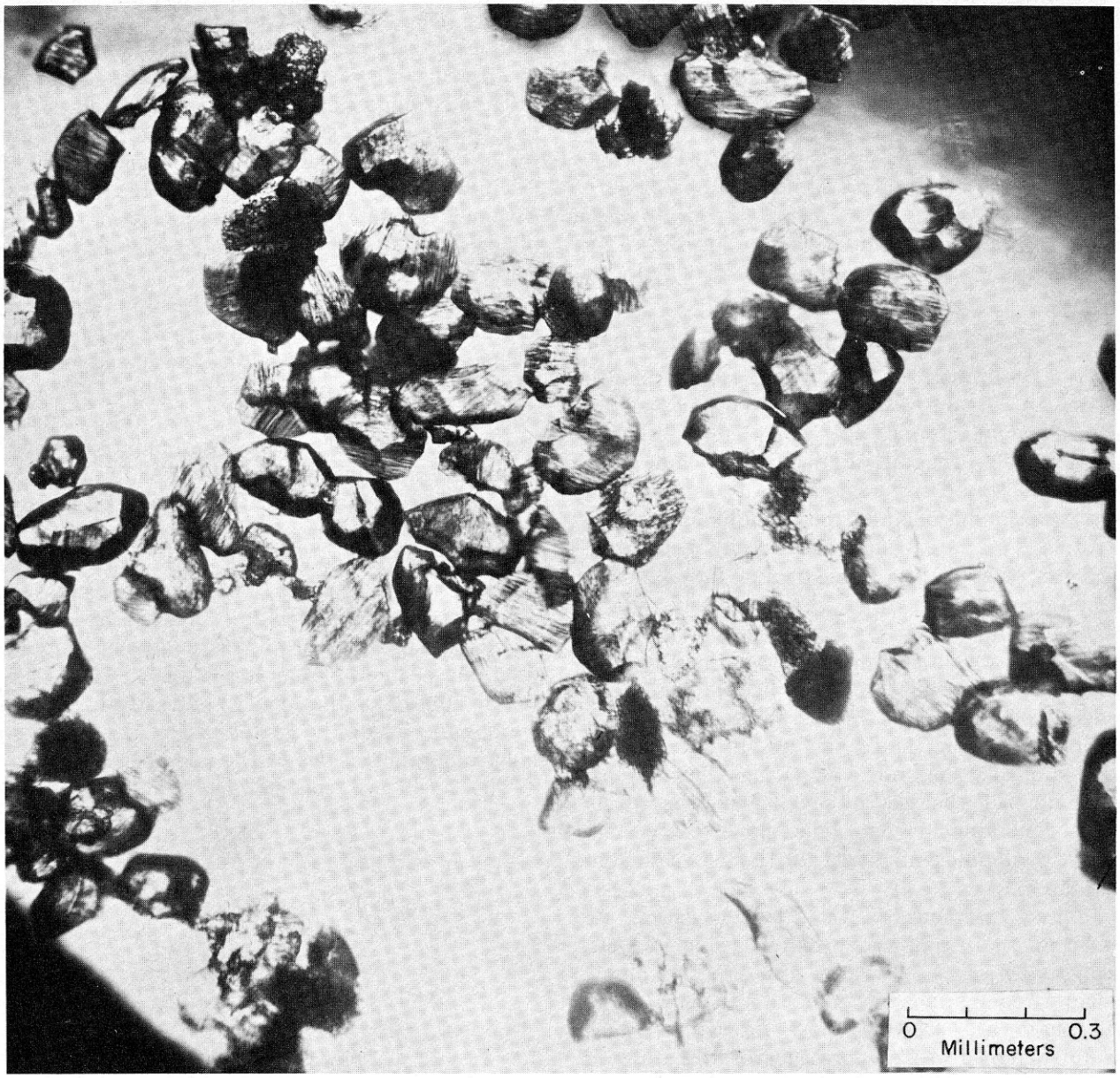

FIGURE 101.—Photograph of crystals of a mixture of calcite and gypsum formed in the mantle cavity of *C. virginica*.

chemical reactions show that the secretion of calcium is not confined to special sites but takes place over the entire edge and outer surface of the mantle. The intensive coloration of the granules by alizarin suggests that they contain a considerable amount of calcium, probably bound in organic compounds of the globules. Amoebocytes present in the material secreted by the mantle also may be involved in the mobilization of calcium during the formation or repair of shells.

Sometimes the mineral crystals formed by the mantle are not incorporated in the conchiolin but accumulate in the pallial cavity and are eventually ejected. On several occasions fairly large quantities of a white powdered material were found in front of the discharge areas of oysters which were kept in glass trays in running sea water in the laboratory. The material consisted of crystals (fig. 101) which, according to the X-ray analysis kindly performed by Marie Lindberg of the Geochemistry and Petrology Branch of the Geological Survey of the U.S. Department of the Interior, were found to consist of a mixture of

calcite and gypsum (hydrous calcium sulfate), with the latter present only as a minor constituent. The oysters appeared to be normal in every respect and showed good growth of shells. The presence of gypsum is of interest since it is not a normal constituent of oyster shell. What particular disturbance in the calcium metabolism produced its formation is unknown.

SOURCES OF CALCIUM

It has been suggested (Pelseneer, 1920; Galtsoff, 1938) that lamellibranchs may remove calcium directly from sea water. Pelseneer (1920) cites an example of a young *Anodonta cygnea* which in 2 months removed all the calcium from 5 l. of water in which it was kept. Definite proof of the direct absorption of calcium by the oyster mantle is given by the experiments with *C. virginica* (Jodrey, 1953) in which radioactive Ca^{45} was used. Calcium turnover was also studied by Hirata (1953) in mantle-shell preparations made by cutting off the adductor muscle and the visceral organs, and leaving the intact mantles spread over their respective valves. The mantle remained alive for several days and deposited the shell material, although at a lower rate than does the intact oyster. Jodrey placed a mantle preparation in 500 ml. of aerated sea water with a Ca^{45} activity of 5.8 microcuries. At least part of the calcium of the newly formed shell substance came directly from the sea water, and the deposition of calcite took place in tissue isolated from the circulatory and digestive systems. The experiments also demonstrated that the greater portion of calcium in the mantle appears to be inert. Only 2.5 percent of the total calcium content was renewed every 24 minutes, the turnover being 0.6 mg. of calcium per minute per gram of mantle. In addition to entering the mantle directly calcium can be taken up by other organs of the oyster and transported to the mantle (Wilbur, 1960).

MINERALOGY OF CALCIUM CARBONATE IN MOLLUSCAN SHELLS

Calcium carbonate is known to occur in 12 mineral forms (Prenant, 1924), but only three of these have been found in animals. In the shells of mollusks, calcium carbonate usually occurs as calcite and aragonite. There are many species in which both minerals occur together although in different parts of the shell. Prenant (1928), who contributed much to the study of calcification, found that besides calcite and aragonite the animal tissue may contain small spheres (sphaerolithes) or tiny needles of the mineral called "vaterite", after the mineralogist Vater who discovered it. Vaterite was reported to be present in the connective tissue of certain gastropod mollusks, cestodes, and trematodes, and in the fat tissue of insects (Diptera). Its presence in the tissues of the oyster has not been reported.

The various forms of calcium carbonate secreted by animal tissue can be identified by their crystallographic properties, birefringence, density, and chemical reaction. Some of these distinctive characteristics are summarized in table 12, taken from Prenant (1924).

Impurities always present in material secreted by living forms can sometimes make the mineralogical identification of calcium carbonate doubtful. Calcite and aragonite can be distinguished by means of the polarizing microscope. Calcite crystals examined under crossed nicols give a brilliant picture of various colors, and a distinct black cross appears when the optical axis is aligned parallel to the axis of the microscope (fig. 94.) In the case of aragonite, hyperbolic arched lines appear instead of the black crosses. Exact identification of minerals can of course be made by X-rays, but this method is rarely available to the biologist.

Among various chemical identification methods the Meigen color reaction can be most easily employed (Bøggild, 1930, p. 238). In a weak solution of cobalt nitrate aragonite becomes violet, the intensity of coloration increasing as the solution is warmed. Calcite, however, remains pale blue even in a heated solution.

The conditions under which a mollusk secretes calcium carbonate in a specific mineralogical form are not at present understood. It is reasonable to presume that the organic matrix of the shell is somehow involved in this process. Roche, Ranson, and Eysseric-Lafon (1951) found that in the shells of mollusks consisting both of calcite and aragonite the conchiolin associated with the calcite of the prismatic layer had higher concentrations of glycine and tyrosine than were present in the nacre of the same shell consisting of aragonite (see ch. II, p. 41). The causal relationship between the mineralogical forms of carbonate and amino acids of its conchiolin has not been demonstrated.

A hypothesis that carbonic anhydrase, an enzyme present in the tissues of the mantle, plays

TABLE 12.—*Distinctive properties of principal mineral forms of calcium carbonate found in invertebrates* [1]

Name	Chemical composition	Optical System	Birefringence	Index of refraction	Density	Meigen reaction
Calcite	$CaCO_3$	Rhomboedric, uniaxial	Strong (0.172)	1.658–1.486	2.714	Negative.
Aragonite	$CaCO_3$	Monoclinic, biaxial	Slightly weaker, (0.156)	1.686–1.530	2.95	Positive.
Vaterite	$CaCO_3$	Sphaerolithes, optically negative	Weak	About 1.55	2.5–2.65	Do.
Amorphous	$CaCO_3$	Isotropic		Near 1.5	2.25–2.45	
Hydrated carbonate	$CaCO_3\ 6H_2O$	Prisms or Monoclinic tablets	Near 0.085	About 1.5	1.777	

[1] From the data published by Prenant, 1927.

an important role in the formation of calcium deposits in molluscan shells has been advanced by Stolkowski (1951). According to this theory the enzyme exerts its effect by orienting the calcium carbonate molecules in the aragonite crystal lattice. The action of carbonic anhydrase in this admittedly very complex process is not, however, satisfactorily explained and should be more thoroughly investigated before its role in the formation of aragonite or calcite in mollusk shells is definitely established. In its present state the hypothesis fails to explain the existence of shells in which both aragonite and calcite are present. Recently Stenzel (1963) reported that in the shells of *C. virginica* aragonite covers the areas of attachment of the adductor muscle, the imprint of Quenstedt's muscle, and is found in the ligament.

Another explanation of the formation of the less stable aragonite instead of calcite suggests that strontium and magnesium carbonates influence the formation of aragonite in shell. Some support to this idea is found in the fact that in vitro the crystallization of aragonite is facilitated by strontium and lead salts. This observation made by Prenant (1924) apparently influenced Trueman's (1942) hypothesis that strontium, magnesium, and probably other salts found in living mollusks influence the crystallization of aragonite.

That there may be some correlation between the predominance of the particular mineralogical form of calcium carbonate and the temperature of the surrounding water has recently been suggested by some geologists. Through quantitative X-ray analysis of shells they have demonstrated that in certain polyclad worms (Serpulidae) and in some gastropods and pelecypods (*Mytilus, Volsella, Pinctada, Anomia,* and others) the concentration of aragonite in shells increases with increasing temperatures (Epstein and Lowenstam, 1953; Lowenstam, 1954). In *Mytilus*, for instance, only the shells of warm water species are composed entirely of aragonite, whereas those from colder waters contain varying amounts of both calcite and aragonite. This interesting ecological observation does not, however, provide a clue to the nature of the biochemical processes which control the predominance of one or another crystallization system.

RATE OF CALCIFICATION

The calcification rate of the left valve of *C. virginica* is significantly higher than that of the right one, as can be readily seen by examining newly formed shells. The calcareous material deposited by the left mantle is thicker and heavier than that deposited during the same time by the right mantle (Galtsoff, 1955). I made the following observations on shell growth rate of adult *C. virginica*. After the new growth of shell along the valve edge was carefully removed the oysters were placed in tanks abundantly supplied with running sea water. About 2 months later the areas of newly deposited shells on each valve were measured with a planimeter, carefully removed from the shell, rinsed in distilled water, dried in air, and weighed. The results are summarized in table 13. In every case the amount of calcified material deposited over a unit of area was considerably greater on the left

TABLE 13.—*Areas of new growth and rate of deposition of shell material by* C. virginica *in mg. per day per cm.² during April to June 1954, Woods Hole, Mass.*

Oysters	Area of new shell	Weight per cm.²	Deposition per cm.² pay day	Days under observation	Ratio weight of left to weight of right valve
	Cm.²	*Mg.*	*Mg.*	*No.*	
Five-year-old, Narragansett Bay					
Left valve	5.80	156.0	2.8	55	2.6
Right valve	5.16	59.3	1.1		
Adult, Narragansett Bay					
Left valve	7.1	123.0	1.8	68	6.2
Right valve	7.7	19.9	0.3		
Adult, Narragansett Bay					
Left valve	6.1	74.2	1.09	68	2.9
Right valve	8.8	25.5	0.37		
Two-year-old, New Hampshire					
Left valve	3.68	163.8	2.98	55	3.2
Right valve	4.20	52.0	0.95		
Very old, New Hampshire					
Left valve	6.83	71.2	1.3	55	2.2
Right valve	7.35	33.0	0.6		

valve (lower) than on the right one (upper), the difference varying from 2.2 to 6.2 times.

The rate of deposition of calcified material by the surface of the mantle may also be studied by inserting between the mantle and shell small pieces of plastic or other nontoxic material of known area and weight. Results obtained with this method vary greatly. Observations made on 16 adult oysters at Woods Hole during the period of August 9 to 20, 1953, show that in 15 oysters the daily rate of shell deposition per square centimeter varied from 0.4 to 2.1 mg. One oyster deposited 14.2 mg. in 2 days or 7.1 mg. per day. The amounts of shell material deposited by 20 Narragansett Bay oysters kept in laboratory tanks for 68 days during the period of April to June varied from 0.1 to 0.79 mg. of shell substance per day cm.^{2}. In some of these oysters the presence of the plastic material induced pathological conditions which resulted in the formation of leathery capsules similar to the blisters frequently found on the inside of shells near the adductor muscle. The formation of such blisters was accompanied by deposition of calcite greatly in excess of the rate of calcification under normal conditions.

Seasonal variation in rate of shell deposition over the inner surface of the valves was also studied, using 20 adult oysters for each set of determinations. Observations were continuous from June 1954 until the end of February 1956. To avoid possible injury to the mantle while introducing pieces of plastic, the oysters were fully narcotized in magnesium sulfate solution and insertions made when the mantle was completely relaxed and did not respond to touch. Thin sheets of plastic were cut into rectangular pieces 0.5 cm.^{2} in area and weighed before inserting them under the mantle, their weight varying from 5.5 to 6.0 mg. Some of the pieces introduced were ejected by the oysters, but losses were minimized when the insertion was made under full narcosis. The treated oyster was then marked and placed on its left valve in a large tray supplied with running sea water. The temperature of the water was recorded twice a day. Each set of 20 oysters was kept in water as long as the seasonal rise or fall of water temperature did not exceed 2.5° C.

To obtain measurable quantities of shell deposits the pieces of plastic were left inside the oysters for a longer time in winter and in August, after the completion of spawning, than during the rest of the year. The number of days the oysters with inserted pieces were left undisturbed varied as follows: from 10 to 16 days in April to July; from 25 to 30 days in August; from 13 to 18 days in September to November; for 30 days in December; and 70 days in January to March. Observations were continued for 14 months. No shell was formed in January to March except in a few oysters in which the mantle was injured during insertion. These samples were not included in the data plotted in fig. 102. Laboratory observations showed that shell opening and feeding of the oysters at Woods Hole are as a rule temporarily reduced after the discharge of sex products which takes place late in July and early in August. Unequal time intervals in observing shell deposition do not affect the validity of the results since the rates of shell formation shown in figure 102 are expressed as weights of shell deposited per cm.^{2} in 1 day.

At the end of each period the oysters were removed, the pieces of plastic recovered, rinsed in distilled water, dried at 55° C., and weighed. The results summarized in figure 102 are shown as medians (Md.) of the rate of shell deposition per cm.^{2} per day, and as lower (Q_1) and upper (Q_3) quartiles.

The curves show two periods of accelerated shell growth in Woods Hole water, one in May to June and another in October, and no shell growth during winter from December to the end of April when the temperature of the water varied between 1° and 2° C. These observations are in agreement with many field data and with the experiences of practical oyster growers of the North Atlantic states, who found that oysters grow more rapidly in the spring and in the autumn and cease to grow when the water temperature drops to about 5° C. The relatively low rate of shell deposition during the summer is attributable to the inhibitory effect of fully developed gonads. Observations frequently made in the Woods Hole laboratory show that shell growth in the winter will begin within 24 hours after the transfer of oysters from the harbor to much warmer sea water in the laboratory.

Under normal conditions no shell is deposited in winter. In several instances, however, large amounts of shell material were secreted over an area of the mantle which was apparently injured by the insertion of plastic. One of these cases is shown in figure 103. In this oyster a heavy pocket of shell material was deposited on the valve over

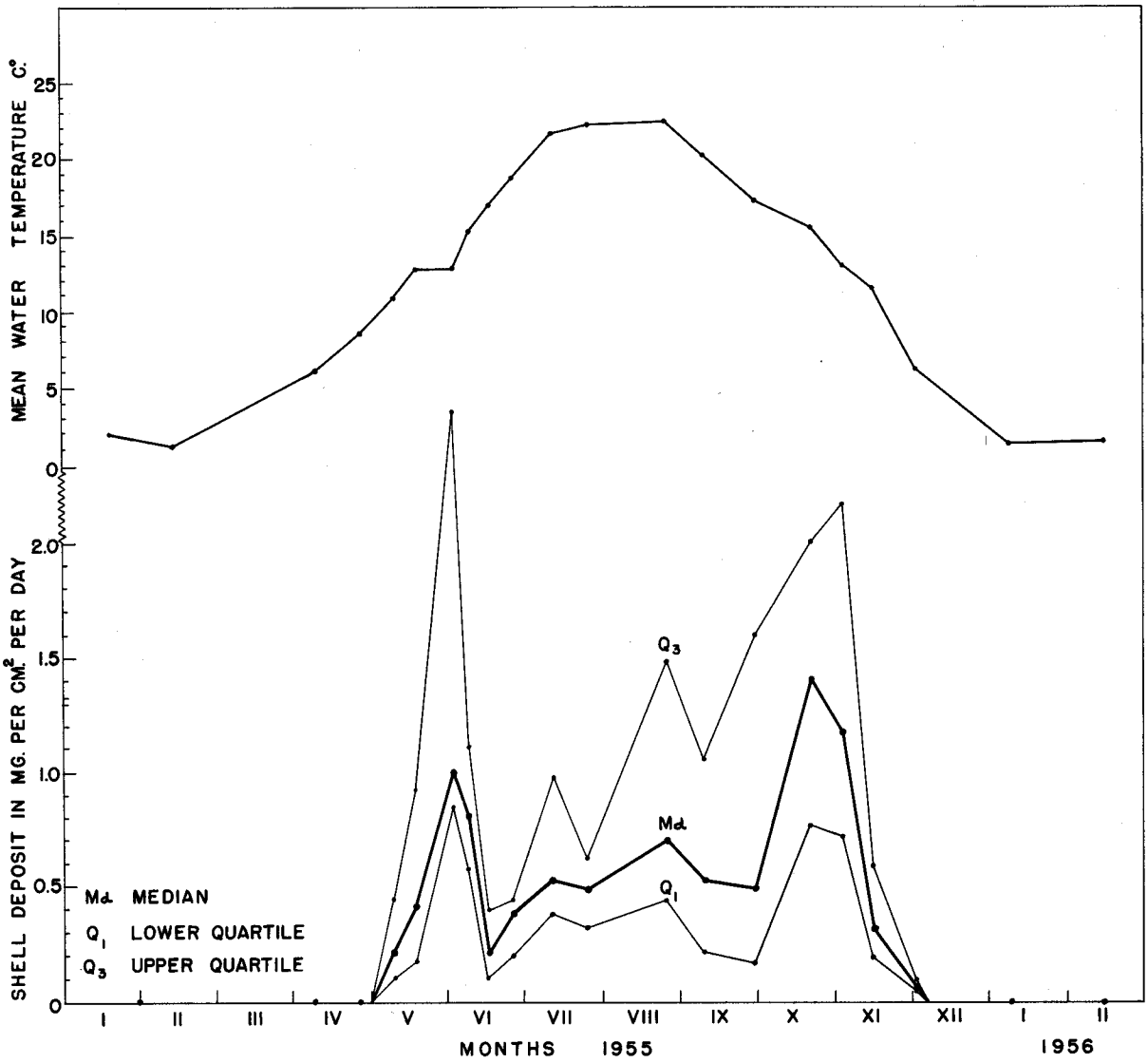

FIGURE 102.—Seasonal changes in the rate of deposition of shell material over the inner surfaces of left (lower) valves.

the area occupied by a piece of plastic, and a shell ridge was formed along the edge of the mantle, which was withdrawn a considerable distance back from its normal position. It can be deduced from these observations that injury to the mantle stimulates the shell secretion and that deposition may take place even at low temperatures when normal shell growth is inhibited. This would indicate that the enzymatic system involved in shell deposition is always present and may become active in response to pathological conditions in spite of the inhibitory effect of winter temperatures.

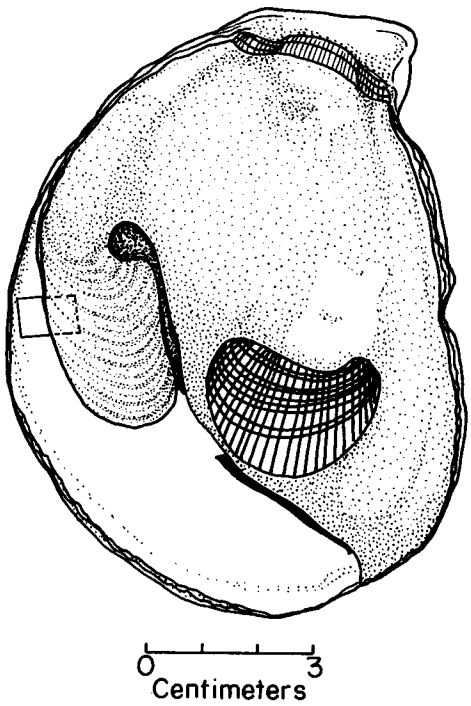

FIGURE 103.—Abnormal deposition of shell material along the edge of the mantle (black line) and over the piece of plastic quadrangle, which was completely encapsulated in a pocket of newly secreted shell. Mantle is shown by stippled area. Winter observation at Woods Hole.

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