VOLUMETRIC STUDIES OF THE FOOD AND FEEDING OF OYSTERS

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Economically considered, probably the most important direct interrelation between a marine animal and plants is that existing between the oyster and its food. We have in the United States alone an industry valued at $18,000,000 per annum, which is immediately dependent upon the supply of microscopic vegetation in our bays and estuaries, a vast food resource useless to man in its original state, but of great present and still greater potential value when transsubstantiated into the flesh of oysters, clams, and other mollusks.

Various investigations have shown that about 95 per cent of the food of the oyster consists of diatoms and that most of the remainder is composed of other equally minute plants or organisms on the more or less debatable borderland between plants and animals. The oyster obtains these microscopic organisms by drawing feeble currents of water between the open shells, straining them through the exceedingly minute orifices in its gills, and passing the filtrate by ciliary action into its mouth, which lies ensconced between two pairs of fleshy palps close to the hinge of the valves. Though the currents induced are feeble they are constant, and during the course of twenty-four hours the water thus minutely strained is many times the volume of the oyster.

It is common knowledge among oystermen and oyster growers that different localities differ markedly in their powers or capabilities for growing and fattening oysters, and the results of various researches have shown that these diversities are correlated with the amount of food available to the sessile oysters. A deficiency may be due to a natural poverty of the waters, to an overpopulation of oysters, or to an absence of currents sufficient to carry the food within reach of the feeble external currents set up by the oysters themselves. Frequently all three of these factors are found to be involved where oysters grow slowly and fail to fatten.

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Certain enthusiasts, some of whom should know better, have held forth the prospect of a time when the entire available bottom of our bays and sounds would be planted in oysters as densely as are the comparatively small areas now utilized. They fail to consider the fact that the natural fertility of the waters imposes some limit upon the production of oyster food, and that a vast increase in the oyster population, such as their imaginations contemplate, would undoubtedly exceed the limits which nature has set.

The microscopic vegetable life of our brackish bays and sounds is probably as abundant as it is capable of becoming under existing conditions. It is dependent primarily upon the quantity of certain mineral salts in solution, and is as strictly limited by the conditions as is the crop yield of a given area of land by the available salts in the soil. The soils can have their fertility artificially increased, but though experiments conducted by the author for the Bureau of ‛Fisheries have shown that the same expedient is partially successful for limited areas of inclosed water, it can never be applied to open waters, as the fertilizer would be speedily carried away. In this connection, however, it is an interesting speculation whether our coastal waters are not to-day richer in fertilizing salts than they have been in the past. The denudation of our forest lands, the erosion due to faulty agriculture, the artificial fertilizers carried away from cultivated fields during periods of heavy rainfall, and the discharge of sewage rich in organic matter have undoubtedly added much to the available fertilizing content of our coastal waters, to the advantage of their microscopic vegetation.

The question of food supply, its availability, and the quantity required for a given area planted in oysters is one of vital importance to the oyster culturist. Of the total oyster supply of the United States, about five-eighths, valued at over $10,000,000, is produced on planted beds, and the future growth of the industry is dependent upon the increase of the area of private bottoms under culture. With the extension of the planting industry to new localities and the inevitable congestion in places naturally favorable for growing and fattening oysters, the value of definite data upon this subject will be greater in the future than in the past.

Empirical methods involving actual planting to determine the suitability of a locality are expensive and often wasteful, and operators with small capital are frequently deterred from taking the risk. Even though the work on a small scale may prove successful, an increase to a large commercial basis may overtax the food supply to such an extent as to make the growth of the oysters slow and their fattening impossible. A number of cases of this kind have come to the author's attention, the most noteworthy being in Lynnhaven Bay, where the increase in the area planted, though the quantity per acre is exceedingly small, has made it almost impossible to fatten oysters properly on certain bottoms formerly satisfactory.

As the economic importance of the subject merits, it has frequently been the matter of investigation and has probably attracted more attention from biologists than has any other direct correlation between marine plants and animals. The nature of the oyster's food was long ago determined and the work of the last twenty years has been hardly more than confirmatory of that which preceded it.

Dean appears to have been the first to attempt the quantitative determination of the oyster food available in the water. He employed a chemical analysis of the water to determine the albuminoid ammonia content, assuming that the results would indicate the comparative food values of different regions.

Subsequent investigators have recognized the grave defects in this method, and, including myself, have all followed the general method of Rafter. Water specimens of definite volume, usually 1 liter, have been collected either by means of a stoppered bottle or jug, from which the cork is pulled after it has been sunk to the bottom, or by a specially designed metal cylinder constructed on essentially the same principle. The suspended matter in the specimen, a large part of which often consists of sand, mud, and débris, is then concentrated in, say, 10 cubic centimeters of water by filtration through sand or precipitation in an Erlenmeyer flask after the addition of a few drops of formalin. A definite quantity of the filtrate is then removed after agitation and the food organisms counted in a Rafter cell, the calculated number of such organisms per liter being regarded as an expression of the food value of the water.

This method has two defects, the first of which is that the water specimen is not drawn from the stratum tenanted by the oyster, but solely from a height of about 12 inches above the bottom. It would be possible to correct this defect by using a shorter, broader bottle or specimen cup, but as the water flows rather slowly into the necessarily narrow inlet, there would enter with it a considerable quantity of material stirred up when the instrument strikes the bottom. As the amount of this material would vary with the bottom, the impact, and the currents, a more serious source of error would arise and the results would become worthless.

To obviate these difficulties I have designed the type of bottle illustrated in text figures 1 to 5. It consists essentially of a brass barrel of a capacity somewhat over 1 liter, two conical valves, and a tripping device. The lower valve is fixed at a height of 2 inches above a broad base, which prevents the instrument from sinking in soft mud, but the barrel and upper valve slide freely on a central column or rod. The instrument is set by engaging the lug (F) over the inclined surface (G) of the stirrup or tripping device (CDEG), which suspends the upper valve (B) and the barrel (A) so as to leave a gap of 2 inches between the two valves and their respective seats, the stirrup being maintained in position by tension on the cord by which the instrument is lowered. By rotating the cam (H) so as to pinch the cord between it and the collar on top of the upper

valve, the instrument may be locked in the set position, but it is automatically unlocked when it is raised by the cord.

As the instrument is lowered there is a free flow of water through the barrel, so that at any given time its contents are taken from the stratum in which it
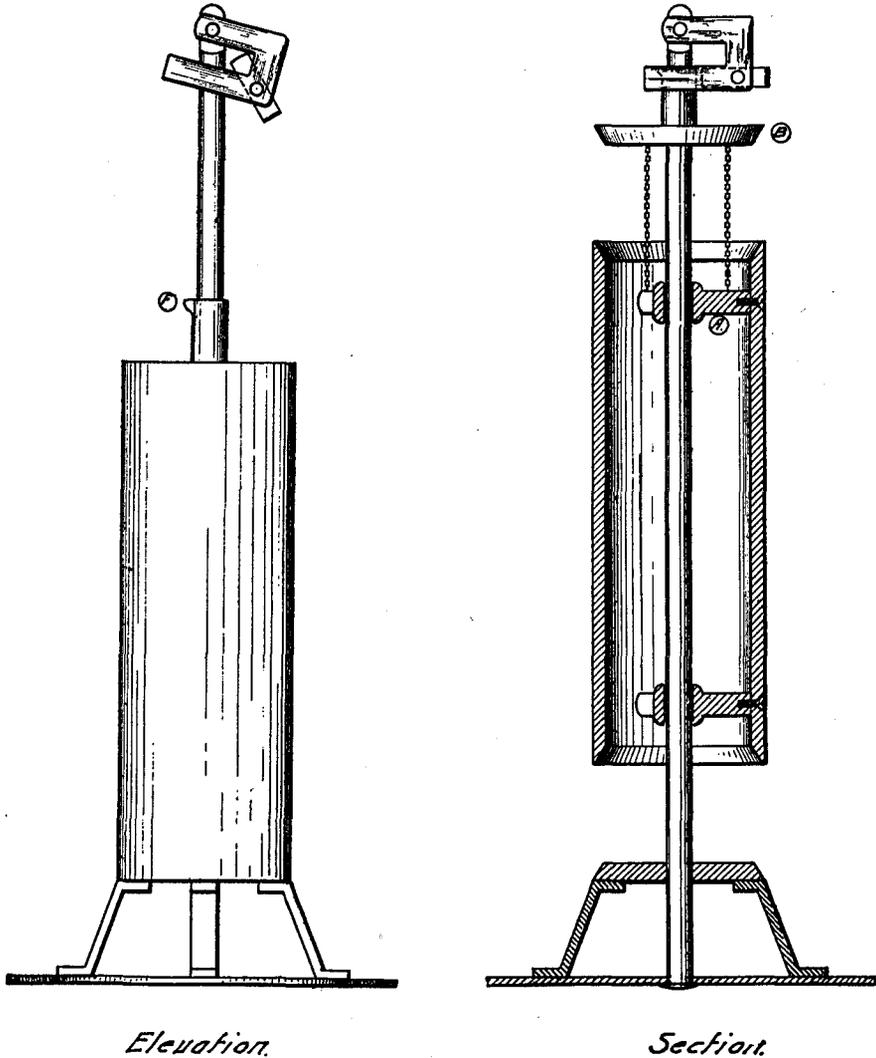

Elevation.

FIG. 1.

Water specimen cup.

Section.

FIG. 2.

rests. When bottom is touched the tension on the cord is relaxed, the tripping device instantly releases the upper valve and the barrel suspended from it, and they fall into their respective seats, inclosing a sample of water before it can be contaminated by the stirred-up bottom deposits. As the barrel is 10 inches

long, the water inclosed is a vertical column of the stratum lying between 2 inches and 12 inches above the bottom, and as the currents do not flow over the beds in horizontal strata, but roll over and over, this specimen is regarded as a fair sample of that in which the oysters are bathed.

The instrument is now used in Massachusetts, Maryland, Virginia, and Louisiana, and actual tests have shown that it takes a water specimen much cleaner and freer from mud and extraneous materials than do the instruments previously employed.

FIG. 3.—Cross section at A, figure 2.

The other defect of the old method of determining the food value of oyster-producing waters arises from the practice of using the number of diatoms or organisms per liter as the measure of their productiveness. It is well known that diatoms, which usually constitute upward of 95 per cent of the food of oysters, differ greatly in size and the species vary in comparative abundance in different regions and from season to season in the same locality. When a numerical expression is employed, it follows therefore that a multitude of small organisms may g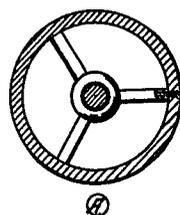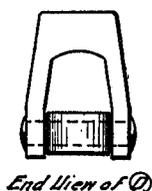ive an apparent superiority to a water specimen as compared with another containing a smaller number of a species of vastly larger size and much greater aggregate volume, and my own experience has shown cases where this error amounted to nearly 400 per cent. The method is attended with grave error as applied to even limited regions and is wholly untrustworthy as a basis of comparison between widely separated localities. It gives seemingly quantitative results, but these, not being volumetric, are deceptive.

Direct volumetric determination can not be made on account of the presence

Top View of E

End View of D

Bottom View of C.

FIG. 4.   FIG. 5.

Details of tripping device of water specimen cup in figures 1 and 2.

of considerable volumes of sand, mud, and extraneous débris in the filtrate, these materials greatly exceeding the food organisms in volume. Grave attempted to overcome the difficulty by listing the food organisms by species,

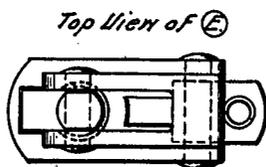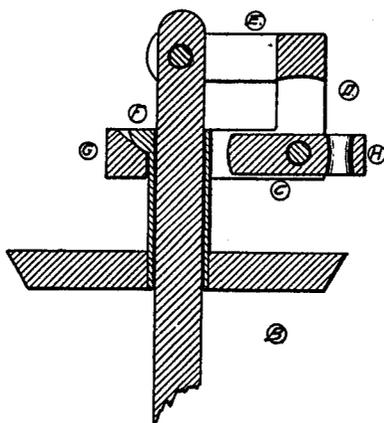but this arrangement, though an advance on previous work, is not capable of comparative use, and any error in identification, not unlikely to occur with persons not diatomists, would be misleading to future investigators.

To overcome these difficulties I have for several years used the following indirect method, which has given satisfactory results. The diatoms and other food organisms are collected and counted, as before indicated, and are listed by species, although their identification by their correct names is not essential. Careful outline camera lucida drawings are made of the zonal and valvular aspects of a number of specimens of each species, and their cubic contents are calculated by geometric methods from planimeter measurements of the draw- ings. The average of a number of such calculations will give the average rela- tion of the volume to the product of length, breadth, and thickness of the species. Using this relation and the average of a number of micrometer meas- urements of the specimens themselves, a simple calculation will furnish an approximately correct expression of the average volume of the species in the region under investigation. If these volumes be employed as multipliers into the numbers of the respective species, determined from the counts in the Rafter cell, we have an approximately correct volumetric expression for the amount of the food content of each specimen of water. As the most convenient unit of measurement I have adopted Van Heurck's "c. d. m." (0.01 millimeter), the unit of volume being the cube of this, "cu. c. d. m." (0.000,001 cubic milli- meter). The following is an illustration of the data required for each species:

Synedra commutata (Matagorda Bay); average length, 4.7 c. d. m.; breadth, 0.5 c. d. m.; thickness, 0.5 c. d. m.; volume = 0.6 (l × b × t) = 0.7 cu. c. d. m.

This method sounds elaborate in its narration, but has not shown itself to be cumbersome in practice, and, moreover, it appears to be the only method so far proposed which gives data of real value. The results are directly compar- able with those obtained in other waters or with those reached in the same waters at different seasons. Five hundred or 600 determinations have been made in the past two years, and, for reasons shown below, the procedure gen- erally was found to require but little more labor than the older misleading and less accurate method.

In oyster investigations it is customary to take a large number of water specimens at adjacent stations, and as the nature of the food content of each varies in quantity rather than in the character of the organisms, the measure- ments of eight or ten species will apply to all water samples from the locality. Only those organisms need be measured which examinations of the stomach contents of the oysters show to be important as food. The counts have to be

made, whatever method be employed. In Matagorda Bay, where the present method was first used, about 150 specimens of water were examined and the additional time required was not over 10 per cent. The following table shows the results and the manner of tabulation, as well as the differences in results attained by the numerical and the volumetric methods:

FOOD VALUE OF WATERS OF MATAGORDA BAY.[a]

[Roman figures indicate volume of organisms, or food value. Bold-face figures indicate number of organisms.]

No.	Species.	A. Between Sand and High Mound signals.	B. Between High Mound and Lake signals.	C. Between Mad Island, West, and Lake signals.	D. Between Shell Island and Mad Island reefs.	E. Between Dog Island and Shell Island reefs.	F. Between Dog Island and Pavilion signal.
1	Coscinodiscus crassus	**500**	---------	**917**	**250**	**100**	**500**
2	lineatus	121,805 / **8,488**	141,470 / **4,042**	142,905 / **4,088**	183,750 / **5,250**	141,750 / **4,050**	122,500 / **8,500**
3	excentricus	10,500 / **1,750**	17,502 / **2,917**	17,760 / **2,960**	12,000 / **2,000**	5,550 / **925**	12,000 / **2,000**
4	Navicula didyma	4,125 / **875**	6,413 / **583**	9,625 / **875**	11,000 / **1,000**	---------	---------
5	elliptica	1,250 / **125**	1,660 / **166**	4,160 / **416**	2,500 / **250**	1,000 / **100**	5,000 / **500**
6	arenaria	937 / **875**	1,145 / **458**	1,688 / **675**	3,750 / **1,500**	250 / **100**	1,250 / **500**
7	Amphora ovalis	2,500 / **500**	---------	625 / **125**	---------	500 / **100**	---------
8	Pleurosigma fasciola	**250**	---------	**125**	---------	**425**	---------
9	obscurum	---------	---------	**125**	---------	---------	---------
10	intermedium	**125**	---------	---------	---------	**225**	**500**
11	tenuissimum	**875**	**292**	**125**	**1,250**	**850**	**500**
12	angulata major	---------	---------	---------	---------	---------	**250**
13	Synedra commutata	5,600 / **8,000**	6,650 / **9,500**	9,100 / **13,000**	25,550 / **36,500**	8,155 / **11,650**	1,400 / **2,000**
14	sp	1,750 / **500**	1,225 / **833**	3,790 / **1,083**	1,750 / **500**	2,275 / **650**	875 / **250**
15	Melosira distans	52,500 / **2,625**	68,340 / **3,417**	73,340 / **3,667**	35,000 / **1,750**	18,160 / **908**	20,000 / **1,000**
16	sp	**250**	---------	**675**	---------	---------	**250**
17	Pyxilla sp	---------	---------	---------	---------	**200**	---------
18	Other diatoms	**1,250**	**500**	**292**	**250**	**800**	**1,000**
19	Prorocentrum micans	18,375 / **2,825**	29,456 / **4,208**	8,750 / **1,250**	8,750 / **1,250**	---------	3,500 / **500**
	Total volume, or food value	219,342	273,861	271,743	284,050	177,640	156,525
	Total number of organisms	**23,108**	**26,416**	**30,898**	**51,750**	**20,083**	**18,250**
	Prairie shore	208,527	287,737	239,024	259,875	159,937	89,925
	Middle of bay	259,774	345,200	267,000	274,350	177,900	254,925
	Peninsula shore	190,049	188,450	314,412	317,625	193,770	153,725

[a] From Survey of Oyster Bottoms in Matagorda Bay, Texas, by H. F. Moore. Bureau of Fisheries Document 610.

FOOD VALUE OF WATERS OF MATAGORDA BAY—Continued.

No.	Species.	G. Between Pavilion and Three-mile signals.	H. Between Three-mile and Seven-mile signals.	I. Between Seven-mile and Grass signals.	J. Between Grass and Dressing Point signals.	K. Live Oak Bay.	L. Above Dressing Point.
1	Coscinodiscus crassus	375	292	792	200	----------	----------
2	lineatus	135,625 / 3,875	163,310 / 4,666	198,310 / 5,666	118,720 / 3,892	157,500 / 4,500	140,000 / 4,000
3	excentricus	17,250 / 2,875	13,248 / 2,208	16,002 / 2,667	9,150 / 1,525	----------	3,498 / 583
4	Navicula didyma	-------- / --------	2,750 / 250	3,212 / 292	2,013 / 188	----------	4,587 / 417
5	elliptica	2,500 / 250	4,170 / 417	12,500 / 1,250	----------	----------	2,500 / 250
6	arenaria	3,438 / 1,375	730 / 292	1,458 / 583	2,500 / 1,000	3,750 / 1,500	5,420 / 2,167
7	Amphora ovalis	625 / 125	1,250 / 250	----------	830 / 166	3,750 / 750	1,665 / 833
8	Pleurosigma fasciola	----------	166	166	----------	----------	166
9	obscurum	----------	----------	125	----------	750	250
10	intermedium	----------	----------	166	492	----------	583
11	tenuissimum	1,500	750	166	888	750	883
12	angulata major	125	166	167	----------	----------	----------
13	Synedra commutata	962 / 1,875	1,517 / 2,167	642 / 917	1,686 / 2,408	1,575 / 2,250	1,166 / 1,666
14	sp	5,250 / 1,500	1,793 / 541	581 / 166	4,812 / 1,375	5,250 / 1,500	11,081 / 3,166
15	Melosira distans	10,000 / 500	----------	20,000 / 1,000	13,500 / 675	----------	----------
16	sp	250	542	167	208	----------	833
17	Pyxilla sp	250	167	125	100	750	----------
18	Other diatoms	----------	125	----------	517	2,250	500
19	Prorocentrum micans	2,625 / 875	5,832 / 883	7,875 / 1,125	14,581 / 2,088	5,250 / 750	11,669 / 1,667
	Total volume, or food value	178,275	194,600	260,580	167,792	177,075	181,586
	Total number of organisms	14,750	13,832	15,540	15,207	15,750	16,964
	Prairie shore	151,050	162,900	191,700	182,470	----------	----------
	Middle of bay	186,599	182,925	357,650	152,525	----------	----------
	Peninsula shore	189,675	238,349	232,250	168,674	----------	----------

In the study of the food actually consumed by the oyster, it has been regarded, heretofore, as sufficient to remove the stomach contents by means of a pipette inserted in the mouth or through an incision in the body walls. This method extracts but an indeterminate portion of the undigested food in the stomach, a considerable proportion remaining in the folds of that organ and in the wide openings of the hepatic ducts, and it removes practically nothing of the intestinal contents. For quantitative work the method is very defective, and it is useless as a basis for those studies of food consumption and the rate of feeding which must have an important place in the oyster investigations of the future.

In order to remove the entire contents of the alimentary canal, I am now using the apparatus illustrated in figure 6, which is essentially a combination of stomach pump and enema, effectually irrigating the entire digestive tube. It consists of a reservoir (A), connected by a flexible siphon tube with a glass canula (B) ligated in the rectum, and of an aspirator (C) connected through the medium of a vial or test tube (D) with another canula (E) inserted in the mouth.

The canulas are made of glass tubing, and their tips are held for a moment in a Bunsen flame to produce a burr, which prevents their slipping from the ligature.

The operation of the apparatus is as follows: The reservoir (A) is lowered until the water surface is about level with the stage F. The oyster is carefully
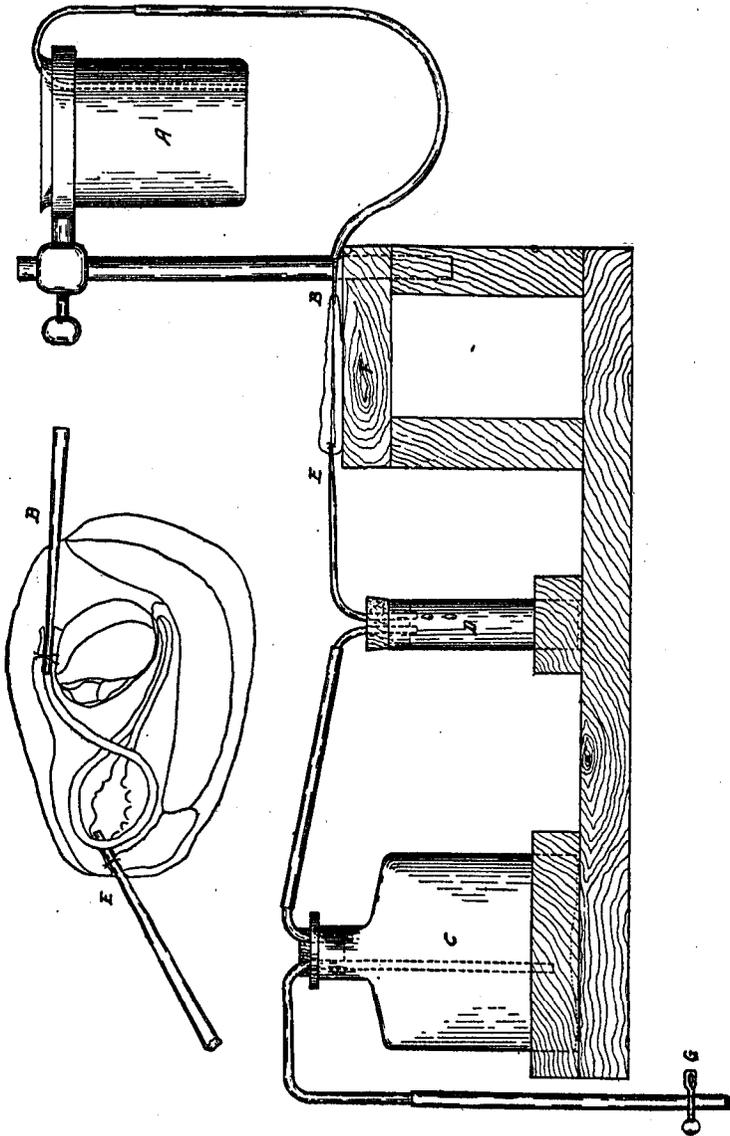

FIG. 6.—Apparatus for extracting contents of alimentary tract of oysters.

removed from its shell and placed on the stage, its rectum is slit for a distance of about one-eighth inch from the anus to facilitate the insertion of the canula, which is ligated in position by means of a needle and thread. The oral canula, which has a wider opening, is inserted in the mouth and ligated by means of a

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needle and thread carried through the tissues. The pinch cock (G) is then released on the siphon of the aspirator, which exhausts the air from the vial or tube (D), draws out some of the stomach contents, and causes a slight collapse of the walls of the alimentary canal. The reservoir (A) is then raised until a flow of water is established through the rectum with a resultant slight turgescence of the intestine. There is thus established a current of water running into the rectum, through the intestine, and out of the mouth, carrying with it eventually the entire alimentary contents, which collect in the tube (D). To facilitate the dislodgment of the more or less impacted fæces, the intestine is occasionally gently tapped with the handle of a scalpel or dissecting needle. With one apparatus about six oysters per hour can be opened and operated on, and dissection shows the entire alimentary canal to be freed of contents. The contents of the tube are treated with a few drops of preservative and are concentrated, by precipitation and the removal of the supernatent water, to a standard volume of 5 or 10 cubic centimeters, after which the organisms are counted by the Rafter method and the volume calculated as previously described. It is usual to take the average of five specimens as the measure of the food content of a given lot of oysters.

For studying the rates of feeding of oysters under different environmental conditions, I have recently used the following experimental methods, which have been found effective:

Pieces of sheet rubber (dentists' " rubber dam ") about 8 inches square, called " aprons, " are prepared by cutting out of the middle semicircular " windows " of about 2 inches radius, over which pieces of no. 25 bolting cloth are cemented with a thick ethereal solution of rubber. A slit about 5 inches long is cut in the rubber parallel to and about ½ inch below the long diameter of the window.

A number of oysters, about 5 inches long, are then thoroughly scrubbed with a brush, washed in fresh water, the shells covered with a thin layer of Portland cement so as to fill all cavities and smooth irregularities in their surfaces, and thoroughly dried in the air.

Each is then inserted in the slit in the middle of an "apron" in such position that the edges of the slit approximate the line running from the dorsal side of the hinge to the point of insertion of the gill at the edge of the mantle. The edges of the slit are then pasted to the shell with rubber solution, care being taken to provide a small fold in the apron at the lip of the shell, to carry it around the dorsal side of the hinge so as not to interfere with the opening of the valves, and to see that there are no gaps between the shell and the rubber at any point.

Security of adhesion can be promoted by first giving the proper parts of the shell several coats of thin rubber solution, the final cementing being performed with a thick paste made by squeezing the ether-softened crude rubber through cheese cloth and reducing it to the desired consistency by shaking it in ether.

The oysters prepared in accordance with the foregoing description are then placed for about three days in filtered sea water, renewed morning and night, at the end of which time they are practically purged of food and usually gaping with hunger. The intestinal contents of five are then determined by means of the apparatus and methods already described.

The remaining oysters are now placed each in a 6-inch Petri dish, the shells resting on a wire support to raise them above the bottom and lying so that the deep valve is downward and in such position that the cloacal or excurrent chamber of the oyster lies below the apron and the oral or incurrent chamber above it. The "apron" is then confined to the sides of the dish by means of a rubber band or cord, and a layer of sand is placed over the window and the surrounding rubber to serve as a filter, as shown in figure 4. A piece of cheese cloth tied over the sand will prevent its being washed away by currents or disturbed by inquisitive fishes and crabs.

When the oysters thus prepared are transferred to their natural environment they are as free to open their valves and feed as if they had never been removed from their beds; the oral chamber is in unobstructed communication with outside waters while the excurrent chamber discharges into the Petri dish, where the fæces are retained while the expelled water passes through the filter. Oysters prepared as described have been kept under close observation under otherwise natural conditions and appeared to feed as freely and normally as neighboring specimens that had never been disturbed. The fæces drop into the dish in a little heap of demicylinders, while extraneous matter was excluded by the apron and filter.

At the end of three and six days, respectively, lots of five of these oysters are taken up, their intestinal contents removed by the method already described and added to the fæces collected from the dishes. As about 95 per cent of the food consists of diatoms whose tests pass unchanged through the alimentary canal, it is evident that by calculating the volume of the combined food organisms of the fæces and alimentary canals by the methods described and deducting the volume of the residual intestinal contents, as determined from the lot of five starved check oysters, we can arrive at a volumetric expression of the average rate of feeding. Determinations of the diatomaceous content of the surrounding water made at intervals during the experiment supply the data for the necessary correction to be applied for dead diatom frustules ingested by the oysters under experiment.

It is perhaps not necessary to use starved oysters for these experiments, but they have been used in order to insure the prompt commencement of feeding as soon as returned to the water, unstarved specimens sometimes "sulking" after repeated handling. A check upon possible error due to any abnormal

appetite at the beginning of the experiment is provided by comparison of the results obtained in the two lots fed for different periods.

My first experiments were with bolting cloth aprons, but it was found difficult to keep them covered with sand, especially close to the edges of the dish, and also to secure good adhesion between the shell and the apron. These defects in some cases permitted the infiltration of fine mud and other extraneous matter. Such difficulties have been obviated by the use of sheet-rubber "aprons" as described. The latter have been in use for four or five months and have proved satisfactory, but there has not been time for the tabulation of the quantitative results.

It is believed that the apparatus and methods of research above described furnish for the first time efficient instruments for strictly quantitative studies of the food and feeding of oysters and similar mollusca, and they also furnish data for determining the amount of water filtered through the gills. In addition to the scientific interest attaching to the studies it is believed that they will lay the foundation for valuable economic data. As is well known to those who have made a study of the oyster fisheries, much time and money is lost in futile attempts to grow oysters in localities which eventually prove unsuitable. In many cases these failures are due to a paucity of food, the oysters failing to fatten. If there could be determined the minimum food unit requisite under varying conditions of bottom, currents, and density of oyster population, the waste of time, money, and effort in useless planting could be largely prevented.

As a preliminary to the determination of such unit, it is necessary to determine with accuracy the relations existing between the oysters and the plants which constitute their diet. We must know the exact relation existing between the food consumed by oysters which are rapidly growing and fattening and by those which are not. We must determine how much more food an oyster will consume in strong currents than when living in sluggish waters equally rich per unit of volume, and it will be necessary to learn also the water food content required to supply the minimum requisite under varying conditions of current.

The experiments already conducted have shown that all of these data can be obtained with considerable accuracy by the means above described, and by conducting further research in regions such as Lynnhaven Bay, where the quantity of oysters on the bottom over considerable areas can be approximately arrived at, they can be given concrete application. The formulation of the desired unit will require much patient research and observation, the study of currents, of the behavior of oysters under various natural conditions, and possibly of the reproductive activity of diatoms and other food organisms, but it is believed that we are now in possession of instruments which warrant an attempt at the solution of the problem.

Oyster with filter apron for study of feeding.