The Ratio of Shell to Meat in *Mytilus* as a Function of Tidal Exposure to Air

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Introduction

The source of calcium for shell deposition in marine lamellibranchs has been shown to be the sea water. FOX and COE (1943) showed that the calcium available for this purpose from ingested food was not sufficient to account for shell growth, while ORTON (1925) showed that shell growth could occur in the almost complete absence of food. ROBERTSON (1941) stated that absorption of calcium ions from sea water was probable; RAO and GOLDBERG (1954) showed that such an intake to the tissues occurs. The utilization of calcium from this source in shell deposition has been shown by WILBUR and JODREY (1952).

RAO (1953) suggests that the intake and deposition of calcium by molluscs is an automatic function, directly dependent on the exposure of the animal to the source of calcium, the sea water. There is support for this in the work of WILBUR and JODREY (1952), who found that the amount of shell deposited by *Crassostrea virginica* was directly proportional to the period of exposure to sea water. RAO went on to show that in a sublittoral population of *Mytilus* the ratio of shell to meat was higher than in a littoral population. He suggested that the sublittoral population was exposed to the source of calcium (the sea water) for a longer period and thus greater accretions of calcium resulted. It has been our experience that, contrary to RAO's findings, bank mussels periodically exposed to air have, in general, thicker shells and less meat than mussels that are never so exposed, which would result in an increased ratio of shell to meat for these littoral mussels.

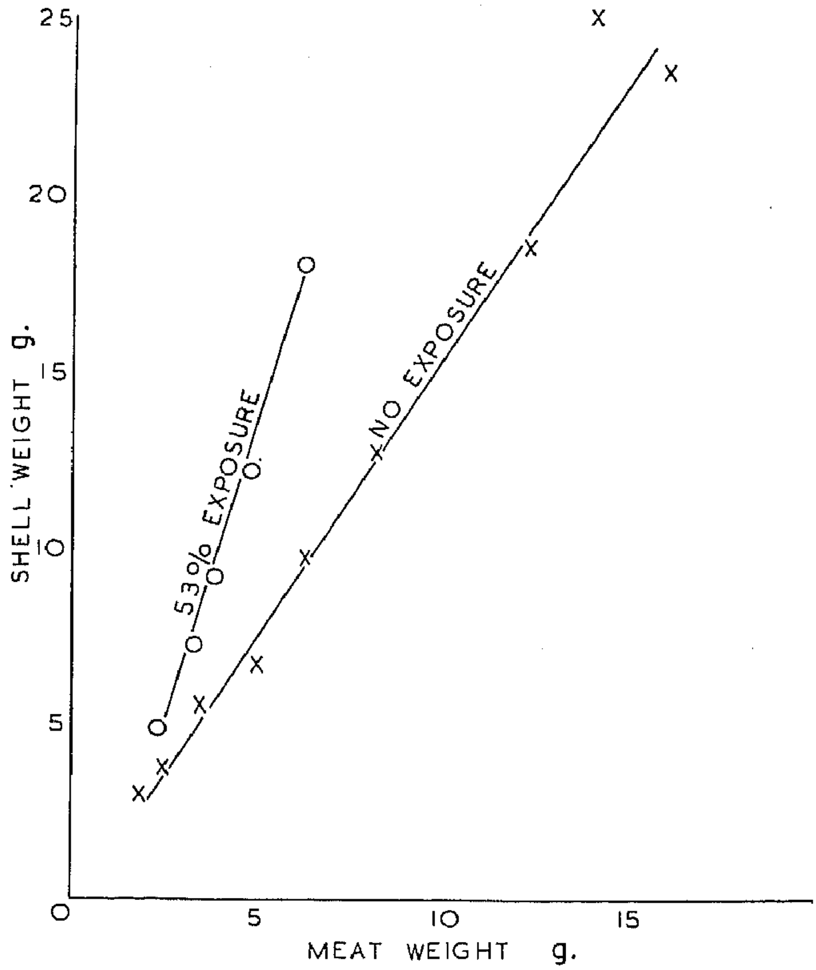

Figure 1. Showing the mean shell weight in relation to the mean meat weight.
o = ratio of shell to meat in littoral mussels.
x = ratio of shell to meat in sublittoral mussels.

Observations

To test these general observations a series of measurements was made on two groups of mussels of varying sizes from two tidal levels in the same area. Tidal recordings, which had been related to a permanent tide pole with an arbitrary zero (Figure 2), had been made in the estuary of the Conway River below the mussel purification tanks. This is a very sheltered position where wave action is at a minimum. The salinity drops to a low level at low water during and after periods of prolonged rainfall. Mussels are found in the area from a depth of about 20 ft. below low water extreme spring tides to a point above mean tide level. One group of mussels was dredged from a point 15 ft. below low water extreme spring tides and the other group was collected from the highest point at which mussels were found on the beach. From an analysis of tidal records over 14 days these latter mussels were found to have been uncovered for 53% of the time during that period.

The sublittoral dredged sample, which consisted of 73 mussels, ranging

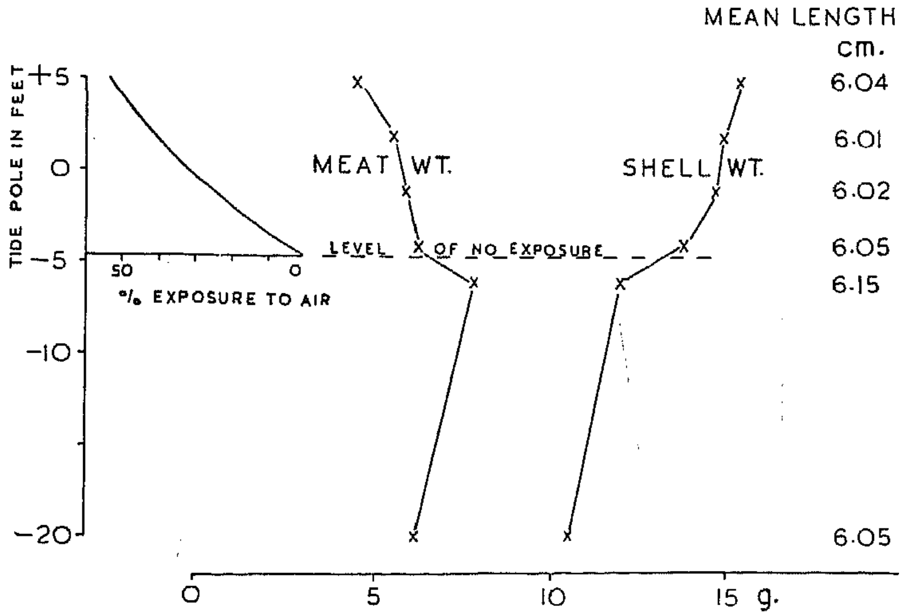

Figure 2. Variation of meat and shell weights in *Mytilus edulis* with variation of tidal level, with related percentage of time exposed to air. The levels are related to readings on a tide pole which had an arbitrary zero.

from 35 mm. to 89 mm. in length, was divided into nine length-groups, each containing between five and eleven mussels. The littoral sample, which consisted of 59 mussels ranging in length from 31 mm. to 69 mm., was similarly treated, being divided into 5 groups each containing between seven and twenty-one mussels. The shells and meat were both weighed wet immediately after opening. The mean shell weights are shown plotted against the mean meat weights in Figure 1. It can be seen that the mussels that had been exposed to air had the higher ratio of shell to meat.

To determine whether the decrease in ratio of shell to meat with decreased time of exposure to air was occasioned by an increase in meat weight or a decrease in shell weight, a series of samples was taken of mussels of approximately the same length at different levels on the beach and from the bed of the river. Four littoral and two sublittoral samples were taken. The shells and meats were allowed to dry on filter paper for two hours at room temperature before being weighed. The results, together with a curve showing time of exposure to air, are plotted in Figure 2. For a given length, meat weight increased with decreasing time of exposure, while shell weight decreased. The sublittoral samples from different depths showed little alteration in ratio of shell to meat with depth, but the sample from the greater depth showed a decrease in both shell and meat weight.

It has been shown (DUGAL and FORTIER, 1941) that an increase in the calcium content of the shell liquor occurs in oysters kept out of water for some days. To determine whether this effect was due to erosion of the shell or to a release of calcium from the tissues, as suggested by JODREY (1952), and whether it occurred over a short period, samples of 50 mussels were taken from the highest level at which mussels were found on the beach, at

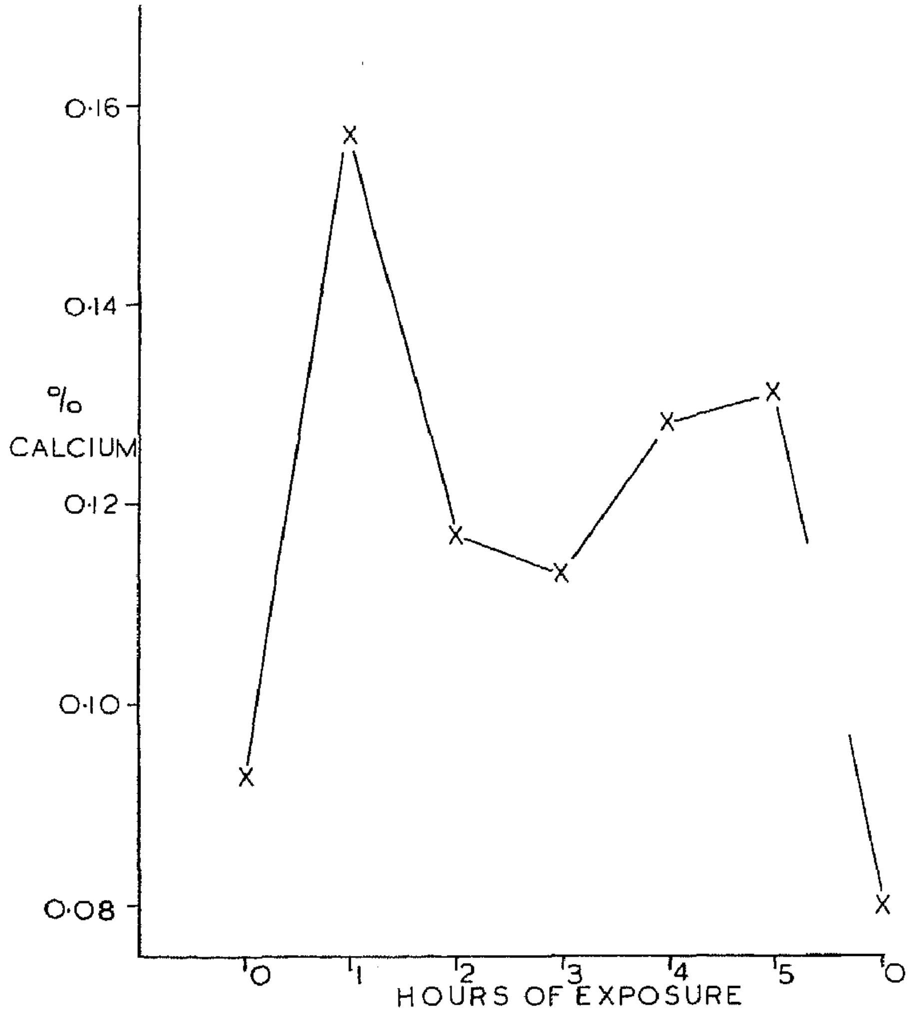

Figure 3. Calcium content of shell liquor and meat of *M. edulis* in relation to hours of exposure to air during a tidal period. Each point is based on a sample of 50 mussels and is the mean of duplicate analyses.

hourly intervals during that part of a tidal period in which they were out of the water. The pooled meats and shell liquor from each sample were analysed for calcium. It can be seen (Figure 3) that the percentage of calcium in the shell liquor and tissue is greater after the mussels have been out of water for some time than immediately after they are uncovered (0 hours exposure in Figure 3). On the following day a duplicate of the first sample was taken immediately after the mussels were uncovered, and this showed a return to a calcium lèvel of the same order as that recorded immediately after they were uncovered on the preceding day. We believe it is probable that the result of the analysis for one hour's exposure is anomalously high; the duplicate analysis gave a much greater divergence in this sample than in any of the others. If the result for one hour's exposure is disregarded, the calcium percentage after a period of exposure to air shows a significant increase, at a probability level of 0·01.

Discussion

The ratio of shell to meat can only be changed by a factor which influences shell growth differently from that of meat. The factors that have been suggested as affecting shell thickness in a natural population of mussels are light, wave action, and tidal exposure to air.

COULTHARD (1929) and HUNTSMAN (1921) have shown that light affects the growth-rate, bright light reducing linear growth. This reduction appears to be a result of change of shape. That this could affect the ratio of length to weight of the shell is apparent, but it is unlikely that it would have an effect on the ratio of shell weight to meat weight because in each case the mussels have equal access to sources of food and calcium.

FOX and COE (1943) suggest, and it is now generally known, that exposure to wave action results in slow growth and thicker shells. They also state that mussels living near or below low water have thinner and narrower shells than mussels from a higher level. In the area in which our observations were made there is not much wave action.

A reduction of salinity at low water would tend to have the same effect on the sublittoral mussels as exposure to air would have on the littoral mussels, tending to keep the mussels closed when salinity dropped below the tolerable level, thus lessening the differences between the samples. It is therefore reasonable to assume that the differences that exist between the samples are primarily due to differences in length of time of exposure to air.

In a population of mussels where length of time of exposure is the only variable, it would be expected that mussels exposed to air for half their life would be only half the size of mussels of the same age that were never exposed, because as the source of calcium was cut off, so would be the source of food; the net result would be that all the mussels had the same proportions with similar ratios of shell to meat. There is, however, another factor operating in the case of the mussels periodically exposed to air in that they are obliged to expend energy to maintain their basal metabolism while they are not feeding. This could result in a reduced proportion of meat in the mussels from the littoral part of the population, which would give higher ratios of shell to meat.

It can be seen from Figure 1 that the littoral mussels (53 % exposure) had much higher ratios of shell to meat than the continually submerged mussels. From Figure 2 it can be seen that this higher shell/meat ratio for the littoral mussels is the result both of a reduction in the meat weight and of an increase in the shell weight for mussels of a given length. The use of reserves to maintain basal metabolism could explain the reduction in meat weight. The erosion of the shell (Figure 3) should result in a lighter shell for the littoral mussels, if no other factors were involved. Erosion of the shell is a function of the basal metabolism, and if the energy consumption during basal metabolism has a greater proportionate effect on the meat than erosion has on the shell, the net result can be expressed, in terms of energy, as a loss in the quantity of meat.

The schematic representation of shell and meat growth in Figure 4 demonstrates the way in which basal metabolism could result in the littoral

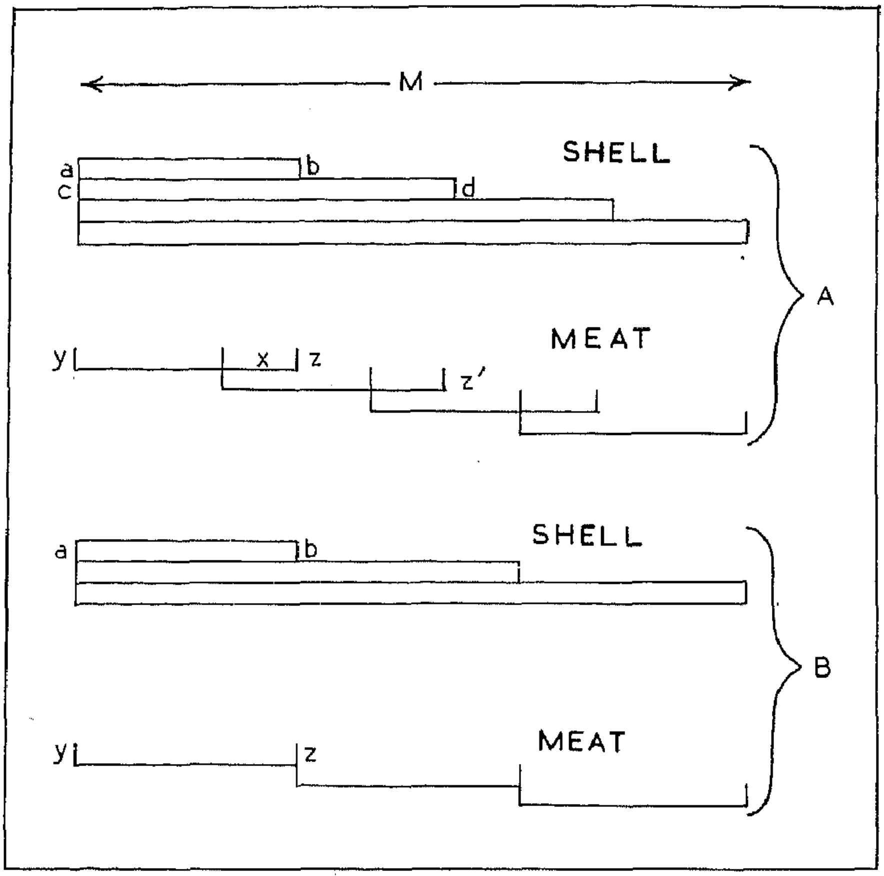

Figure 4. Schematic representation of the growths of shell and meat in (*A*) littoral and (*B*) sublittoral mussels, both having attained length *M*. The effect of basal metabolism on meat growth during exposure to air is represented by *x*. Shell growth (length and thickness) during one growth period is represented by *ab*, and meat growth by *yz*; in addition to the energy loss *x* in mussel *A* there will be a time interval between growth periods. On the assumption of 50% exposure to air and energy loss *x* for mussel *A*, the ratio of the age of mussel *A* to that of mussel *B* will be 8:3, and the ratio of their shell weights 4:3.

mussels having heavier shells than the sublittoral mussels. *A* represents a littoral mussel, *B* a sublittoral mussel, both having attained length *M*. There is evidence to suggest that shell deposition is continuous while the source of calcium is accessible to the mussel—that is, all the time it is covered with water. It is known that shell secretion occurs over the whole of the mantle. If we consider growth in periods of time, in the case of mussel *A*, shell growth *ab*, representing length and thickness, progresses simultaneously with the meat growth *yz*, while the mussel is covered. When the mussel is exposed by the fall of the tide, basal metabolism results in the consumption of reserves of energy, the loss of meat in terms of energy, in excess of the loss of shell by erosion, being represented by the resultant *x*. During the next period of immersion shell is laid down (*cd*), but since the energy lost through basal metabolism must be replaced to maintain the same mean condition, during the second growth period the quantity of meat grows to *z*, and four such growth periods are required to reach size *M*, and four units of shell thickness are produced. In the case of the sublittoral mussel, where there are no losses due to basal metabolism while the animal is not feeding, size *M* is reached in three growth periods, with a consequent reduction in thickness and weight of shells. Thus, if we assume a 50% exposure for mussel *A*, it will take *more* than twice as long to reach the same size as a mussel that is always submerged. In addition to the loss *x*, there will be a time interval between growth periods equivalent to the growth periods. The ratio of the age of mussel *A* to that of mussel *B* will be 8:3, and the ratio of their shell weights 4:3.

The energy loss due to basal metabolism can be the limiting factor in the height above low water at which a suspension-feeding shore animal can grow. It can be seen that a point will be reached when the whole of the energy taken in whilst the animal is immersed will be needed to maintain the basal metabolism during exposure to air.

COULTHARD (1929) showed that 50% exposure to air reduced growth in mussels (*M. edulis*) to a very low level and that mussels at that level had a mean growth during the period June–September of only one-sixteenth of that of mussels which were always submerged.

Summary

Mussels periodically exposed to air have been shown to have a higher ratio of shell to meat than mussels that were not exposed. Shell weight was found to increase, and meat weight to decrease, with increased time of exposure. A hypothesis to account for these differences is outlined. It is suggested that during the time that the mussels are closed through being out of water, the energy demands of basal metabolism reduces the meat more than internal chemical erosion reduces the shell.

A schematic representation is used to show how this could result in thicker shells in littoral than in sublittoral mussels.

It is suggested that the energy requirement of basal metabolism while the mussel is exposed to air could be the factor limiting the height above low water at which mussels are found on the shore.

Acknowledgements

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References

COULTHARD, H. S., 1929. "Growth of the sea mussel". Contrib. Canadian Biol., N. S., 4: 121–36.

DUGAL, L. P., & FORTIER, G., 1941. "Le métabolisme anaerobique chez les Mollusques. II. Variations du calcium et de l'acide lactique chez les huîtres". Ann. ACFAS, 7: 112.

FOX, L., & COE, W. R., 1943. "Biology of the California sea-mussel (*Mytilus californianus*). II. Nutrition, metabolism, growth and calcium deposition". J. Exper. Zool., **93** (2): 205–49.

HUNTSMAN, A. G., 1921. "The effect of light on growth in the mussel". Trans. Roy. Soc. Canada, Ser. 111, **15**: 23–28.

JODREY, Louise H., 1953. "Studies on shell formation. III. Measurement of calcium deposition and calcium turnover in mantle tissue using the mantle-shell preparation and Ca^{45}". Biol. Bull., **104** (3): 398–407.

ORTON, J. H., 1925. "The conditions for calcareous metabolism in oysters and other marine animals". Nature, **116**: 13.

RAO, K. P., 1953. "Shell weight as a function of intertidal height in a littoral population of Pelecypods". Experientia, **9** (12): 465.

RAO, K. P., & GOLDBERG, E. D., 1954. "Utilization of dissolved calcium by a Pelecypod". J. Cell. Comp. Physiol., **43** (3): 283–92.

ROBERTSON, J. D., 1941. "The function and metabolism of calcium in the Invertebrata". Biol. Rev., **116**: 106–33.

WILBUR, K. M., & JODREY, L. H., 1952. "Studies on shell formation. I. Measurement of the rate of shell formation using Ca^{45}". Biol. Bull., **103** (2): 269–76.