OYSTER GROWTH AS AFFECTED BY LATITUDINAL TEMPERATURE GRADIENTS[1]

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INTRODUCTION

The complexity of growth processes in animals makes necessary the use of many different yardsticks for a critical evaluation. The word growth itself is difficult to define but is interpreted, usually, as meaning permanent changes in length or volume. In oysters, growth is especially difficult to study since the body is hidden between the valves. Body size fluctuates seasonally; even the shell may decrease in length under special environmental conditions. Specimens taken from upper Chesapeake Bay after a prolonged period of low salinity showed that the occupied portion of the valves had decreased by an inch. Under such adverse conditions there is considerable body shrinkage and the oyster forms new valve margins within the old shell thus decreasing its total length by as much as one-third. This negative, or reductional, growth is common to many animals and frequently occurs in oysters. Most often the valves do not reflect these transitory body changes and body size cannot be determined without opening the shell. Measurement of growth in oysters is further complicated by the absence of a definitive size and by the fact that sexual maturity may be attained at shell sizes varying from $\frac{1}{2}$ to 2 inches.

For these and other reasons biologists and fishermen are prone to accept shell length as a valid criterion for oyster growth, and certainly it is the easiest measurement to use. State laws regulating oyster harvesting follow suit and the $2\frac{1}{2}$ or 3-inch "market" oyster is a legal standard in most areas where oysters are harvested commercially. However, since the amount of meat in an oyster rather than the size of the shell determines the profit, we find that private oyster growers do not necessarily use the 3-inch standard to determine the harvesting time for their crop. Under most conditions, the private planter determines the harvesting period by the number of pints of meat produced from a bushel of oysters rather than on whether or not the oysters will pass the minimum legal standard. In some areas too, the commercial canner does not purchase oysters on the basis of length but rather on how many cans of meat he can process per barrel of shell stock. Shell growth is, of course, intimately associated with body growth, but the relation between these two is by no means directly proportional. Investigators have recognized these facts for a long time. But, unfortunately, there are occasional reports of rapid increases in shell length which, with or without the writer's intention, are interpreted as meaning rapid meat production. The reading public has been educated to consider shell growth as synonymous with meat growth.

LENGTH VERSUS WEIGHT-VOLUME FOR DETERMINING GROWTH

The difficulty in determining oyster growth from length measurements becomes apparent on examining the results of some of the many experiments we have conducted during the past four years. For example, observations on growth under average conditions show that during the summer months of their first year oysters grow up to 60 mms. in length; during their second summer they may increase from 1 to 10 percent. During the summer months of their third year there is virtually no increase in shell length, although weight and volume may increase from 10 to 20 percent. Obviously, during this third summer the oysters are growing despite the lack of increase in length. Length increases do take place in the third year of course, but during the

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colder months. In contrast, oysters in the colder waters of New England add 70 percent of their annual length increment during the four summer months when mature Gulf oysters are not growing appreciably.

Location	Mean annual temp. 0° C.	Calendar months to grow select oyster: Poor area	Best area	Average area	Months in hiber-nation	Average no. of growing months	Oz.-yield per bushel (USFWS statistics)	Oz.-yield per bushel (biologists' estimate)	Oz.-yield per calendar month	Oz.-yield per growing month
CANADA	6	84	48	66	5	46	-	120	1.8	2.6
LONG ISLAND SOUND	10	80	42	52	4	36	122	120	2.3	3.4
CHESAPEAKE BAY	15	60	18	30	3	24	72	96	3.2	4.0
SOUTH CAROLINA	20	48	18	30	0	30	42	76	2.5	2.5
GULF OF MEXICO	22	48	18	30	0	30	66	72	2.4	2.4

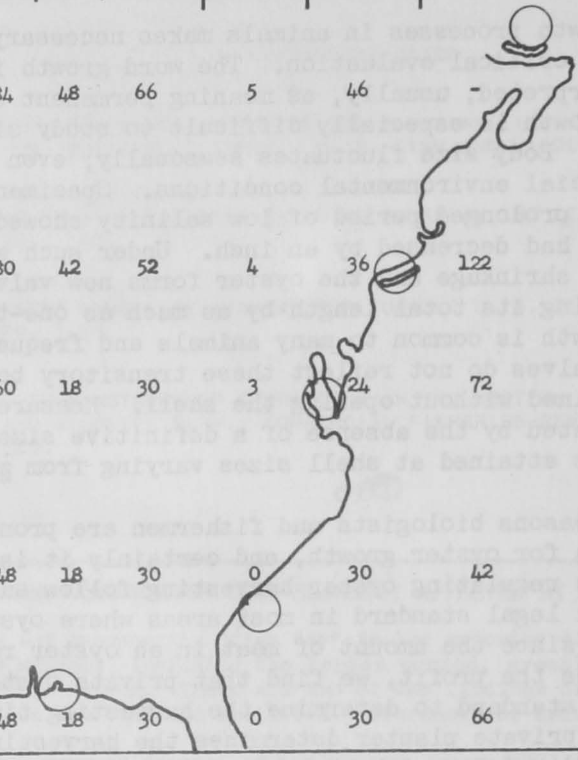

FIGURE 1 - ESTIMATED AVERAGE GROWING TIME AND MEAT YIELD FOR SELECT 3-INCH OYSTERS AT DIFFERENT LATITUDES. YIELD PER MONTH IS DERIVED FROM BIOLOGISTS' ESTIMATE OF YIELD PER BUSHEL.

Interesting changes in growth rates may be obtained experimentally by simulating the tidal conditions to which many oysters are normally exposed. At Pensacola we compared oysters growing under these conditions with control oysters held continuously below the water surface. In the first six months of observations, control oysters gained 35 percent in length and width while experimental oysters showed no gain; control oysters increased 160 percent in weight and experimental oysters 100 percent in weight. In another series of observations we separated oysters growing under very crowded conditions and placed them in individual trays. In the following six months these oysters increased in length only 1 percent, showed no change in width, but increased 40 percent in volume.

It is apparent that under a variety of environmental conditions essentially no changes in length and width may occur while substantial gains are being made in weight and volume, in other words, when the oyster is growing. Our observations in Florida show that significant increases in weight and volume occur each month throughout the year, whereas increases in length and width follow a well-defined seasonal pattern after the first year and occur primarily in the winter months. The regularity of volume increases during all of the growing months as compared to periodic length and width increases has been reported also for New England oysters (Loosanoff 1949). I suspect it is a characteristic of this oyster wherever it grows. For these reasons, the measurement of volume is a far more critical yardstick in the measurement of growth than is the measurement of length. There are certain disadvantages in the use of volume measurements as criteria for oyster growth. It is more time consuming and requires more equipment, but the data obtained are of much greater value for interpreting growth changes under both experimental and natural conditions.

RELATIVE VALUE OF GROWING AREAS

The oyster biologist is interested not only in growth rates in a given environment, but also is frequently concerned with the relative value of two or more growing areas. It may be possible to examine such areas only briefly. In these circumstances, the use of the total volume measurement by itself is of little value in assaying the growth potential of the oyster population. The reasons for this are obvious considering the striking differences found in the character of the shell. In areas infested with boring sponge and clams, the valves may be massive and yet enclose relatively little meat. Conversely, in areas of rapid growth, with the production of thin shells and relative thin oysters, the meat yield may be quite high. Even in circumscribed areas, variations in population density and types of cultch radically influence shell thickness and thus affect the relationship of total oyster volume to meat yield. We have several series of data illustrating these differences and our results parallel those obtained by H. F. Moore in his experimental plantings in Louisiana at the turn of the century (Moore 1910). Moore found in seed plantings of similar age that crowded oysters averaged greater length but only half the meat production of uncrowded oysters; that oysters growing on clam shell cultch produced the same amount of meat per bushel as larger and longer oysters growing on oyster shell cultch in the same area. Thus, in comparing oyster samples even from adjacent reefs, neither greater length nor greater volume is necessarily an index of greater meat yield.

TOTAL OYSTER VOLUME TO SHELL VOLUME INDICATES POTENTIAL YIELD

It is a simple operation to shuck measured samples of oysters from one or several locations and determine the relative yield at harvest time. However, for the biologist who may wish to determine the potential yield of a particular area or type of culture technique, it is much more difficult. He must sample oysters both in and out of season, when they are spawning and when they are hibernating. Under varied seasonal conditions, the yield from a sample may have little bearing on what those same oysters would produce under the optimum conditions found at harvest time. For example, we determined the yield of similar-aged oysters growing as "singles" and another group growing under crowded conditions. In May, the single oysters produced 30 percent more meat than did the crowded oysters. Two months later the yield ratio had reversed and the crowded oysters produced nearly 25 percent more than the singles. This change in meat production was not due to any sudden improvement in the crowded oysters but simply to the fact that they were heavy with spawn while the single oysters had all completed the spawning process. There are still other local conditions which may contribute to such misleading results, and it is essential for the biologist to have some yardstick usable at any time to evaluate the potential yield from an oyster population at its peak of condition.

We have found in our work that the ratio of total oyster volume to shell volume provides such a yardstick. Under poor growing conditions, where meat yield is low, this ratio approaches but, of course, never reaches 1.0. As oysters improve in meat-yielding capacity, this ratio approaches and may surpass 2.0. In other words, the larger the body space in proportion to shell, the higher the ratio. In the Pensacola area, the best oysters have a total volume:shell volume ratio of about 1.8 and the poorest oysters have a ratio of about 1.2.

This ratio has many convenient uses, some of which I shall indicate briefly: since it is based on the total internal capacity which the oyster has at some time created for its body, this ratio reflects the volume of oyster meat when the animal is, or was, at peak size; this ratio is independent of meat volume at the time of examination and hence is not affected by seasonal fluctuations in meat quality, or by variations due to spawning, etc.--it can even be used on the intact shells of oysters long dead; it eliminates the subjective impressions gained from rapid shell growth and over-all large-appearing oysters; when used in conjunction with meat volume, the ratio helps to evaluate the effects on body size of disease, pollution, and semi-permanent environmental changes.

We have found this ratio useful in comparing oysters grown under different experimental conditions in adjacent environments, and it should be equally useful in comparing oysters which have grown in environments widely separated geographically.

Since distinctive differences in the meat yield per bushel exist in the commercial production of oysters at different geographical locations, it is of interest to learn whether these differences have a biological foundation based on the oysters' ability to grow or whether they are artificial differences based on harvesting techniques.

The U. S. Fish and Wildlife Service in compiling production figures for the several oyster-growing areas makes use of certain factors for converting bushels of oysters harvested to pounds of meats produced (Anderson and Peterson 1952). These conversion factors vary from over 7 pounds per bushel in New England to less than 3 in South Carolina. These figures indicate to some extent the quality of the oysters, but they reflect primarily the harvesting methods used in the different states. In order to estimate the meat-yielding capacity of oysters from different geographical areas, it is necessary to determine the meat yield and age of a standard-size oyster. I have selected for this purpose the 3-inch "market" oyster, taking into consideration the number of calendar months necessary to produce such an oyster and in how many of these months the oyster actually grows. (Many biologists have contributed helpful information for my use in compiling these data, and I wish to express here my appreciation for their assistance.[2] I wish to emphasize, too, that any faults in the interpretation of this material are entirely my own.)

DIFFERENTIAL OYSTER GROWTH AT DIFFERENT LATITUDES

Although some of the data are quite meager, I believe that a clear-cut differential in oyster growth does exist at different latitudes. The Chesapeake oyster produces the greatest volume of meats in unit time on the basis of both calendar months and growing months. If we consider rate of growth from the biological point of view, rather than the commercial, and eliminate the hibernation months, oysters in the warmest areas produce the least amount of meats in unit time, and the other regions considered are intermediate.

The relatively poor growth of the southern oyster suggests that the Gulf of Mexico is on the periphery of the geographical distribution for this species, Crassostrea virginica. It suggests too, that parts of the Gulf may be classified as a distinctly marginal environment. Although there is clear evidence for the existence of enormous populations here in the recent past, we have no knowledge of the annual recruitment in these populations. It may well be that in the presence of static population levels overfishing by man has been the decisive factor in causing the rapid decline of the species in such areas as the Texas coast. This hypothesis may explain man's failure to restore barren areas by small-scale plantings. It is reasonable to assume that in marginal areas and in the presence of many enemies the oyster can perpetuate itself only when the adult population is very large. Admittedly,

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there are other areas in this latitude which provide an excellent environment for oyster populations. This situation merely emphasizes the fact that the suitability of an environment is dependent on the interaction of many ecological factors. Any single factor, such as the temperature gradient, is rarely a limiting factor in the survival of the species, although it may have far-reaching effects on the quality of the individuals making up the population.

These conclusions are not contradicted by reports of rapid shell growth in southern oysters (Ingle 1950). Although 3- to 4-inch oysters are frequently grown in the Gulf States in a year's time and 6-inch oysters in 30 months are not rare, oysters occasionally attain a length of 3 inches in 6 months in the Chesapeake Bay and 6-inch specimens have been reported that were only 17 months old (Beaven 1952). Because of the hibernation period at this latitude, these 6-inch specimens represent approximately 15 months of growing time. Surprise has been expressed in the literature (Gunter 1951) that Gulf oysters may increase as much as 0.3 mms. per day in shell length, but this may be compared with the 6-inch Chesapeake Bay oysters which must have grown at similar or faster rates. All of these examples describe a few unusual oysters or oysters growing under exceptional circumstance, and hence do not present a true picture of average growth rates. Moreover, oyster-shell length is of only relative importance in determining meat yield. In South Carolina, for example, clustered reef oysters with an average length of 3 inches are harvested when 2 years old and yield approximately 42 ounces of meats per standard bushel. Select single oysters growing in this area may require 3 years to attain the same length, but yield up to 120 ounces of meats per bushel.

In discussing the reasons for the apparently greater meat yield of oysters grown in colder waters, we need not consider the obvious differences resulting from the harvesting of cultivated oysters in the North as contrasted with the harvesting of clustered reef oysters for canning purposes in many southern areas. I should like to mention, however, that harvesting techniques may be of greater importance than the environment in determining the meat yield from oysters as well as from any other aquatic farm crop.

Oysters in northern areas are harvested primarily at or near hibernation temperatures when they have naturally accumulated the maximum amount of food reserves. In southern areas, where hibernation temperatures are the exception, the oyster does not build up large food reserves in its tissues and during the harvesting season its energy requirements are supplied by daily food consumption. As a result, the meats are smaller on the average than meats from oysters harvested in colder waters. This hypothesis is corroborated by circumstances occasionally found in the South. In some years sudden increases in water temperatures well above the level necessary for mass spawning may exist for some time before any spawning takes place in the spring (Hopkins 1935). In my opinion this is because the oysters, having little stored glycogen available, require days or even weeks to accumulate sufficient food material for the maturation of the gonads. Geographical differences in oyster-meat production have in the past been attributed to salinity differentials in the growing areas, i.e., greater production from more saline waters. However, I suggest that the effects of the temperature gradient offer a more logical explanation for these production differences.

We should recognize why oysters living in cold waters are able physiologically to store more food reserves than warm-water animals. The reasons underlying this condition justify the conclusion that northern oysters grow faster than southern oysters. Scientists have learned that the rates of many biological processes are dependent on temperature. The temperature coefficient for such biological processes, or Q_{10} as it is called, is approximately 2. This means that for each 10-degree rise in temperature within the tolerance levels of the animal, the speed of metabolic activity is approximately doubled. In the case of the oyster, we may interpret this to mean that month by month throughout the year, minimum food and oxygen requirements of the southern oyster are about twice as great as for the northern oyster. Since this greater food requirement is accompanied by a presumed decrease in food availability in the South, it appears reasonable that southern oysters have to devote much more of their energies to the problem of existing. Although water pumping and feeding rates may be similar at different temperature levels, the percentage of food consumed which can be devoted to body building, that is to growth and to storage, must be significantly greater in New England, for example, than it is in the South Atlantic and Gulf areas.

SUMMARY

1. Field and experimental observations indicate that volume rather than the customary length measurements provide a more critical evaluation of growth in the oyster.

2. The ratio of total oyster volume to shell volume provides a useful single index for estimating the meat-yielding potential of an oyster population when continuing observations are impractical.

3. Oyster growth varies geographically, responding to differences in the latitudinal temperature gradient.

4. Oysters in the latitude of Chesapeake Bay tend to grow faster and produce more meat in unit time than oysters growing north or south of this region.

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