negative. Weights of meats of heavily infected oysters and moderately infected oysters are compared, per unit of shell capacity, with the negative and lightly infected group. The data show that the average mean of meat weights of heavily infected oysters was about 33 per cent less than that of the controls and that the moderately infected oysters were intermediate in loss of weight. Mathematical analyses of the data support the conclusion that disease plays a major role in reduction of meat weights.

Analysis of the data also shows that reduction of weights is not only a matter of disease but of season, summer losses accruing from disease being significantly greater than those of early spring months.

Experimental studies which eliminate factors of nutrition point to lysis of tissues as one of the major processes resulting in loss of weight. In these studies reduction of bits of excised gill tissues which were heavily infected with the fungus is compared with that of normal excised tissues when bacterial and other contaminants are excluded.

Statistical methods and procedures are fully described.

Distribution of Oyster Larvae in Relation to Hydrographic Conditions

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Observed Distribution of Salinity and Circulation Pattern

In the summer of 1950 the Chesapeake Bay Institute of The Johns Hopkins University, in cooperation with the Virginia Fisheries Laboratory, undertook an intensive study of the physical and chemical hydrology of the James River oyster seed bed area. A detailed discussion of the observed current velocities and salinities is presented elsewhere (Pritchard, 1952). The discussion here will concern the circulation pattern and mixing processes, as indicated by the observations of velocity and salinity.

First, consider briefly the character of the salinity distribution. Figures 1 and 2 show the surface salinity distribution over the seed bed area of the James River for low and high water, respectively, on September 2, 1950. The following common features are noted: (1) an increase in salinity from the head of the estuary, where the fresh water enters, toward the mouth; (2) a salinity gradient across the estuary with higher salinities on the left side of the estuary than on the right side (directions are taken relative to an observer standing at the head of the estuary and facing toward the mouth); (3) the tidal fluctuation does not greatly alter the general picture, but rather shifts the pattern up and down the estuary.

In Figure 3 examples of the vertical distribution of salinity are given. These mean salinity vs. depth curves are similar to an inverse tangent function, with an upper and lower layer of slight vertical gradients separated by a halocline of relatively rapid change in salt content with depth. At the bottom, and to some extent at the surface, the curve shows increased gradients apparently related to boundary effects. The character of the vertical distribution does not change greatly with longitudinal distance. Consequently, the horizontal gradients do not vary appreciably with depth.

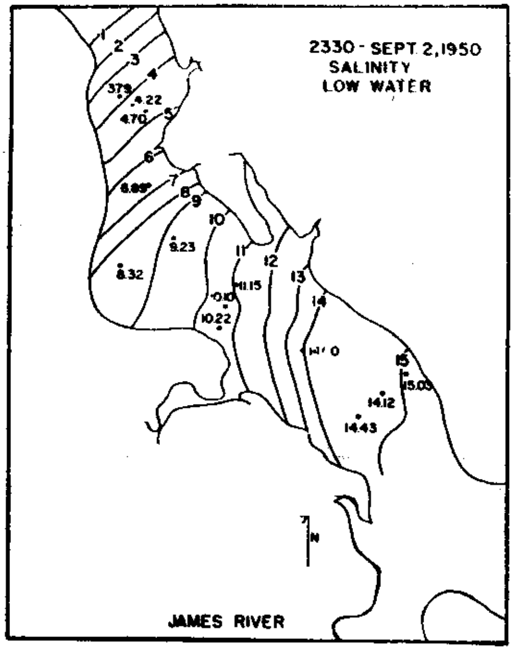


FIGURE 1

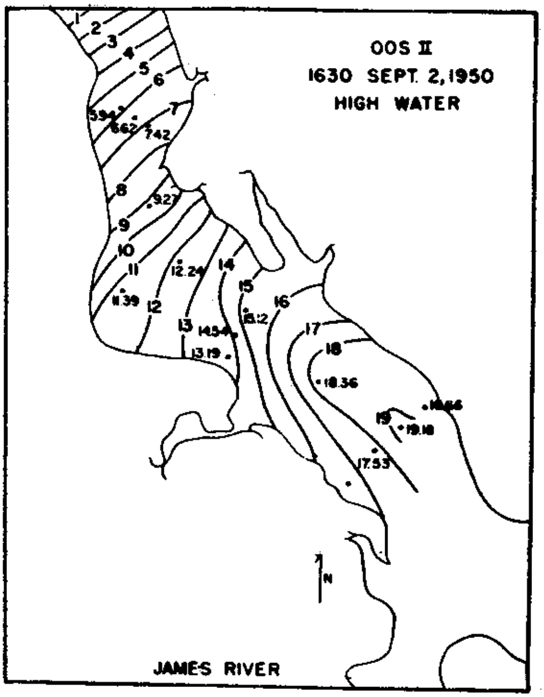


FIGURE 2

The most obvious water movements in the James River estuary are oscillatory tidal currents. Time averages of hourly current observations taken over one or more tidal cycles reveal that superimposed upon the oscillatory tidal currents is a net circulation pattern which appears from investigations of other estuaries of the Atlantic Seaboard to be typical of many coastal plain estuaries at mid-latitudes.

Currents which are directed upstream toward the head of the estuary are designated as flood currents, while those directed toward the mouth of the estuary are designated as ebb currents. If the magnitudes of all ebb current velocities taken at a single station over several tidal cycles are averaged and plotted against depth, a graphical presentation of the mean vertical distribution of ebb velocities is obtained. The mean vertical distribution of flood velocities may be obtained in a similar manner. Figure 4 gives such a presentation for three different periods of observation at a typical station near the center of the James River estuary. The ebb velocities are relatively large at the surface, and decrease with depth, while the flood velocities are relatively small at the surface, but increase to a depth of about 17 feet where the influence of bottom friction results in a decrease in magnitude as the bottom is approached. The two sets of curves cross at about ten feet where the magnitude of the mean ebb current is the same as the magnitude of the mean flood current.

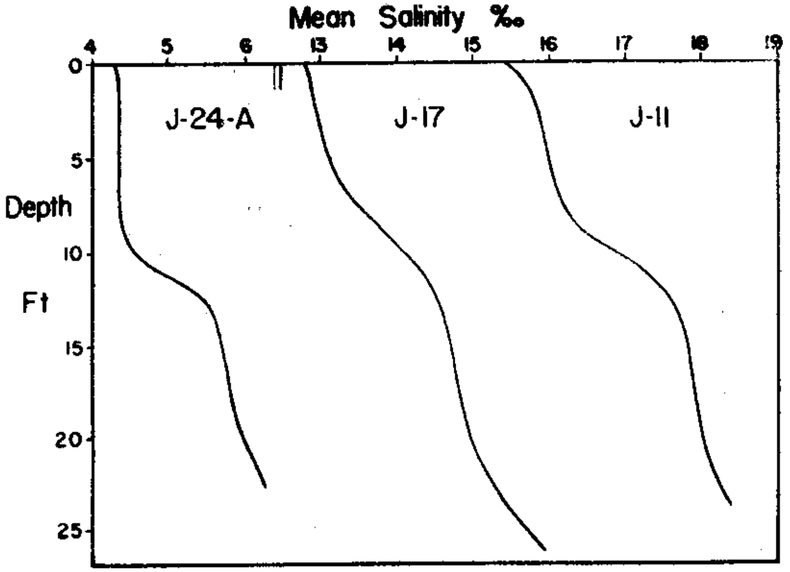


FIGURE 3

Averaging of the ebb and flood current observations together results in the net velocity-depth curves shown in Figure 5. Above ten feet in depth the current is directed down the estuary and is designated as positive. Below ten feet the current is directed up the estuary and is designated as negative.

The boundary between the surface layers which have a net movement down the estuary and the deeper layers which have a net movement up the estuary may be designated as a surface of no net motion. The depth of this surface varies slightly both in the longitudinal and in the lateral direction. Figure 6 shows a cross-section of the James River estuary upon which the observed surface of no net motion has been drawn. The figure reveals that this surface slopes downward from the left side of the estuary toward the right side. This results in a deeper layer of positive flow on the right side, where the mean salinity is low, than on the left side, where the mean salinity is high.

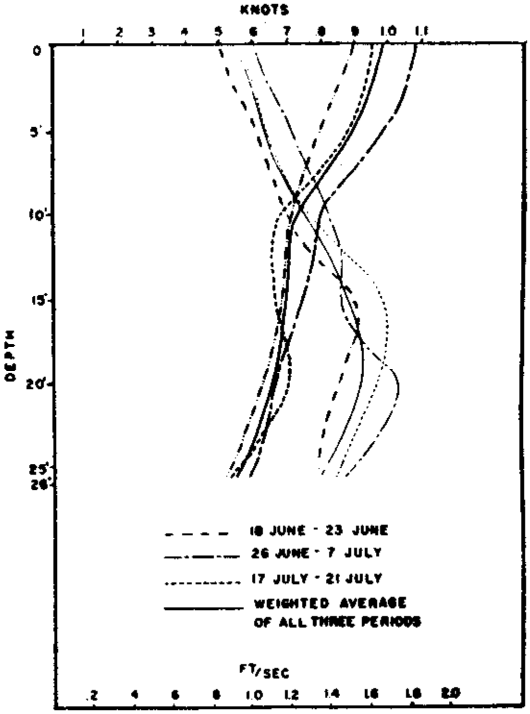
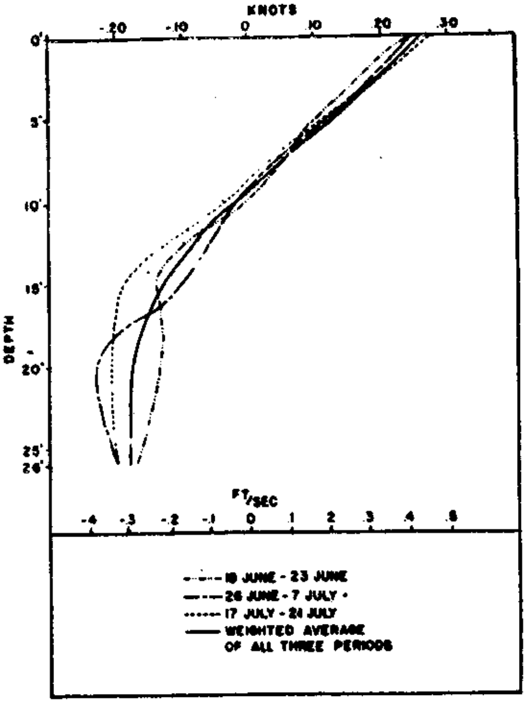


FIGURE 4

From the standpoint of the distribution of salinity and of the circulation pattern the James River estuary may be considered as composed of two layers. In the upper layer there is a net horizontal flow down the estuary. In the lower layer there is a net horizontal flow up the estuary. The upper layer has a lower mean salt content than the deeper layer. In order to maintain volume continuity, there must pass through each section seaward during any period of time an amount of fresh water equal to the amount of fresh water introduced from the river during that time interval (neglecting evaporation from and precipitation on the surface of the estuary itself). Thus, since the upper layer is transporting seaward a net amount of fresh water equal to the fresh water inflow, there must be a flux of salt into the upper layer to maintain the salinity distribution. This may be accomplished by two processes: (1) a net transfer of relatively higher salinity water from the lower layer to the upper layer, resulting in a net vertical velocity directed upward across the boundary between the two layers; and (2) a random flux of salt upward due to eddy turbulence. The first process leads to an augmentation of the volume of flow in the lower layer.



FIGUBE 5

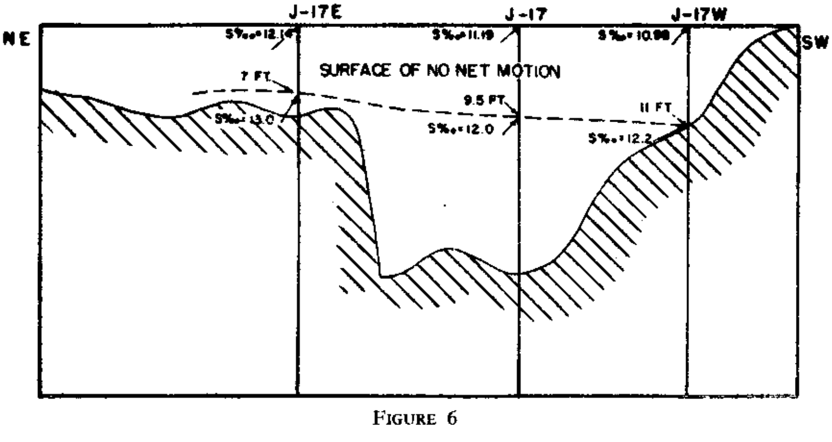


FIGURE 6

A schematic presentation of the flow pattern in a vertical section taken along the central axis of the James River estuary is given in Figure 7.

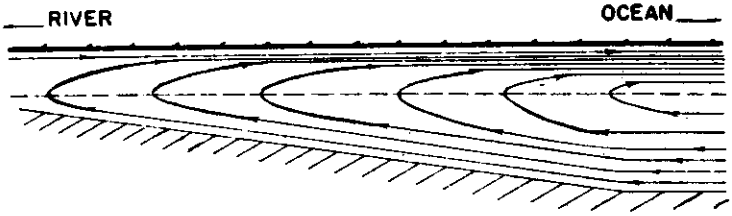


FIGURE 7

The Mixing Processes

It is beyond the scope of the paper to present the complete theoretical development required to obtain the magnitude of the mixing processes which contribute to maintaining the distribution of dissolved and suspended material in the James River. The principles involved will be briefly discussed.

The mean time rate of change of concentration of any material in solution or in true suspension in a natural body of water is given by the sum of the spacial derivatives of the mean advective flux and the non-advective flux of the material in question. Thus, in the case of salt content, the equation giving the mean time rate of change is

$$\partial\bar{s}/\partial t = -\frac{\partial}{\partial x_i}(\bar{v}_i\bar{s}) - \frac{\partial}{\partial x_i}<v_i's'>$$

where s is salt concentration, t is time, v_i is vector velocity (having the three components v_1, v_2, and v_3) and x_i represents the three spacial coordinates x_1, x_2, and x_3. The superscript — and the symbol < > both indicate time averages. The instantaneous salt concentration s is considered to be composed of a mean concentration $\bar{s}$ plus a random concentration s′. Similarly the velocity v_i is composed of a mean velovity $\bar{v}_i$ plus a random velocity v_i'.

The term $\bar{v}_i\bar{s}$ represents the mean advective flux of salt, and can readily be obtained from observations of salt content and velocity. The term $<v_i' s'>$ represents the non-advective flux of salt, and cannot be readily determined directly because the spectrum of random velocities contains turbulent components having the time and space which are below the sensing ability of present day marine instrumentation. Pritchard (1952) has shown, however, that an adequate application of boundary conditions allows the indirect determination of the non-advective flux by employing the observed mean salinities and velocities in a modified form of equation (1). The modifications employed are based upon simplifying considerations peculiar to a coastal plain estuary as the James River.

The non-advective flux term $<v_i' s'>$ is more generally called eddy diffusion and expressed as $-A_i\,\partial\bar{s}/\partial x_i$, where A_i is the so-called diffusivity or Austausch coefficient. If it is assumed that the mixing processes are such that the diffusivity is the same for all dissolved or suspended substances, then the results of the evaluation of the salt balance provides information required to predict the time change of any dissolved or suspended material carried by the water. In a practical application it is of course necessary to make some reasonable assumption as to the initial distribution of the material.

The results of studies in the James River estuary have shown that the salt balance is maintained primarily by two processes—the mean horizontal advection and the vertical mixing term. Of secondary but still significant importance is the mean vertical advection term. The horizontal mixing term is not important in maintaining the salt balance in the James River.

Application to Oyster Larvae Distribution

The application of the general principles of circulation and mixing in the James River to oyster larvae distribution is encouraging. Oyster biologists have long pondered about the processes whereby oyster larvae apparently move "upstream" from beds of mature oysters to setting bars further up an estuary. The net movement of the deeper layers provides a mechanism for this up-estuary movement of the larvae.

There is no agreement as yet as to whether the oyster larvae which produce the profitable set of seed oysters in the James River originate from mature oysters in the immediate vicinity of the seed beds, or whether the supply is from further down the estuary, for example, from the mature oysters in the Hampton Roads area. Every few years the oyster population in the portion of the seed bed nearest the head of the estuary is destroyed by freshets. The return flow of the deeper layers provides a mechanism for the replenishment of these beds from the surviving bars further downstream.

Another feature of the circulation pattern appears to be related to the distribution of seed oysters, and consequently to the distribution of oyster larvae. As mentioned above, the upper boundary of the sub-surface layers of water having a net motion toward the head of the estuary occurs at shallower depths on the left side of the estuary than on the right side. This lateral distribution of the net motion implies a slow upwelling of the deeper waters over the shallow bars of the northeast side of the river. Thus oyster larvae brought up the estuary in the deeper layers would tend to be concentrated over the bars on the northeast side. Dr. Jay Andrews has reported that the northeast side of the river has much higher production of oyster seed than the southwest shore.

Bousfield (1952) in a recent paper before the American Society of Limnology and Oceanography described the distribution of barnacle larvae in Miramichi Estuary. This estuary is remarkably similar in physical structure to the James River. Bousfield made use of the above described studies on the James River in explaining the observed distribution of the larvae in Miramichi Esturay.

Mr. Bousfield kindly sent the writer some of the illustrations from his treatise prior to publication. A portion of one of his graphs is presented in Figure 8. A vertical-longitudinal section of Miramichi Estuary is shown, running from the fresh water in the river on the left to the mouth of the estuary on the right. At selected stations along this section the vertical distribution of the larvae of *Balanus improvisus* is shown by the shaded areas. In the upper section the distribution of the early stages I and II is given. In the lower section the distribution of the late Cyprid stage is shown. It is seen that the early stages are concentrated in the surface layers and are found in the lower portion of the estuary. The late stage occurs in greater concentrations below mid-depth and is found further up the estuary.

Bousfield, by comparison with the James River study, has estimated that the surface of no net motion occurs at about nine feet. Above this depth, as described above, the net flow is directed down the estuary toward the sea, and would carry those larvae which remained in this layer out of the estuary. At depths greater than nine feet, however, the net flow would be directed up the estuary, and hence carry the larvae in this layer away from the mouth up into the estuary.

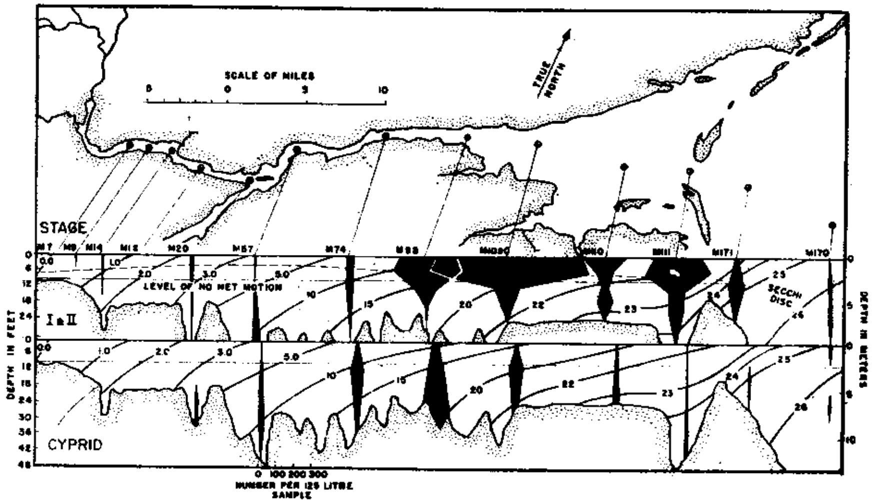


Figure 8

The observed distribution of oyster larvae in the James River estuary has not revealed any such clear-cut vertical relationship as described for the barnacle larvae in Miramichi Esturay, even though the hydrography has been more precisely defined. It is believed that the reason for this is related to our inability, to date, to sample adequately the larvae distribution, particularly the late stage larvae. Even though setting in the James River is very high, calculations show that the concentration of late stage larvae in the overlying water sufficient to produce the large observed set needs to be, on the average, only about one larva per 100 liters. Since the basic sample employed in filtering out the larvae was 100 liters, it is apparent that a clear picture of the relative distribution of the late stage larvae could not be obtained by our sampling procedures.

Specific applications of the results of our theoretical study of circulation and mixing to observed distributions of oyster larvae have met with less success than might be hoped for on the basis of the above qualitative relationships. During our study of the James River estuary in the summer of 1950 samples were obtained for the purpose of determining the distribution of oyster larvae. The counting of the oyster larvae in such samples is a tedious and time-consuming task, and only one series of observations are as yet available for our consideration. Dr. Andrews has kindly made available this series which was obtained at the surface over the Wreck Shoal oyster bar.

The samples were collected at aproximately two hourly intervals during the period August 31 to September 3, 1950. The observed hourly current velocities have been employed in converting this time series of observations to an approximate spacial distribution.

In Figure 9 a portion of the series has been plotted against longitudinal distance from the Wreck Shoal station for the high water slack and for the low water slack nearest the time of the observation. It is possible in many cases

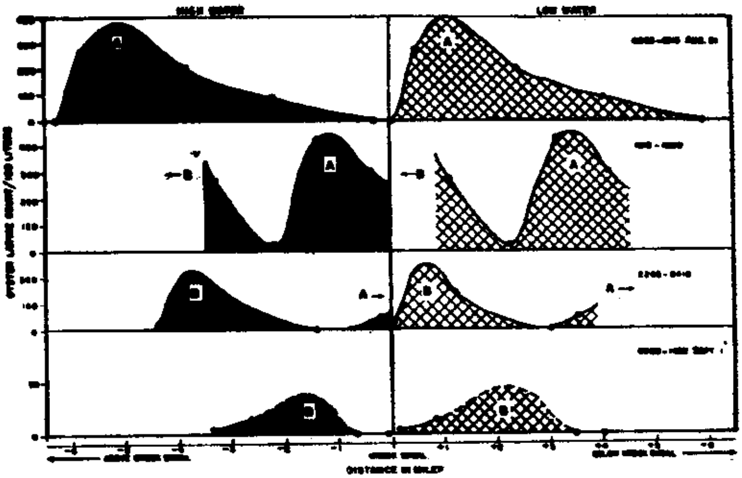


FIGURE 9

to identify peak concentrations of the oyster larvae as these concentrations move downstream past the station. It should be borne in mind that this plot represents but one dimension of a three-dimensional distribution. During the period between one high water slack and the next the processes of mixing alter the distribution. For these reasons we would not expect the shape of the concentration curves to be the same from one tidal period to the next .

One feature which appears from the figure is the relatively peaked distribution of the more prominent "groups" of oyster larvae. It is this feature of the observed distribution which differs most markedly from the distribution which would be expected from a consideration of the mixing processes.

The principles employed in the development of the salt balance equation may also be employed in describing the time change of any dissolved or suspended material carried by the water. The studies of the salt balance provide means for estimating the effect of the circulation and mixing on the distribution of any other substance partaking freely of the water movements. Oyster larvae, while having the ability to swim, are generally considered to be incapable of anything but random movements. Consequently, we might expect that they could be considered theoretically the same as dissolved material.

The application of the results of our studies of the salt balance to an assumed initial distribution of oyster larvae allows the prediction of the variations in the spacial distribution of the larvae with time. Preliminary results of such application give computed distribution similar in shape to the observed larvae distributions if the age of the larvae is assumed to be two or three tidal cycles.

Dr. Andrews has suggested (personal communication) that the larvae collected were in general two or three days old, or from four to six tidal cycles. The computed distributions after four tidal cycles appear much less sharply peaked and spread over a larger area than the observed larvae distributions.

The discrepancies between the observed and computed distributions of oyster larvae may indicate a failure of the theoretical treatment. However, experiments with dye in large scale models of estuaries indicate that dissolved or suspended material spreads at a considerably faster rate than is suggested by the observed larvae distributions.

Another possibility suggested by the difference between observed and computed larval distributions is that the oyster larvae cannot in fact be considered the same as dissolved material but rather exhibit some ability, independent of the physical character of the circulation and mixing processes, to remain closely grouped. Such a tendency could be the result, for example, of the larvae near the periphery of a particular brood dying at a faster rate than those near the center of the group. The possibility of the oyster larvae having a "swarming" tendency has been suggested previously by oyster biologists.

The study described here illustrates the fact that the physical scientists, when attempting to apply physical theories to biological problems, must take into account the possible modifying factors peculiar to the organism involved. Some responsibility must then rest with the biologists to supply information concerning the organism which might modify the influence of the physical factors.

REFERENCES

Pritchard, D. W. 1952. The Physical Structure, Circulation, and Mixing in a Coastal Plain Estuary. Chesapeake Bay Institute Technical Report No. III, March 1952.

Bousfield, E. L. 1952. Ecological Control of the Distribution of Barnacle Larvae in the Miramichi Estuary. Presented at meeting of American Society of Limnology and Oceanography, Ithaca, New York, September 8-10.

A Critique of Present Biological Research on Oysters

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Research on oysters of one variety or another has been carried on in the United States for almost 50 years, and even before 1900 experiments on transplanting oysters were being attempted. It appears that far more research has gone into oysters than any other species of marine animal. However, the results have been used in only limited ways by the industry. Let us stop to consider for a moment the oyster industry as it is now and its condition 50 years ago.

Harden F. Taylor (1951) and his associates showed a drastic decline in production. According to their statistics, 172,885,000 pounds of oyster meats were produced per year during 1889-1892, representing 16.1 per cent of all food fish produced in the United States. By 1908, the catch had declined to 152,046,000 pounds of oyster meats, 9.6 per cent of all food fish, and by 1938-40 the average catch amounted to 89,740,000 pounds, representing 3.1 per cent of all food fish.

The decline has been common to all areas along the Atlantic Coast, but less on the Gulf. Statistics for 1950 indicate the same relative position of the various states and little change in the production. The causes for these fluc-