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Effects of Turbidity on Some Larval and Adult Bivalves

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Abstract

The article is devoted to an analysis of the experiments on effects of turbidity upon larval and adult bivalves. Studies of the American oyster, **Crassostrea virginica,** the larvae of the same species, and of **Venus mercenaria** are emphasized although several other species are also considered. Turbidity was caused by several substances, including natural silt and the clay-like substance, kaolin. Exposures of adult mollusks lasted from three hours to several weeks. Larvae of oysters and clams were grown in different concentrations of turbidity for periods as long as two weeks. Very small quantities of silt, etc., sometimes stimulated normal activities of adult and larval mollusks. This may be due to absorption by particles of suspended materials of toxic substances present in the water and to slight mechanical stimulation of the gills of adults. However, concentrations as small as 0.1 of one gram per liter of water significantly reduced the rate of water pumping and strongly affected the character of shell movements of the adults. Different turbidity-creating substances, when present in the water in the same concentrations, affected the experimental animals in a different degree. Different species of mollusks, their eggs and larvae were affected to different degrees by the same concentrations of the same turbidity-creating substances. Results suggested extension of the studies to sizes and shapes of suspended particles and to determining whether effects are mechanical or chemical. Data indicated that lamellibranchs feed most effectively in relatively clear water.

INTRODUCTION

SINCE OYSTERS, CLAMS, AND MUSSELS are widely distributed and constitute important fisheries, various aspects of their biology have been extensively studied. Baughman's (1947) bibliography of oysters, alone, contains references to thousands of articles devoted to the biology and ecology of these mollusks. Since the appearance of Baughman's review, many new articles have been written about oysters, principally *Crassostrea virginica* and related forms, including the hard shell clam, *Venus mercenaria,* and the common edible mussel, *Mytilus edulis.*

A study of the literature shows that efforts directed toward understanding the biology of these bivalves have not been equally distributed but confined, as a rule, to selected fields which, at one time or another, appeared to be in vogue among biologists. For example, while salinity and temperature and their effects upon bivalves have been described and discussed by many authors, studies of the effects of other environmental factors, such as turbidity, have been virtually neglected. This lack of interest has persisted even though many important bivalves are inhabitants of shallow waters of estuarine regions, where turbid conditions are often created by river discharge, wind action, or dredging operations.

Obviously, it is of interest to biologists, shellfish growers, and administrators to know how turbidity affects various mollusks and their larvae. This knowledge is also needed to evaluate the numerous complaints that are brought against either the U.S. Corps of Army Engineers or dredging companies engaged in operations which result in an abnormally high turbidity of the water over shellfish beds. If dredging is carried on during the summer, when mollusks are propagating, and setting is a failure, dredgers are accused of, and often sued for, creating unfavorable conditions for the existence of bivalve larvae. During these lawsuits, and similar legal proceedings, federal and state biologists are often requested to testify or act as experts. Unfortunately, since there are few experimental data on the effects of turbidity on bivalves of different species and ages, people who act as experts have little material on which to base their opinions. This is especially true in relation to larvae, which were assumed to be extremely sensitive to abnormal turbidity. Because until recently no dependable method for growing bivalve larvae was known, obviously, no systematic studies of the effects of environmental factors upon these organisms could be conducted. Fortunately, such a method has been developed and is now widely used in many laboratories and several commercial shellfish hatcheries (Loosanoff, 1945, 1954; Loosanoff and Davis, 1950).

The purpose of this article is to review the studies on effects of turbidity on larval and adult bivalves made during recent years. Before proceeding with a discussion of the experimental results it may be advantageous to mention that the rate of water propulsion in an adult bivalve or, as we call it, the rate of water pumping, a criterion of physiological activity, has been determined by different methods and under different conditions for a number of species, especially oysters. These studies were reviewed recently, at considerable length, by Jørgensen (1955, 1960). Because of these excellent reviews it is not necessary to discuss again the various aspects of this broad field. It will be sufficient to mention, for those who are not too familiar with the anatomy of bivalves, the contributions of Kellogg (1915), Yonge (1928) and Nelson (1938), which describe the feeding and water propulsion organs of these mollusks. We may also refer to the studies on the behavior of adult oysters, *C. virginica,* exposed to different concentrations of unicellular algae, including *Chlorella* sp., *Nitzschia closterium,* and *Prorocentrum triangulatum,* which showed that these mollusks fed most efficiently when the numbers of food cells were relatively small (Loosanoff and Engle, 1947) or when the water contained little suspended material (Loosanoff and Tommers, 1948). This point of view was in agreement with the theoretical deductions of Kellogg (1915) and Yonge (1928).

On the other hand, Lunz (1938), in his studies of the gross effects of dredging upon oysters in South Carolina waters, came to the conclusion that these operations were not injurious to oysters because he could establish no correlation between the condition of the oyster meats and the turbidity caused by dredging. Moreover, he maintained that dredging operations, regardless of the considerable turbidity that they created, did not unfavorably affect the spawning of oysters or setting of their larvae. In other words, according to Lunz, oysters in the areas where the dredging was carried on, remained practically undisturbed, even though the water was made quite turbid.

Considering the discrepancy between Lunz' conclusions and ours, it was thought desirable to verify at least some aspects of the question in dispute by designing and executing a series of critical experiments which could show convincingly the extent of the effects of turbidity-creating substances upon the behavior of some bivalves.

METHODS

The oysters used in the experiments were selected for their uniformity. They were about four years old and measured between 90 and 95 mm in length and 60 to 68 mm in width. Their average volume was approximately 95 cc. Before being used the oysters underwent a period of observation to ascertain that no sick individuals were in the group. Furthermore, to be certain that the oysters were not unduly disturbed or handled too much immediately prior to being used in the experiments, the rubber aprons employed in determining their rate of water pumping were attached to their shells several weeks prior to the beginning of the observations.

The methods employed in these studies were virtually the same as those in our observations on effects of different concentrations of microorganisms upon feeding activities of adult oysters (Loosanoff and Engle, 1947). During these experiments shell movements and rate of water pumping by oysters, under normal conditions and after the addition of different quantities of turbidity-creating substances, were recorded on kymographs. Considering the importance of observing undisturbed mollusks, so strongly advocated by MacGinitie (1941), the oysters were placed in the running water of the apparatus chamber at least 12 hours before an experiment was begun. At that time the only change was the starting of the kymograph, which in no way reflected on or was felt by the oysters because the kymograph was located on a stand not connected with the oyster chamber foundation and, furthermore, was supported by a thick rubber mat to eliminate disturbing vibrations.

After the oysters had been in flowing sea water for several hours and their normal pattern of behavior had been recorded, turbid water was introduced into the chamber. This, again, was accomplished merely by manipulating a series of cocks without disturbing the oysters. After the experimental animals had been in the turbid water for the required time, regular sea water was substituted for the turbid water, again by merely opening and turning off cocks.

During the studies the temperature of the water ranged between 17.0° and 23.0°C, the salinity was steady near 27.0 parts per thousand and the pH of silt suspensions and of sea water ranged from 7.9 to 8.1. Provisions were made so that the temperatures of the turbid and regular sea water did not vary from each other by more than 0.5°C. Since presence of silt in water can considerably reduce the quantity of dissolved oxygen, the turbid water was always vigorously aerated. This method was also helpful to drive out unwanted gases that may form in the water because of the addition of silt and other substances.

The materials used to make sea water turbid were fine silt collected from the tidal flats of Milford Harbor; kaolin (aluminum silicate), a clay-like substance; powdered chalk; calcium carbonate; and Fuller's earth (Loosanof and Tommers, 1948). The latter, however, was used in only a few experiments. All these materials are sometimes found under natural conditions in estuarine waters. Silt, a complex mixture of inorganic and organic materials, is very common, of course, and is usually present in various quantities in sea water. Heavy rains resulting in a heavy river discharge, dredging, and also boat traffic may noticeably increase quantities of suspended silt. Kaolin, as well as other clay-like substances, is often found in various mixtures of soils that form foundations of oyster beds. Large quantities of clay are also brought down by rivers. Since oyster shells are made largely of calcium carbonate, minute particles of this substance can often be found suspended in the water over oyster beds. Fuller's earth, which consists chiefly of shells of small diatoms, is also a natural material.

The silt used in the experiments was prepared as follows: Soft mud collected from the upper layer of the tidal flats of Milford Harbor was agitated in river water. The heaviest particles were permitted to settle and then discarded, while the material still in suspension was filtered through a No. 20 plankton net. This fine suspension was kept in glass vessels until it settled to the bottom, a procedure which sometimes requires several days. The water was then decanted and the silt dried in the sun in large enamel trays. The dry material was later pulverized and placed into air-tight jars. Before using the material it was resuspended in the water, in the form of minute particles, by prolonged, vigorous stirring.

RESULTS

Silt was the first material to be studied. Even when such a small quantity of silt as 0.1 g/liter was present, the behavior of the adult oysters was noticeably affected (Figure 1). For the group as a whole, the average reduction in the

FIGURE 1. Kymograph record of shell movements (1st line) and rate of pumping (2nd line) of an oyster kept for the first three hours in normal sea water and then exposed to turbid water containing 0.1 g/liter of silt. Each vertical mark of the second line designates the discharge of 278 cc of water pumped by the oyster.

rate of pumping was 57 per cent and in more severe cases the decrease was nearly 90 per cent (Table 1). In one or two instances, however, the oysters appeared to be stimulated and pumped faster. Even at this low concentration of silt the type of shell movement was changed indicating that the oysters were not acting normally.

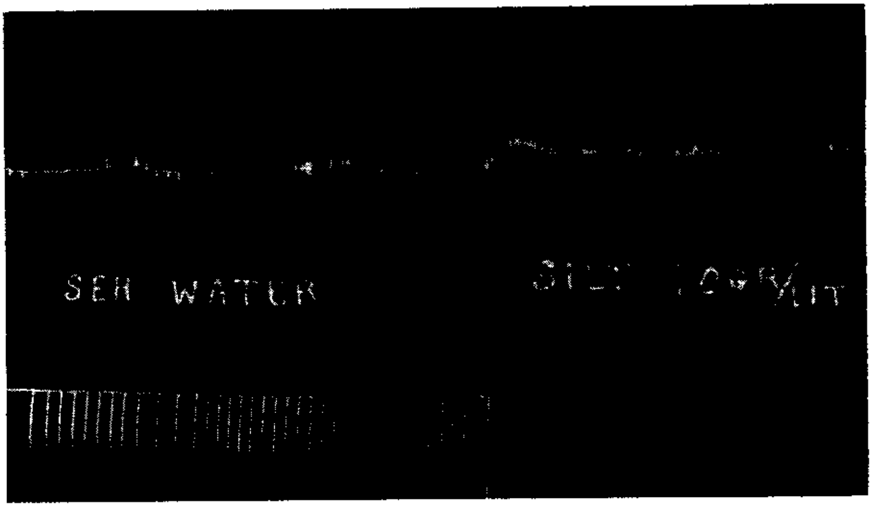

FIGURE 2. Kymograph record showing shell movements (1st line) and rate of pumping (2nd line) of an oyster subjected to sea water and then to turbid water containing 1.0 g/liter of silt. Each vertical mark on the second line designates the discharge of 237 cc of water pumped by the oyster.

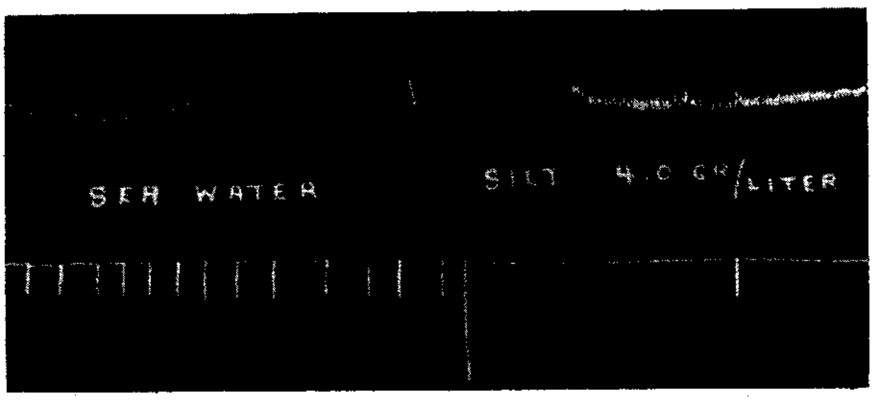

FIGURE 3. Kymograph record of shell movements (1st line) and rate of pumping (2nd line) of an oyster exposed to normal sea water and then to turbid water containing 4.0 g/liter of silt. Each vertical mark of the second line designates the discharge of 272 cc of water pumped by the oyster.

TABLE 1

EFFECTS OF DIFFERENT CONCENTRATIONS OF TURBIDITY-CREATING SUBSTANCES ON PUMPING RATES OF OYSTERS. RATE OF PUMPING IN SEA WATER AT THE BEGINNING OF THE EXPERIMENTS WAS TAKEN AS 100 PER CENT.

Substance	Concentration g/liter	Number of Oysters	Range of Change in %	Average Reduction in %
Silt	0.1	22	+18 to — 87	57.0
"	0.25	21	—12 to — 92	74.5
"	0.5	16	+15 to —100	68.5
"	1.0	22	—18 to —100	81.0
"	2.0	17	—41 to —100	85.0
"	3.0	10	—83 to —100	93.7
"	4.0	18	—62 to —100	94.0
Kaolin	0.1	24	+16 to — 77	46.0
"	0.25	22	—35 to — 95	68.0
"	0.5	25	+10 to — 93	68.5
"	1.0	16	—14 to —100	71.0
"	2.0	15	—66 to —100	78.0
"	4.0	16	—27 to — 95	85.0
Chalk	0.1	18	—12 to — 59	38.0
"	0.5	18	—44 to — 86	76.0
"	2.0	18	—68 to — 94	87.0
"	4.0	19	—79 to — 94	89.0
Fuller's Earth	0.5	8	—32 to — 80	60.0

Greater concentrations of silt resulted in stronger effects on both shell movements and rate of water pumping (Table 1, Figure 2). In such heavy concentrations as 3.0 and 4.0 g/liter the average reduction in rate of pumping was over 90 per cent (Figure 3).

Although such large quantities of silt seldom occur in nature they may, nevertheless, be created during a period of unusually heavy floods or occur, and sometimes persist for weeks or months, within areas where extensive dredging is carried on, especially if the methods employed are such that large quantities of disturbed bottom material are allowed to escape into the water.

In turbid waters the oysters formed and discharged large quantities of silt-containing pseudo feces. Stomach examinations, however, showed that not all of the silt was rejected in this way; some was ingested, together with large quantities of mucus that was formed by the gills. In some instances, although the shells remained open and moving, the oysters did not pump. Occasionally, especially in heavier concentrations of silt, the oysters closed their shells entirely for extended periods. In long-term experiments not discussed in this paper oysters sometimes remained closed for a period of several weeks, opening their shells slightly from time to time, as if testing the water, and then closing the shells again without resuming pumping.

The shell movements of oysters kept in turbid waters were clearly associated with frequent ejection of large quantities of silt and mucus accumulating on the gills and palps. These movements closely resembled those of oysters which were kept in heavy concentrations of live microorganisms, such as *Chlorella, Nitzschia,* or commercial yeast (Loosanoff and Engle, 1947). Thus, the results of these two series of studies showed a strong similarity in the behavior of oysters in turbid waters regardless of whether the turbidity was caused by a large number of live microorganisms or merely common silt.

This similarity was even more strongly emphasized by observations that in both series of experiments, when the flow of silt or plankton-laden water was substituted with regular sea water, the oysters quickly recovered and both the rate of pumping and shell movements returned to normal (Figure 4). The behavior of oysters during the recovery period resembled the so-called "cleansing reaction" which we noted in the above-mentioned studies on feeding of oysters when large quantities of phytoplankton cells were present in the water. The consistency of our results, therefore, strongly supports the contention that lamellibranchs, such as oysters and clams, feed most efficiently in relatively clear water. This contention remains valid even though Yonge (1948) showed that some bivalves, such as *Spisula subtruncata*, are provided with special anatomical adaptations to live in silty environment. These forms, therefore, may not be regarded as strictly clear water inhabitants but, nevertheless, it has not been disproven experimentally that they, too, feed more effectively in clearer waters.

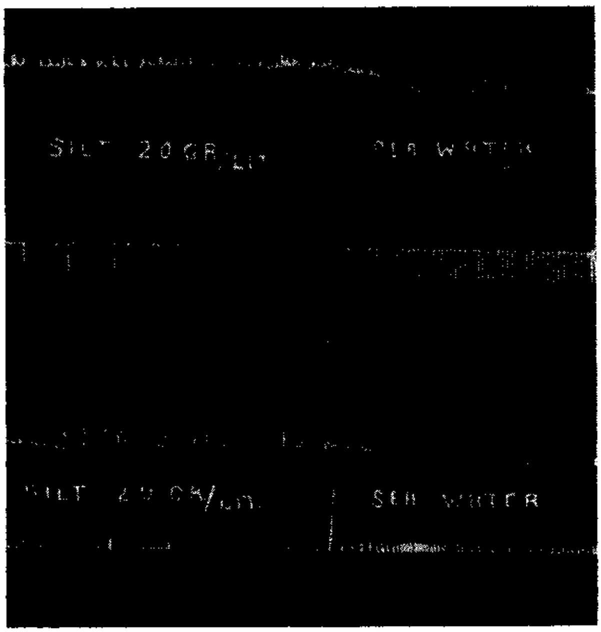

FIGURE 4. Kymograph record showing shell movements (1st & 3rd lines) and rates of pumping (2nd & 4th lines) of two oysters exposed to turbid water containing 2.0 g/liter of silt and then to normal sea water. Each vertical mark on the 2nd line designates the discharge of 244 cc of water pumped by one oyster, while each mark on the 4th line shows the discharge of 251 cc of water pumped by the second oyster.

Another series of experiments was designed to determine whether a gradual, rather than a sudden increase in turbidity is better tolerated by oysters. As usual, the oysters were kept in running sea water until they opened their shells and began pumping. After the normal pattern of each oyster's

FIGURE 5. Kymograph record showing shell movements (1st line) and rate of pumping (2nd line) of an oyster exposed to gradually increasing concentrations of silt ranging from 0.1 g/liter to 0.5 g/liter. The oyster remained in each concentration for 2 hours. Each vertical mark on the second line designates the discharge of 250 cc of water pumped by the oyster.

behavior was established they were exposed to a concentration of 0.1 g/liter of sea water. Again, regardless of the low silt concentration, the oysters showed, by the change in their shell movements and reduction in rate of pumping, that they were unfavorably affected (Figure 5). After two hours the concentration of silt was increased to 0.25 g/liter and, after an equal period of time, to 0.5 gram. Under these conditions the rate of pumping decreased progressively with each increase in the concentration of silt and some oysters showed a typical "fighting" type of shell movement, indicating that they were expelling feces. After exposure to a concentration of 0.5 gram of silt the sea water was turned on to replace the turbid water. Within a few minutes all oysters resumed active pumping at a significantly faster rate.

In such stronger concentrations of silt as 1.0, 2.0, 3.0, and 4.0 g/liter, in each of which the oysters remained for two hours, they were strongly affected but, nevertheless, even in the heaviest concentration a few oysters continued to pump some water. However, a comparison of the rates of pumping recorded during the initial experiments with those in which the turbidity was increased gradually failed to show that because of the gradual increase in turbidity the rate of pumping was more normal.

Another experimental approach consisted of observing oysters when they were exposed to silt for relatively long periods, extending for 48 hours. The concentrations used were 1.0, 2.0, 3.0, and 4.0 g/liter. Regardless of heavy concentrations, the oysters, if taken as a group, remained open more than half the time, although some of them were open only 8 per cent of the total time. However, even among the oysters that remained open some did not pump water at all and, in general, the pumping rate was reduced approximately 90 per cent. The shell movements were abnormal, clearly different from those exhibited by the same oysters while still in regular sea water.

When, after the 48-hour exposure to turbid water, the oysters were again subjected to the flow of normal sea water, many of them, for some time, did not show the usual recovery-type of shell movement nor did they resume a rapid rate of pumping, as is normally observed after exposure of oysters to turbid water for relatively short periods. Apparently, longer exposures affected them unfavorably, perhaps by injuring the delicate ciliary mechanisms of their gills and palps. This conclusion is strongly supported by our other long-range experiments, not discussed in this article, where oysters and sea mussels, *M. edulis,* eventually died if kept in turbid water for several weeks.

Mortality will occur only if mollusks are kept in relatively large quantities of water, not less than 25 or 50 gallons per individual. Under radically different conditions, such as those employed by Fox, Sverthrup and Cunningham (1937), where a large mussel was placed in a small quantity of water, sometimes only 1.0 liter, the mollusk will be able, within a few minutes, to remove from suspension the turbidity-producing substances, rendering the water clear. When placed in a large quantity of water, however, the mussel or oyster may pump vigorously at first, removing from the water, in the form of pseudo feces, some algae or silt, but will become exhausted long before the turbidity is significantly lowered, cease pumping and close its shell. Eventually, the animal dies.

Mortality of experimental mollusks kept for long periods in large quantities of water containing heavy concentrations of turbidity-creating substances was probably due, in part, to clogging of the gills with silt or other materials, which interfered with normal respiration and feeding of these bivalves. The relatively high temperature at which these experiments were conducted (about 20°C) also probably contributed to the lethal effect. Being unable to open their shells and cleanse their gills, these animals were, nevertheless, compelled to function at a rapid metabolic rate and, as a result, soon died from starvation and suffocation. This inference appears logical because at the above temperature *M. edulis* in our waters normally feeds from 97 to 99 per cent of the time (Loosanoff, 1942), while *V. mercenaria* and *C. virginica* remain open, and probably feeding, approximately 90 per cent of the time (Loosanoff, 1939; Loosanoff and Nomejko, 1946). Ellis (1936) also showed that erosion silt strongly interfered with the feeding of fresh water mussels because they remained closed between 75 to 95 per cent of the time. In Ellis' experiments, mussels that died in turbid water always contained large quantities of silt in the mantle cavity and gills, a condition that we also observed in dead and dying *C. virginica* and *M. edulis* used in our long-term experiments.

Studies of oxygen consumption in various species of oysters, mentioned by Jørgensen (1960), show that it is tripled when the water temperature rises from 10° to 28°C and doubled when it rises from 16° to 28°C. Jørgensen concludes, therefore, that within their natural range of existence feeding conditions for bivalves became poorer at higher temperatures. Since our experiments were conducted at relatively high temperatures and since, because of turbidity, the oysters could not feed effectively, their uncompensated rapid metabolic rate was an indirect cause of the comparatively rapid death.

In concluding the description of the effects of silt upon oysters it should be mentioned that the addition of minute quantities, considerably smaller than 0.1 g/liter, may often reflect favorably on the behavior of oysters by inducing somewhat more rapid pumping. This observation is identical to that made in our studies of feeding oysters with different quantities of living algae (Loosanoff and Engle, 1947). We agree with Jørgensen (1955) that when only very small amounts of suspended matter are present in the water the rate of pumping may be independent of these concentrations.

Clay-like kaolin was the second material used to make the water turbid. Concentrations ranged from 0.1 to 4.0 g/liter. As in the case of common silt, even such small quantities of kaolin as 0.1 g/liter considerably decreased the rate of pumping of oysters and also somewhat changed the character of their shell movements (Table 1, Figure 6). As the concentration increased, the abnormal aspects of the behavior of oysters became gradually more prominent (Figure 7). When concentrations were as high as 3.0 or 4.0 g/liter (Figure 8) the shell movements became abnormally vigorous, indicating that the oysters were continuously cleansing their gills. As usual, large quantities of pseudo feces were discharged under these conditions but, nevertheless, some oysters kept their shells open for long periods and pumped water, although the rate of pumping was markedly reduced.

As in the experiments with silt, the oysters, when again exposed to regular sea water, quickly resumed a normal or even faster-than-normal rate of water pumping and their shell movements also soon became normal.

FIGURE 6. Kymograph record showing shell movements (1st line) and rate of pumping (2nd line) of an oyster exposed to sea water, then to a concentration of 0.1 g/liter of kaolin, and returned to sea water. Each vertical mark on the second line designates the discharge of 255 cc of water pumped by the oyster.

FIGURE 7. Kymograph record showing shell movements (1st line) and rate of pumping (2nd line) of an oyster exposed to sea water and then to gradually increasing concentrations of kaolin ranging from 0.1 g/liter to 0.5 g/liter. Each vertical mark on the second line designates the discharge of 245 cc of water pumped by the oyster.

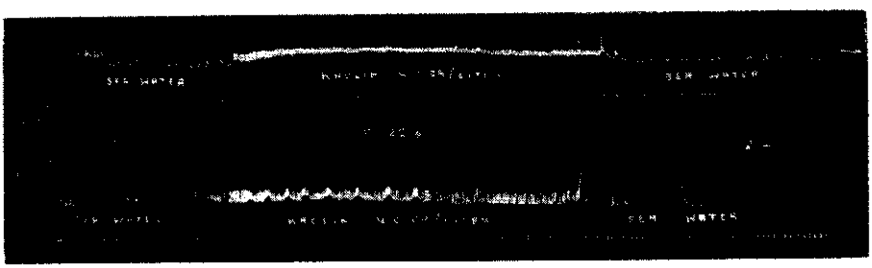

FIGURE 8. Kymograph record showing shell movements (1st & 3rd lines) and rates of pumping (2nd & 4th lines) of two oysters exposed to sea water, then to a concentration of 4.0 g/liter of kaolin, and again to sea water. Each vertical mark on the second line designates the discharge of 249 cc of water and the fourth line, 265 cc of water pumped by the oysters.

Experiments with pulverized chalk (calcium carbonate) closely corroborated the conclusions formed during studies of effects of two other turbidity-creating materials (Table 1). Again, the presence of chalk in the water depressed the rate of water pumping and usually radically changed the type of shell movement (Figure 9). After the oysters were returned to sea water they quickly showed signs of recovery.

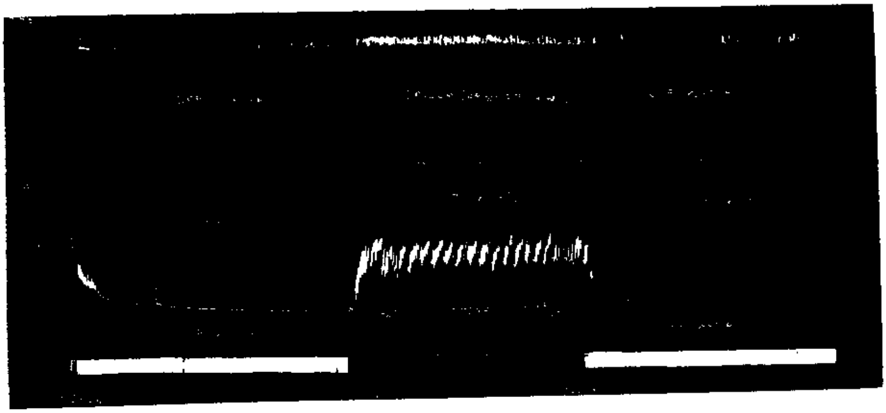

FIGURE 9. Kymograph record showing shell movements (1st & 3rd lines) and rates of pumping (2nd & 4th lines) of two oysters exposed to sea water, then to a concentration of 2.0 g/liter of chalk and again to sea water. Each vertical mark on the second line designates the discharge of 255 cc of water and the fourth line, 219 cc of water pumped by the oysters.

A limited number of experiments in which Fuller's earth was used supported, in general, the conclusions formed during observations on the action of the three other materials.

Observing the development and survival of molluscan eggs, especially during early stages in different concentrations of silt and related substances is, of course, a necessary and important step in evaluating the effects of turbidity. However, as already mentioned, until recently no reliable studies could be made of various aspects of larval physiology or ecology because no simple, standard method for cultivation of bivalve larvae was available. Since the new method was developed, it has been used extensively in studying various ecological requirements of larvae, including their reactions to turbidity. This work has been carried on at our laboratory by Harry C. Davis.

Davis, using the same turbidity-creating substances that were employed in earlier experiments with adult oysters (Loosanoff and Tommers, 1948), studied their effects on eggs and larvae of oysters, *C. virginica,* and clams, *V. mercenaria.* The methods employed in these studies, including use of a rotating wheel to maintain turbidity at definite constant levels, have already been described (Davis, 1960).

Davis found that silt was much more harmful to oyster eggs than to those of clams (Table 2). For example, in concentrations of only 0.25 g/liter of silt only about 73 per cent of the oyster eggs survived, while over 95 per cent of the clam eggs developed to straight hinge stage. In a concentration of

0.5 g/liter practically all the clam eggs developed to straight hinge stage, while only 31 per cent of the oyster eggs survived this treatment. In stronger concentrations, 1.0 and 2.0 g/liter, practically no oyster eggs developed, while 39 per cent of the clam eggs developed normally, even at the concentration of 2.0 g/liter.

In suspensions of kaolin and Fuller's earth, on the contrary, oyster eggs showed a much higher survival than clam eggs. For example, in a concentration of 1.0 g/ liter of kaolin and Fuller's earth practically all oyster eggs developed to straight hinge stage, while only 37 per cent and 57 per cent of clam eggs survived (Table 2).

TABLE 2

PERCENTAGE OF EGGS OF OYSTERS *(C. virginica)* AND CLAMS *(V. mercenaria)* DEVELOPING TO STRAIGHT HINGE LARVAE IN DIFFERENT CONCENTRATIONS OF TURBIDITY-CREATING SUBSTANCES. THE NUMBER OF EGGS IN CONTROLS DEVELOPING TO THE STRAIGHT HINGE STAGE IS TAKEN AS 100 PER CENT (AFTER H. C. DAVIS).

Concentrations G/liter	Silt		Kaolin		Fuller's earth	
	Oyster	Clam	Oyster	Clam	Oyster	Clam
0.125	95	95	99	82	104	75
0.250	73	96	100	82	103	61
0.500	31	99	104	52	102	41
1.000	3	79	107	37	98	57
2.000	0	39	94	49	79	50
3.000	0	0				
4.000	0	0	76	42	26	45

Of the materials tried, silt was more harmful to oyster eggs than either kaolin or Fuller's earth (Table 2). In the two latter materials some oyster eggs developed normally even in concentrations of 4.0 g/liter, while in a concentration of only 1.0 g/liter of silt practically none of the eggs reached straight hinge stage.

Davis (personal communication) also found that, as in the case of eggs of the two species, silt was more harmful to oyster larvae than to clam larvae. For example, at 0.75 g/liter of silt growth of oyster larvae was significantly affected, and at 1.5 g/liter or higher concentrations, growth was negligible. No oyster larvae survived in concentrations of 3.0 and 4.0 g/liter. As a striking contrast, clam larvae grew normally in a concentration of 1.0 g/liter of silt. The majority survived for 12 days and even showed some growth in 3.0 and 4.0 g/liter. However, it is doubtful that any clam larvae could grow to metamorphosis at these two concentrations.

Again, as with eggs of the two species, kaolin and Fuller's earth were less harmful to oyster larvae than to clam larvae. Whereas 0.5 g/liter of kaolin caused approximately 50 per cent mortality of clam larvae in 12 days, and virtually no clam larvae survived in concentrations of 1.0 g/liter of either Fuller's earth or kaolin, growth of oyster larvae was not appreciably affected by 1.0 g/liter of kaolin.

Davis also established the remarkable fact that some oyster larvae may survive for at least 14 days in concentrations of 2.0 g/liter of silt and up to 4.0 g/liter of kaolin or Fuller's earth.

When minute quantities of silt, kaolin or Fuller's earth were added to water containing straight hinge larvae of these species, growth of these organisms was stimulated, often exceeding that of controls. It is thought that this was a result of adsorption by particles of suspended material of the toxic substances produced in larval cultures by bacteria or algae. It is also possible that some of the particulate materials added to the water of larval cultures carried along a positive growth factor as some soil solutions do. In view of the consistency of such results these possibilities should be investigated so that, perhaps, methods based on these findings can be developed to improve handling of larval cultures of different aquatic invertebrates.

DISCUSSION

This article is devoted principally to an analysis of the studies of effects of turbidity on adult oysters, a brief account of which has already been presented (Loosanoff and Tommers, 1948), and of recent studies by my associate, H. C. Davis, on effects of turbidity on larvae of our two most common bivalves, the American oyster, *C. virginica,* and the hard clam, *V. mercenaria.* These studies, together with Ellis' (1936) work on fresh water mussels, Fox et al (1937) on the California mussel, *Mytilus californianus,* and Jørgensen (1949, 1955, 1960), are the few experimental contributions available at present.

The majority of the observations on adult oysters were of comparatively short duration, the oysters being kept in turbid water from 3 to 6 hours. However, even these observations strongly pointed to the conclusion that oysters are very sensitive to turbidity, regardless of what particulate materials are responsible for it.

When the turbidity of the water is noticeably increased, the oysters begin to react to it by decreasing their rate of water pumping and by changing the character of shell movements which, in stronger concentrations of turbidity-creating substances, clearly indicates that the oysters are seriously disturbed physiologically. In general, there is a correlation between increase in turbidity and decrease in rate of pumping (Table 1). In strong concentrations oysters may cease pumping entirely. Eggs (Table 2) and larvae of bivalves are also affected by heavy turbidity, although they seem to display considerable tolerance toward certain substances. Larvae of different species may react differently.

When adult mollusks were exposed to different concentrations of silt-laden water for periods lasting 48 hours, they were affected at the end of this period and their recovery, upon return to normal sea water, was considerably slower than after shorter exposures of only a few hours. It is assumed that the delicate ciliary mechanism of the gills and palps of the experimental bivalves was somewhat injured during the longer exposures.

If subjected to even more prolonged exposures in turbid water, mollusks eventually die because under such conditions they are not able to respire or feed normally. If, instead of a sudden exposure of the oysters to turbid water, they are submitted to slow and gradual increases in turbidity, the shell movements and rate of water pumping are not basically different from those observed in the same concentrations when the oysters experience a relatively rapid transition from clear to turbid water.

Oysters, and some other bivalves from different geographical regions, may display different physiological capabilities by showing different levels of tolerance to the same degrees of turbidity. Our observations were made on

Long Island Sound oysters, which are accustomed to living in comparatively clear water. In other sections of our Atlantic coast, North and South Carolina for example, oysters exist in waters which are extremely turbid. Perhaps these southern oysters, which seem to show a greater tolerance to turbidity, belong to groups that are physiologically different from the northern, clear water oysters. Studies comparing the behavior of oysters of these different geographical groups under the same turbidity conditions would be extremely desirable and informative.

According to Jørgensen (1955) different species of bivalves are not equally sensitive to the same amounts of turbidity in sea water. Jørgensen also appears to share our contention that different groups of the same species may show a difference in tolerance towards the presence of suspended silt, depending upon the condition of their normal habitat; in other words, they may display differences which we believe may exist between the northern and southern oysters *(C. virginica).* Recent studies of Imai and Sakai (1961) on the Japanese oyster, *Crassostrea gigas,* also show that local races display differences in adaptability to environmental conditions.

It is also possible that even though southern oysters do live in turbid waters, their existence, to a certain degree, is unfavorably affected by this condition. This is a possibility because in spite of the long periods of warm weather, during which southern oysters are able to feed, their meats are normally much poorer than those of oysters of the New England or Middle Atlantic states where summers are much shorter. This is clearly demonstrated by the ratio of pounds of meat shucked per standard bushel of oysters grown in the different areas. Perhaps turbidity is not the only factor contributing to the relatively poor condition of the meats of southern oysters. Diseases and long spawning periods may be partially responsible also but, nevertheless, turbidity cannot be entirely dismissed as one of the factors involved.

Several aspects of the studies mentioned in this article should be considerably expanded. For example, effects on the same organism of different particulate materials present in the same concentrations should be determined and understood. This will extend the observations to sizes and shapes of suspended particles and to their effects on eggs, larvae and, finally, adult animals.

We know that certain lamellibranchs possess the ability to select, by the elaborate sorting devices of the gills, food particles from suspended matter (Loosanoff, 1949; Jørgensen, 1955), while other species do not possess this ability. Studies of this nature, extended to a number of filter-feeding forms, will show whether the effects of different particulate substances are purely mechanical, purely chemical or a combination of the two.

This will also lead to an understanding of the biological significance of the conglomerates of the particulate material in sea water which, at times, exist in large quantities in such places as Long Island Sound. According to Dr. Gordon Riley of Yale University (personal communication) the base of the aggregates is an amorphous material of uncertain composition, consisting probably of bacterial slime with particles of silt, phytoplankton, and bacteria imbedded in it. We usually notice it in April and June, when large areas of Long Island Sound contain masses of these slimy conglomerates. However, being of unstable nature, they are easily disrupted by wave action and part of the material of which they are composed descends to the bottom where beds of clams, oysters, and other filter-feeding invertebrates are located. Obviously, the role of these aggregates, which are partly responsible for turbidity over molluscan beds, should be determined. Still another aspect of this phenomenon, that is entirely unknown at present, is the role which the mechanical and chemical characteristics of the aggregates plays in the existence and survival of bivalve larvae. Possibly, because diatoms are found imbedded in the aggregates, bivalve larvae and eggs become trapped in them also.

It is realized that our results and conclusions expressed in this article cannot be generalized for the entire group of lamellibranchs. Our experiments should be merely considered as a pioneering step towards the solution of an important ecological problem in the existence of filter-feeding invertebrates. However, even the limited information so far obtained on this subject strongly indicates that we should always consider with caution and suspicion any conditions where turbidity of sea water in shellfish-producing regions is raised considerably above the normal level.

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The Contribution of Estuaries to the Offshore Winter Flounder Fishery in Rhode Island

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Abstract

The winter flounder, **Pseudopleuronectes americanus** (Walbaum), has been found to be one of the important demersal fishes of Rhode Island. The contribution of particular breeding areas and the significance of shallow estuarine environments to the offshore flounder fishery were studied by means of mark-