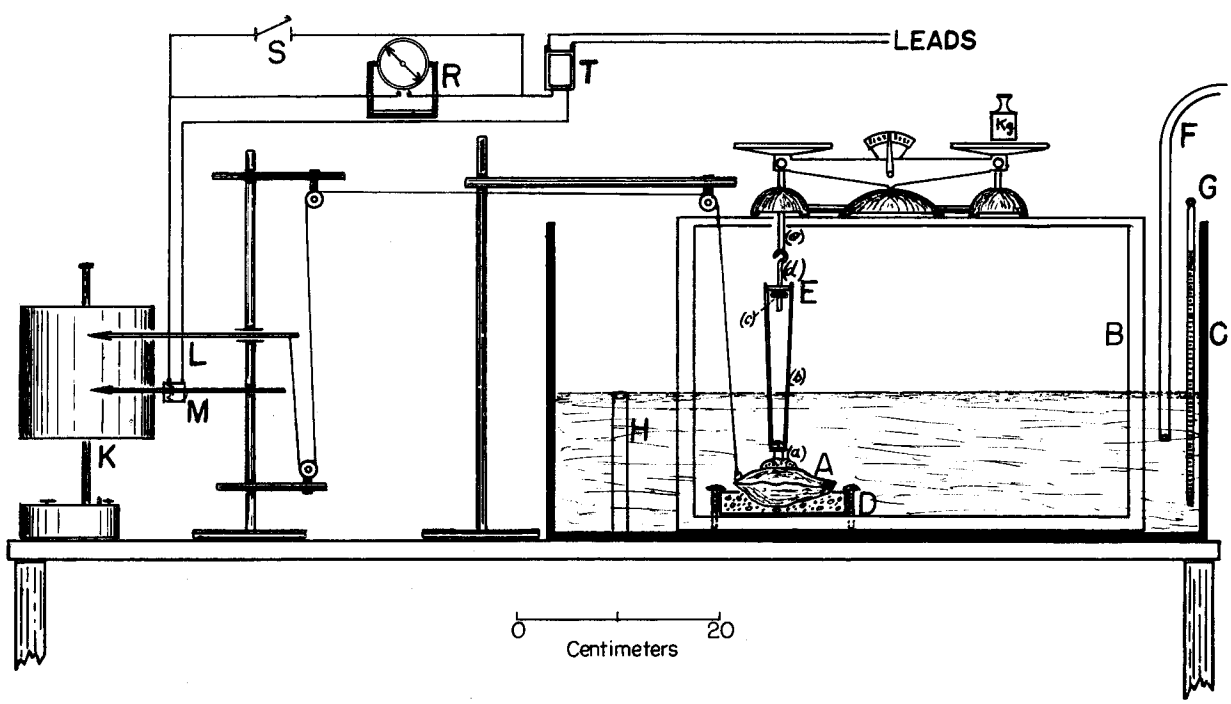

FIGURE 159.—Method of determining the resistance of the adductor muscle of *C. virginica* to a pulling force. A—cement base, bolted to wooden frame D and placed in tank B; a—galvanized iron screw; b—bars of the stirrup E; c—adjusting nut; d—hook for connecting the stirrup to the balance; e—left pan of the balance; F—seawater intake; H—overflow; K—kymograph; L—writing lever; M—signal magnet and pen; R—Telechron timer; T—transformer.

placed on frame D. The length of the hook is adjusted by turning the nut (c). The two pans of the balance are placed in a zero position, and the desired weight is put on the right pan. The right valve of the oyster is connected to the writing lever (L) of the kymograph (K). The writing pen (M) is attached to a signal magnet which is activated by an electric timer (R) and transformer (T). The timer is made by mounting a plastic disc on the axis of a Telechron motor making one revolution every hour. A short piece of copper wire at the periphery of the disc, indicated in figure 159 by the arrows, completes the circuit every 30 minutes (at the vertical position of the arrow). The weight of the balance is sufficient to keep the platform from floating when it is placed under water. Sea water is supplied through the intake (F); the overflow (H) controls the water level. This setup was successfully used in a large number of tests made both in the air and under water.

Occasionally the bond between the cement cup and the surface of the shell was insufficient for a pull of 8 to 10 kg. and had to be adjusted by using a stronger mixture and slightly roughening the surface of the valve. In the majority of cases the connection between the valve and the cement cap remained intact even when the pulling force of about 10 kg. was applied and occasionally the muscle itself was torn in the middle.

The purpose of the test was twofold: to study the behavior of the adductor under variable pulling force and to determine the time required to cause the loss of tonus by the muscles that were being stretched by weights varying from 2 to 10 kg. directly over the muscle scar.

New England oysters kept in the harbor near the laboratory were used in all the tests. The oysters were about 5 inches in height and appeared to be in good condition with the shells undamaged by boring sponge.

TESTS MADE IN AIR AND IN WATER

Adult oysters exposed to air at room temperature are able to withstand the pulling force of several kilograms for several days. Under the weight of 7 to 8 kg. the adductor muscle opened immediately (fig. 160). A force of 8 kg. (2,185.8 g./cm.^{2} of cross-sectional area of the adductor) caused immediate stretching of the adductor to about one-third of the maximum gaping distance, which was attained within 6.5 hours. During the 5 hours following the initial stretching there was no shell movement but the adductor retained its tonus level; the response to pricking (several small upward strokes on the record) was very slight. Final stretching to 1.5 cm. gaping distance of the valves was relatively rapid. At this stage the adductor lost the tonus and failed to respond to stimulation. Upon removal of the weights the muscle regained its elasticity and contracted (right side of fig. 160). For several hours an oyster weighing only 18.2 g., exclusive of shell, was capable of maintaining a constant tonus level against the pull of 8 kg.

In all tests in which the pulling force of 10 kg. per oyster was applied (from 2.5 to 3.0 kg./cm.^{2} of the muscle area) the muscle stretched immediately and the gape of the valves reached the maximum width of 15 to 18 mm. The muscle failed to respond to pricking or to the application of 0.1 *N* hydrocholoric acid but retained a certain degree of elasticity and was able to counteract the pulling force of the ligament. As soon as the muscle was cut off the valves opened several millimeters beyond their former position.

Individual variations in the time required for a muscle to reach maximum stretching are considerable. The time needed to produce tonus loss is inversely related to the weight applied to the valves. The pulling force of 0.5 kg. (131 to 136 g./cm.^{2}) applied for 15 days had no effect on the opening of the oyster shell in the air (at room temperature of 15° to 18° C.). At the pulling force of about 500 g./cm.^{2} the loss of tonus and failure to respond to stimulus developed in 300

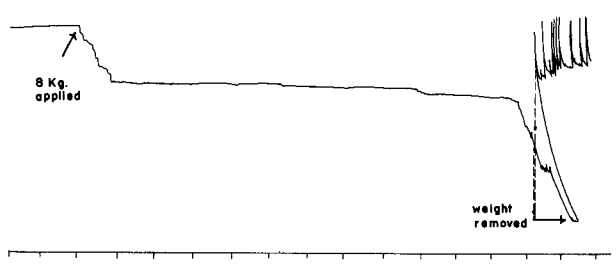

FIGURE 160.—Record of shell movement of *C. virginica* kept in air under the pulling force of 8 kg. (2185.8 g./cm.^{2} of cross-sectional area of the adductor muscle). Arrows indicate time when the weight was applied (upper left) and removed (lower right). Temperature 18° to 23° C. Total weight of oyster meat 18.2 g.; of shell 166 g. Maximum gap (right end of the curve) 1.5 cm. The distortion of the lowermost position of the lever with reference to the horizontal axis is marked by the heavy arrow. Time interval: 0.5 hour.

hours. To avoid desiccation the oyster in this experiment was surrounded by a small moist chamber. With the increase in weight the time of complete loss of tonus rapidly decreases (fig. 161).

Muscles which were kept for several hours under a pulling force of about 1.7 kg./cm.^{2} of cross-sectional area suffered a temporary injury which resulted in abnormal shell movements after the return of the oysters to sea water (fig. 162). The two tracings reproduced in this figure are almost identical, although in the case of oyster A a pulling force of 6 kg. was used while 8 kg. were applied to oyster B. In both instances the pulling force per unit of muscle scar area was the same, 1,676 in A and 1,675 g./cm.^{2} in B. After a few days in running sea water both oysters completely recovered and their shell movements became normal.

In oysters kept in sea water the relationship between the weight applied to the valves and the time needed to attain tonus loss is less regular and individual differences are much greater than for oysters left in the air. With a pulling force of about 1.5 kg./cm.^{2} of muscle area some of the oysters showed tonus loss in less than half an hour while others remained closed for many hours. The relationship between the increasing pulling force and the time required to develop loss of tonus is shown in figure 163.

Changes in the character of shell movements of

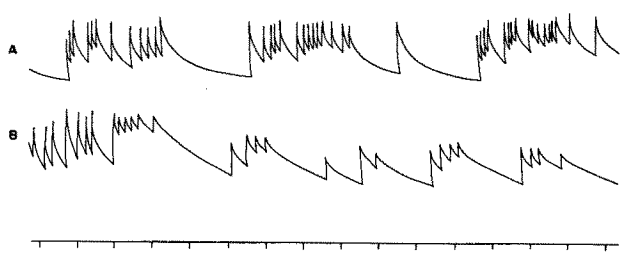

FIGURE 162.—Shell movements of *C. virginica* in sea water after the removal of weight of 6 kg. or 1,676 g./cm.^{2} of muscle area (upper line) and 8 kg. or 1,675 g./cm.^{2} of muscle area (lower line) applied to the valves. Weights were removed after complete loss of tonus was attained in 43.52 and 52 hours exposure in air at temperature 23° to 24° C. Water temperature 13.5° C. Time interval: A and B, 0.5 hour each.

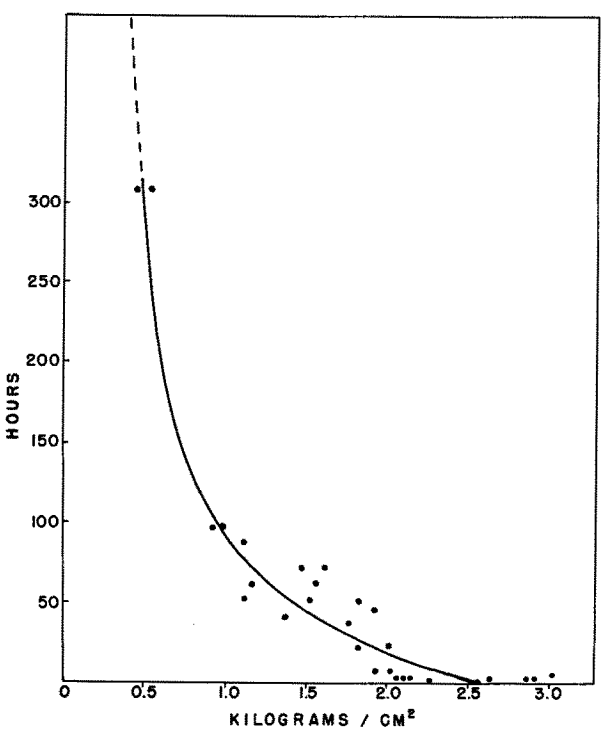

FIGURE 161.—Time in hours required to obtain loss of tonus of the intact adductor muscle kept under constant pull in kg./cm.^{2} of the cross-sectional area of the adductor. Experiments with *C. virginica* kept in air at temperatures between 18° and 24° C.

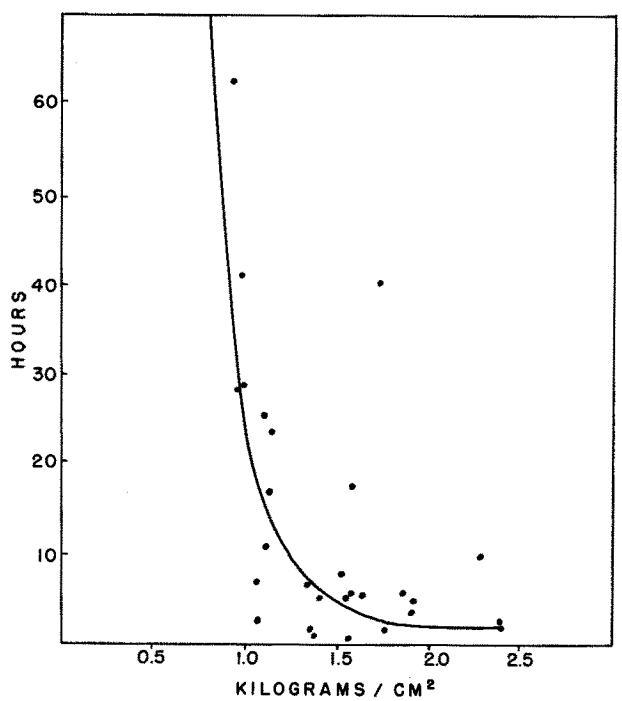

FIGURE 163.—Time in hours required to obtain complete loss of tonus in the adductor muscle of *C. virginica* kept in water under a constant pulling force expressed in kg./cm.^{2} of the cross-sectional area of the adductor muscle. Temperature 13.9° to 18.0° C. At the pulling force of 0.59 kg. complete tonus loss was obtained in 274 hours (11.5 days).

an oyster kept under the continuous pull of the relatively light weight of 2 kg. (606 g./cm.^{2} of cross section of muscle area) are shown in figure 164. The five lines represent excerpts of about 7.5 hours duration from a continuous recording made at a temperature of 13.9° to 14.1° C. and salinity of 31.3 °/oo. In line A the movements are normal. Their amplitude is increased after the application of a pulling force of 2 kg.; at the same time the frequency of contraction decreases (line B). This condition continues until the 67th hour (line D, middle part) when the muscle begins to stretch and the number of contractions greatly increases. At the 71st hour (end of line D) the muscle does not respond to stimulation. After removal of the weight (line E) shell movements are restored. The frequency of contractions during the recovery period is greater than under normal conditions. Within the next 48 hours normal shell movements of the type shown in line A are resumed.

Similar experiments in the air at higher temperatures varying from 18.5° to 24.0° C. gave slightly different results shown in figure 165. The pulling

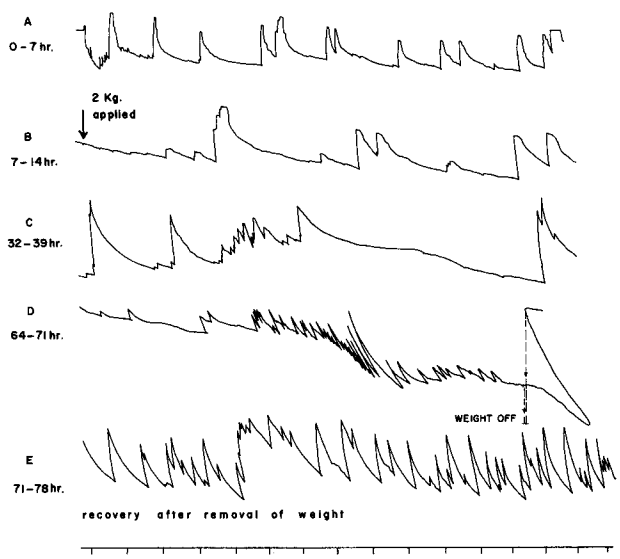

FIGURE 164.—Shell movements of *C. virginica* in sea water under continuous pull of 2 kg. (606 g./cm.^{2} of cross-sectional area of the adductor muscle). Temperature 13.9° to 14.1° C. Salinity 31.3 °/oo. A—normal shell movements before the application of weight. B—immediately after the application of weight. C—after 32 hours; note increased gaping. D—after 64 hours; wide gaping, complete loss of tonus and lack of response to stimulation. Maximum valve opening 1.5 cm. E—increased muscular activity during the recovery period following the removal of the weight. Time interval: A, B, C, D, and E, 0.5 hour each.

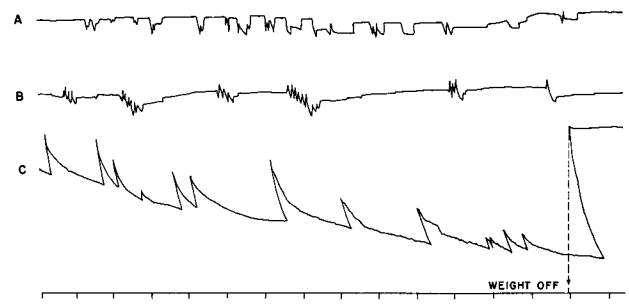

FIGURE 165.—Excerpts of the continuous records of shell movements of *C. virginica* in air under the pulling force of 2 kg. (590 of the cross-sectional area of the adductor). A—line ends at the 96th hour after the application of force; B—at 190th hour; C—at 274th hour when the muscle failed to respond to stimulation. Widest gap of valves 1.5 cm. Temperature 18.5° to 24° C. Time interval: A, B, C, 0.4 hour each.

force of 2 kg. per oyster applied in this case was equivalent to 590 g./cm.^{2} of the cross-sectional area of the muscle. Loss of tonus was attained in this case after 274 hours (line C) when the gap between the valves reached the maximum of 1.5 cm. Pathological condition of the muscle was apparent after 96 hours (line A) and became pronounced at 190 hours (line B). After removal of the weights the oyster was left in running sea water but failed to recover and died in 2 days.

A lighter weight (315.5 g./cm.^{2} of muscle area) applied to an adult oyster kept in running sea water at temperatures ranging from 13.9° to 18.0° C. produced very slow changes in the normal shell movements (fig. 166). The upper line of figure 166 represents normal movements recorded immediately after the application of the weight. A noticeable increase in the amplitude of contractions began on the 3rd day and continued through the 11th and 12th days. During the 13th and 14th days the amplitude of up and down strokes was greatly reduced; loss of tonus and failure to respond to stimulation developed by the 18th day. The last line shows the typical staircase contraction following the removal of the weight, indicating that the muscle retained some of its elasticity. At the maximum amplitude of the contractions (9th and 11th days) the oyster periodically lifted the weight of 1 kg. to the height of about 1 cm. Ten days after the end of the test the oyster recovered completely and its shell movements became normal.

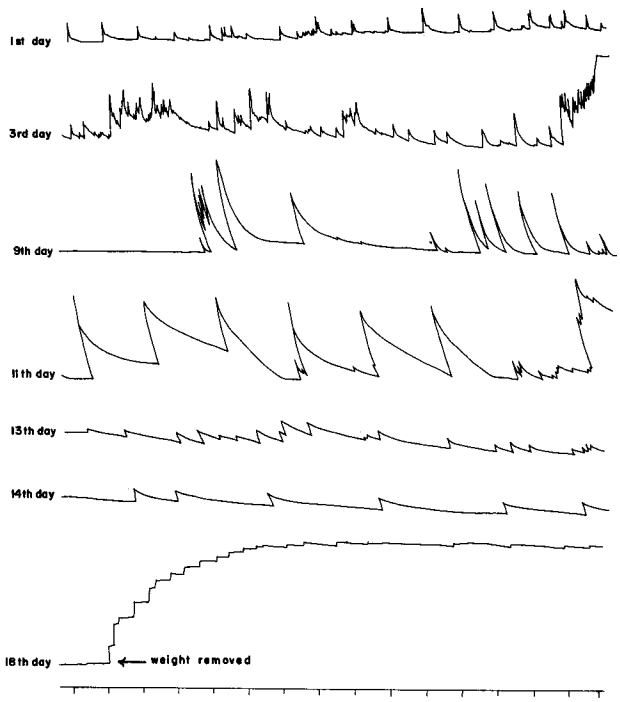

FIGURE 166.—Shell movements of *C. virginica* in running sea water under a continuous pull of 1 kg. (312.5 g./cm.^{2} of the cross-sectional area of the adductor muscle). Temperature 13.9° to 18.0° C. Time interval: 0.5 hour.

If much greater weight (4 kg. per oyster or 1,150 g./cm.^{2} of muscle area) is applied shell movements become abnormal at the very beginning of the test. This is demonstrated in the records of two Cotuit (Mass.) oysters (*C. virginica*) and one *C. gigas* shown in figure 167.

The stretching of the adductor muscle by a pulling force not exceeding 4 kg. per oyster did not interfere with their feeding; a strong current was maintained by the gills, and the feces were formed and discharged in a normal way. However, the secretion of mucus by the mantle and gills was greatly increased. Vast quantities of slimy material accumulated at the mantle edge and were discarded as pseudofeces.

The resistance of the adductor muscle to a pulling force exceeds by many times the force required to overcome the elasticity of the ligament and close the shell. This additional force is apparently needed to keep the valves hermetically sealed. The ability to keep the valves tightly closed has definite survival value. Mollusks possessing it are able to protect themselves against desiccation when exposed to air, or against adverse conditions caused by the presence of toxic substances in the water. Powerful muscular mechanism also helps

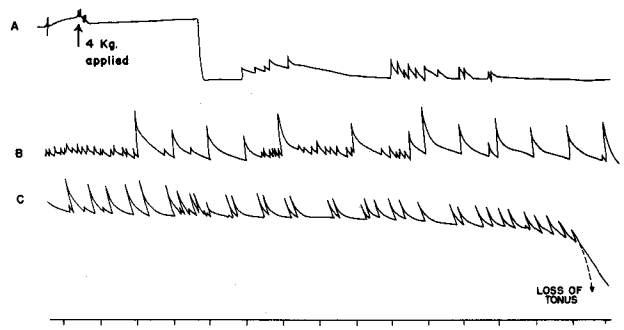

FIGURE 167.—Shell movements of two Cotuit oysters, *C. virginica* (lines A and B), and *C. gigas* (line C) in sea water under a continuous pull of 4 kg. or about 1,150 g./cm.^{2} of cross-sectional area of the adductor muscle. Temperature 14.5° to 16.5° C. Salinity 32.0 to 32.3 °/oo. The exact time of tonus loss is shown by the broken line and arrow. Time interval: A, B, and C, 0.5 hour each.

them to resist attacks of starfishes, crabs, and other enemies that attempt to pry open their valves.

CYCLES OF SHELL MOVEMENTS

There is no indication of any periodicity in muscular activity in the kymograph records of shell movements of oysters that were kept in running sea water in the laboratory or kept outside on a suitable platform submerged from a pier (Loosanoff and Nomejko, 1946). Brown and his associates (Brown, 1954; Brown, Bennett, Webb, and Ralph, 1956) claim, however, that *C. virginica* possesses a persistent lunar cycle of activity with the maxima occuring at about 12.5 hour intervals. Oysters used for obtaining tracings of shell movements were kept for a fortnight or longer in about 4 or 5 l. of sea water which was not changed but was adjusted by occasional addition of distilled water to compensate for evaporation. The mean daily cycles were calculated for 15-day periods by obtaining the average value of opening for each hour of the day and applying to the data a very complicated method of adjustment. The main conclusions reached by the authors were that: (1) oysters and quahogs display "statistical rhythms of opening of shell while the overt rhythms are not apparent from kymograph records", (2) short periods of opening tend to occur about 6:00 a.m. and more or less prolonged periods of openings happen through much of the remainder of the day. The observations and their mathematical treatment are of interest from a theoretical point of view, but the ecological

significance of the times of maxima and minima of activities in the daily cycle of the oyster are difficult to imagine at the present time.

BIBLIOGRAPHY

ANTHONY, R.
1918. Réflexions à propos de la genèse de la striation musculaire sous l'action des causes qui la déterminent. La question de la structure des fibres a contractions rapides dans les muscles adducteurs des mollusques acéphales. Archives de Zoologie Expérimentale et Générale, tome 58, Notes et Revue, numéro 1, pp. 1–10.

BALDWIN, ERNEST.
1957. Dynamic aspects of biochemistry. 3d ed. Cambridge University Press, London, 526 pp.

BANDMANN, H. J., und H. REICHEL.
1955. Struktur und Mechanik des glatten Schlissmuskels von *Pinna nobilis*. Zeitschrift für Biologie, Band 107, pp. 67–80.

BANFIELD, WILLIAM G.
1958. Collagen and reticulin. *In* Sanford L. Paley (editor), Frontiers in cytology, ch. 17, pp. 504–519. Yale University Press, New Haven, Conn.

BARNES, GORDON E.
1955. The behavior of *Anodonta cygnea* L., and its neurophysiological basis. Journal of Experimental Biology, vol. 32, No. 1, pp. 158–174.

BAYLISS, L. E., R. BOYLAND, and A. D. RITCHIE.
1930. The adductor mechanism of *Pecten*. Proceedings of the Royal Society of London, series B, vol. 106, pp. 363–376.

BAYLISS, WILLIAM MADDOCK.
1924. Principles of general physiology. 4th ed. Longmans, Green and Company, London, 882 pp.

BENSON, ANDREW A., JOHN T. HAYS, and RICHARD N. LEWIS.
1942. Inhibition in the slow muscle of the scallop, *Pecten circularis aequisulcatus* Carpenter. Proceedings of the Society for Experimental Biology and Medicine, vol. 49, No. 2, pp. 289–291.

BORRADAILE, L. A., and F. A. POTTS.
1961. The Invertebrata. A manual for the use of students. 4th ed., Revised by G. A. Kerkut. Cambridge University Press, London, 820 pp.

BOWDEN, J.
1958. The structure and innervation of lamellibranch muscle. *In* G. H. Bourne and J. F. Danielli (editors), International Review of Cytology, vol. 7, pp. 295–335.

BRONN, H. G.
1862. Die Klassen und Ordnungen der Weichthiere (Malacozoa), wissenschaftlich dargestellt in Wort und Bild. Dritten Bandes, erste Abtheilung. Kopflose Weichthiere (Malacozoa Acephala). C. F. Wintersche, Leipzig, 518 pp.

BROWN, FRANK A., Jr.
1954. Persistent activity rhythms in the oyster. American Journal of Physiology, vol. 178, No. 3, pp. 510–514.

BROWN, FRANK A., Jr., M. F. BENNETT, H. M. WEBB, and C. L. RALPH.
1956. Persistent daily, monthly, and 27-day cycles of activity in the oyster and quahog. Journal of Experimental Zoology, vol. 131, No. 2, pp. 235–262.

BRÜCK, ARTUR.
1914. Die Muskulatur von *Anodonta cellensis* Schröt. Ein Beitrag zur Anatomie und Histologie der Muskelfasern. Zeitschrift für wissenschaftliche Zoologie, Band 110, pp. 481–619.

CASPERS, HUBERT.
1951. Rhythmische Erscheinungen in der Fortpflanzung von *Clunio marinus* (Dipt. Chiron.) und das Problem der lunaren Periodizität bei Organismen. Archiv für Hydrobiologie, Supplement, Band 18, pp. 415–594.

CLARKE, C. H. D.
1949. Fluctuations in populations. Journal of Mammalogy, vol. 30, No. 1, pp. 21–25.

COLE, LAMONT C.
1951. Population cycles and random oscillations. Journal of Wildlife Management, vol. 15, No. 3, pp. 233–252.
1957. Biological clock in the unicorn. Science, vol. 125, No. 3253, pp. 874–876.

COUTANCE, A.
1878. De l'énergie et de la structure musculaire chez les Mollusques Acéphales. J. B. Baillière et Fils, Paris, 63 pp.

DEROBERTIS, E. D. P., W. W. NOWINSKI, and FRANCISCO A. SAEZ.
1954. General cytology. 2d ed. W. B. Saunders Company, Philadelphia, Pa., 456 pp.

ENGSTRÖM, ARNE, and J. B. FINEAN.
1958. Biological ultrastructure. Academic Press, New York, 326 pp.

EVANS, C. LOVATT.
1926. The physiology of plain muscle. Physiological Reviews, vol. 6, No. 2, pp. 358–398.

FLORKIN, MARCEL.
1949. Biochemical evolution. Edited, translated, and augmented by Sergius Morgulis. Academic Press, New York, 157 pp.

FLORKIN, MARCEL, and GHISLAINE DUCHATEAU.
1942. Sur la composition de myosines d'Invertébrés et sur les degrés d'Homologie des protéines animales. Acta Biologica Belgica, tome 2, pp. 353–354.

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 of the U.S. Bureau of Fisheries, vol. 44, for 1928, pp. 1–39. (Document 1035.)
1953. How strong is the oyster? National Shellfisheries Association, 1952 Convention Addresses, pp. 51–53.
1958. Observations on muscle attachments, ciliary motion, and the pallial organ of oysters. Proceed-

ings of the National Shellfisheries Association, vol. 48, August 1957, pp. 154–161.

GALTSOFF, PAUL S., WALTER A. CHIPMAN, Jr., JAMES B. ENGLE, and HOWARD N. CALDERWOOD.
1947. Ecological and physiological studies of the effect of sulfate pulp mill wastes on oysters in the York River, Virginia. [U.S.] Fish and Wildlife Service, Fishery Bulletin 43, vol. 51, pp. 59–186.

GLAISTER, DEBORAH, and MARGARET KERLY.
1936. The oxygen consumption and carbohydrate metabolism of the retractor muscle of the foot of *Mytilus edulis*. Journal of Physiology, vol. 87, No. 1, pp. 56–66.

GRÜTZNER, P.
1904. Die glatten Muskeln. Ergebnisse der Physiologie, Band 3, Abteilung 2, pp. 12–88.

HALL, C. E., M. A. JAKUS, and F. O. SCHMITT.
1945. The structure of certain muscle fibrils as revealed by the use of electron stains. Journal of Applied Physics, vol. 16, No. 8, pp. 459–465.

HANSON, JEAN, and J. LOWY.
1957. Structure of smooth muscles. Nature, vol. 180, No. 4592, pp. 906–909.
1959. Evidence for a sliding filament contractile mechanism in tonic smooth muscles of lamellibranch molluscs. Nature, vol. 184, No. 4682, pp. 286–287.
1961. The structure of the muscle fibres in the translucent part of the adductor of the oyster, *Crassostrea angulata*. Proceedings of the Royal Society of London, series B, Biological Sciences, vol. 154, pp. 173–196.

HAYASHI, TERU, RAJA ROSENBLUTH, and HAYES C. LAMONT
1959. Studies of fibers of acto- and paramyosin from lamellibranch muscle. [Abstract.] Biological Bulletin, vol. 117, No. 2, p. 396.

HOPKINS, A. E.
1931. Temperature and the shell movements of oysters. [U.S.] Bureau of Fisheries, Bulletin No. 1, vol. 47, pp. 1–14.
1936. Activity of the adductor muscle in oysters. Physiological Zoölogy, vol. 9, No. 4, pp. 498–507.

HOPKINS, HOYT S.
1930. Muscular differentiation in oysters exposed for diverse periods of time. [Abstract.] Anatomical Record, vol. 47, No. 3, p. 305.

HUBENDICK, BENGT.
1958. On the molluscan adhesive epithelium. Arkiv för Zoologi utgivet av Kungl. Svenska Vetenskapsakademien, andra serie, band 11, No. 3, pp. 31–36.

HUMPHREY, GEORGE FREDERICK.
1944. Glycolysis in extracts of oyster muscle. Australian Journal of Experimental Biology and Medical Science, vol. 22, part 2, pp. 135–138.
1946. The endogenous respiration of homogenates of oyster muscle. Australian Journal of Experimental Biology and Medical Science, vol. 24, part 4, pp. 261–267.
1949. Adenosinetriphosphatases in the adductor muscle of *Saxostrea commercialis*. Physiologia Comparata et Oecologia, vol. 1, pp. 366–375.
1950. Glycolysis in oyster muscle. Australian Journal of Experimental Biology and Medical Science, Vol. 28, part 2, pp. 151–160.

HUXLEY, H. E.
1960. Muscle cells. *In* Jean Brachet and Alfred E. Mirsky (editors). The cell, biochemistry, physiology, morphology, vol. 4, Specialized cells: part 1, ch. 7, pp. 365–481 Academic Press, New York.

JOHNSON, WILLIAM H., JOSEPH S. KAHN, and ANDREW G. SZENT-GYÖRGYI.
1959. Paramyosin and contraction of "catch muscles". Science, vol. 130, No. 3368, pp. 160–161.

JOHNSON, WILLIAM H., and ANDREW G. SZENT-GYÖRGYI.
1959. The molecular basis for the "catch" mechanism in molluscan muscle. [Abstract.] Biological Bulletin vol. 117, No. 2, pp. 382–383.

JOLYET, F., et, J. SELLIER.
1899. Contributions à l'étude de la physiologie comparée de la contraction musculaire chez les animaux invertébrés. Bulletin de la Station Biologique d'Arcachon, Travaux des Laboratoires, Année 1899, pp. 49–92.

JORDAN, H. J.
1938. Die Physiologie des Tonus der Hohlmuskeln, vornehmlich der Bewegungsmuskulatur "hohlorganartiger" wirbelloser Tiere. Ergebnisse der Physiologie, Biologischen Chemie und Experimentellen Pharmakologie, Band 40, pp. 437–533.

KATZ, JULIUS.
1896. Die mineralsichen Bestandthiele des Muskelfleiches. Archiv für die gesammte Physiologie des Menschen und der Thiere, Band 63, pp. 1–85.

KAWAGUTI, SIRO, and NORIAKI IKEMOTO.
1957. Electron microscopy of the smooth muscle of a mussel, *Mytilus crassitesta* Lischke. Biological Journal of Okayama University, vol. 3, Nos. 1–2, pp. 107–121.
1958. Electron microscopy on the adductor muscle of the scallop, *Pecten albicans*. Biological Journal of Okayama University, vol. 4, Nos. 3–4, pp. 191–205.
1959. Electron microscopy of the adductor muscle of the thorn oyster, *Spondylus cruentus*. Biological Journal of Okayama University, vol. 5, Nos. 1–2, pp. 73–87.

KELLOGG JAMES L.
1892. A contribution to our knowledge of the morphology of lamellibranchiate mollusks. Bulletin of the U.S. Fish Commission, vol. 10, for 1890, pp. 389–436.

KOBAYASHI, SATARÔ.
1929. Lactic acid and glycogen in the adductor muscles of the oyster, *Ostrea circumpicta* Pils. Science Reports of the Tôhoku Imperial University, series 4, Biology, vol. 4, No. 1, fasc. 2, pp. 193–205.

KROGH, AUGUST.
1938. The salt concentration in the tissues of some marine animals. Skandinavisches Archiv für Physiologie, band 80, pp. 214–222.

LAJTHA, ABEL.
1948. The muscle proteins of invertebrates. Pubblicazioni della Stazione Zoologica di Napoli, vol. 21, fascicolo 3, pp. 226–231.

LEENHARDT, H.
1923. Sur la présence d'un muscle pédieux chez les Ostréidés. Bulletin de la Société Zoologique de France, vol. 48, pp, 379–380.

LOOSANOFF, VICTOR L., and CHARLES A. NOMEJKO.
1946. Feeding of oysters in relation to tidal stages and to periods of light and darkness. Biological Bulletin, vol. 90, No. 3, pp. 244–264.

LOWY, J.
1953. Contraction and relaxation in the adductor muscles of *Mytilus sedulis*. Journal of Physiology, vol. 120, Nos. 1 and 2, pp. 129–140.
1955. The lamellibranch muscle. Contractile mechanism. Nature, vol. 176, No. 4477, pp. 345–346.

MARCEAU, F.
1904a. Sur les fonctions respectives des dux parties des muscles adducteurs chez les lamellibranches. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, tome 138, pp. 1343–1345.
1904b. Sur le mécanisme de la contraction des fibres musculaires lisses dites à double striation oblique ou à fibrilles spiralées et en particulier de celles des muscles adducteurs des Lamellibranches. Comptes Rendus Hebdomadaires des Séances de l'Academie des Sciences, tome 139, pp. 70–73.
1905a. Recherches sur la physiologie et en particulier sur les lois de la production de travail mécanique par les muscle adducteurs des Acéphales. Bulletin de la Station Biologique d'Arcachon, Travaux des Laboratoires, Huitième (8) Année, p. 41–47.
1905b. Sur la production de travail mécanique par les muscles adducteurs des Acéphales. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, tome 141, p. 278.
1909. Recherches sur la morphologie, l'histologie et la physiologie comparées des muscles adducteurs des mollusques acéphales. Archives de Zoologie Expérimentale et Genérale, série 5, tome 2, fascicule 6, pp. 295–469.

NEEDHAM, DOROTHY MOYLE.
1932. The biochemistry of muscle. Methuen and Company, Ltd. London, 166pp.

NELSON, THURLOW C.
1921. Report of the Department of Biology of the New Jersey Agricultural College Experiment Station, New Brunswick, N.J., for the year ending June 30, 1920. Published by the State, Trenton, N.J., pp. 317–349.
1922. Report of the Department of Biology of the New Jersey Agricultural College Experiment Station, New Brunswick, N.J., for the year ending June 30, 1921. Published by the State, Trenton, N.J., pp. 287–299.
1923a. Report of the Department of Biology of the New Jersey Agricultural College Experiment Station, New Brunswick, N.J., for the year ending June 30, 1922. Published by the State, Trenton, N.J., pp. 315–343.
1923b. The mechanism of feeding in the oyster. Proceedings of the Society for Experimental Biology and Medicine, vol. 21, pp. 166–168.
1923c. On the feeding habits of oysters. Proceedings of the Society for Experimental Biology and Medicine, vol. 21, pp. 90–91.
1938. The feeding mechanism of the oyster. I. On the pallium and the branchial chambers of *Ostrea virginica*, *O. edulis* and *O. angulata*, with comparisons with other species of the genus. Journal of Morphology, vol. 63, pp. 1–61.

ORTON, J. H.
1929. Oyster. Encyclopaedia Britannica, vol. 16, pp. 1003–1006. 14th ed. Encyclopaedia Britannica, Inc., Chicago, Ill.
1935. Biology of shell-movements of the oyster. Science, vol. 82, No. 2118, pp. 105–106.

PALMGREN, PONTUS.
1949. Some remarks on the short-term fluctuations in the numbers of northern birds and mammals. Oikos, vol. 1, fasc. 1, pp. 114–121.

PHILPOTT, D. E., MARGIT KAHLBROCK, and A. G. SZENT-GYÖRGYI.
1960. Filamentous organization of molluscan muscles. Journal of Ultrastructure Research, vol. 3, No. 3, pp. 254–269.

PLATEAU, FÉLIX.
1884. Recherches sur la force absolue des muscles des invertébrés. I. Force absolue des muscles adducteurs des mollusques lamellibranches. Archives de Zoologie Expérimentale et Générale, série 2, tome 2, pp. 145–170.

RIESSER, OTTO.
1936. Vergleichende Muskelphysiologie. Ergebnisse der Physiologie, Biologischen Chemie und Experimentellen Pharmakologie, Band 38, pp. 133–250.

RITCHIE, A. D.
1928. The comparative physiology of muscular tissue. Cambridge University Press, London, 111 pp.

RÖCHLING, ELFRIEDE.
1922. Der Kolumellarmuskel von *Helix pom.* und seine Beziehung zur Schale. Zeitschrift für Wissenschaftliche Zoologie, Band, 119, pp. 285–325.

SCHEER, BRADLEY T.
1948. Comparative physiology. John Wiley and Sons, New York, 563 pp.

SCHWALBE, G.
1869. Ueber den feineren Bau der Muskelfasern wirbelloser Thiere. Archiv für mikroskopische Anatomie, Band 5, pp. 205–259.

SHUKOW, E. K.
1936. Die Labilitätsänderung der glatten muskulatur als Faktor des Überganges der Klonischen Verkürzungen in den Tonus. Journal of Physiology of U. S. S. R., vol. 20, No. 1, pp. 87–97. [In Russian with German summary.]

SZENT-GYÖRGYI, A.
1951. Chemistry of muscular contraction. 2d ed. Academic Press, New York, 162 pp.

TABULAE, BIOLOGICAE.
1926. Chemische Zusammensetzung der Mollusken, by G. Grimpe and H. Hoffman. *In* Tabulae Biologicae, Band 3, pp. 455–461. W. Junk, Berlin.

TAMURA, TADASHI.
1929. The power of the adductor muscle of the oyster, *Ostraea circumpicta* Pils. Science Reports of the Tôhoku Imperial University, series 4, Biology, vol. 4, No. 1, fasc. 2, pp. 259–279.
1931. The power of the adductor muscle of the lamellibranchs, inhabiting in the South Sea Islands. Science Reports of the Tôhoku Imperial University. series 4, Biology, vol. 6, No. 3, pp. 347–390.

UEXKÜLL, J. von.
1909. Umwelt und Innenwelt der Tiere. Julius Springer, Berlin, 259 pp.
1912. Studien über den Tonus. VI. Die Pilgermuschel. Zeitschrift für Biologie, Band 58, pp. 305–332.

WEBER, HANS H.
1958. The motility of muscle and cells. Harvard University Press, Cambridge, Mass., 69 pp.

WELSH, JOHN H.
1938. Diurnal rhythms. Quarterly Review of Biology, vol. 13, No. 2, pp. 123–139.

WIERSMA, C. A. G.
1957. Neuromuscular mechanisms. *In* Bradley T. Scheer (editor), Recent advances in invertebrate physiology, a symposium, pp. 143–159. University of Oregon Publications, Eugene, Oreg.

WINTON, F. R. ;
1930. Tonus in mammalian unstriated muscle. Journal of Physiology, vol. 69, No. 4, pp. 393–410.