COMPARISON OF VARIOUS ALLOMETRIC RELATIONSHIPS IN INTERTIDAL AND SUBTIDAL AMERICAN OYSTERS¹

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ABSTRACT

The allometric relationships for the possible combinations of whole weight, dry body weight, soft body weight, shell weight, height, and length were computed for intertidal and subtidal South Carolina oysters. All relationships between intertidal and subtidal oysters involving dry body weight were significantly different. The percent moisture in the tissues was 81.1% for subtidal oysters and 83.4% for intertidal oysters and did not vary with size. Height appears to be the most useful parameter for predicting other biomass parameters from field data.

The American oyster, *Crassostrea virginica* (Gmelin), is one of the principal biomass components of many southeastern estuarine ecosystems, especially that of the North Inlet Estuary, Georgetown, S.C. (Figure 1). This study of intertidal and subtidal oysters was undertaken for two principal reasons: first, quantitative estimates of various oyster biomass parameters from linear or weight measurements would facilitate secondary productivity studies; second, comparison of the morphology of intertidal and subtidal oysters from a quantitative view would give a more exact meaning to the observed differences between the two forms.

Wilbur and Owen (1964) have noted that the size relations between an intact organism and one of its parts or between two of its parts over a wide size range can usually be expressed by an allometric equation or a power function of the following form:

$$Y = aX^{\mathbf{b}}.$$
 (1)

Y is some measure of a part, X is a measure of the whole body or another part, and a and b are constants. Equation (1) can be expressed in linear form by a logarithmic transformation as:

$$\log Y = \log a + b \log X. \tag{2}$$

The fitted coefficients, a and b, can easily be determined from a set of data using least-squares regression techniques.

MATERIALS AND METHODS

On March 21, April 11, May 2, July 25, October 3, and December 5, 1970, groups of intertidal and subtidal (1 m below mean low water) oysters were collected from the North Inlet area. Individual oysters were separated from clumps and scrubbed with a wire brush to remove fouling organisms. The whole live weight of an individual oyster was determined to the nearest 0.01 g and varied from 1.70 to 105.50 g. The oysters were then opened, the whole bodies and shells were separated from each other, and each was dried to a constant weight in an oven at 60°C. On May 31 and July 25, the weight of each soft body was determined, and the long and short axes of each shell were measured to the nearest 0.1 mm with vernier calipers.

The statistical treatments used in this study follow the methods of Steel and Torrie (1960), and the computations were carried out on an IBM 7040 computer.³

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FIGURE 1.-A map showing the location of North Inlet near Georgetown, S.C.

RESULTS

Table 1 gives the allometric coefficients for Equation (2) which best fitted the observed data for the various morphological relationships. The 95% Confidence Intervals (C.I.) are included for log a and b in order to allow an indirect comparison of these values for intertidal and subtidal oysters. The coefficients of a pair of equations were considered significantly different only if the range of log a or $b \pm$ its 95% C. I. did not overlap. In addition, Table 1 gives the number of pairs of data used (n) and the coefficient of determination (r^2) which gives an estimate of how well the data fit the allometric model. (Perfect fit would be $r^2 = 1.0$.)

All relationships involving dry body weight

were significantly different for intertidal and subtidal oysters.

The dry body weight/whole weight relationships for intertidal and subtidal oysters had significantly different b values, while the log avalues were not significantly different. These findings mean that the growth relationships for intertidal and subtidal oysters varied with size; that is, the fitted lines are not parallel (Figure 2).

The shell weight/dry body weight relationships for intertidal and subtidal oysters had significantly different log a values, but similar bvalues. The subtidal ratio of shell weight/dry body weight is significantly higher than the similar intertidal relationship (Figure 2).

The dry body weight/soft body weight fitted

Relationship $\frac{\gamma}{x}$	Tidal level	Coefficients ± 95% C.I.		•	
		log a	ь	* 3	*
dry body weight	Inter	-1.687 ± 0.044	0.960 ± 0.032	0.92	298
whole weight	Sub	-1.539 ± 0.123	0.828 ± 0.081	0.77	107
shell weight	Inter	1.538 ± 0.026	0.966 ± 0.045	0.90	187
dry body weight	Sub	1.652 ± 0.040	0.934 ± 0.097	0.77	107
dry body weight	Inter	-0.779 ± 0.016	0.970 ± 0.036	0.97	80
oft body weight	Sub	-0.741 ± 0.020	0.931 ± 0.042	0.97	70
try body weight	Inter	-2.383 ± 0.172	2.214 ± 0.197	0.87	80
height	Şub	-1.889 ± 0.198	1.794 ± 0.232	0.78	70
lry body weight	Inter	-1.832 ± 0.133	2.694 ± 0.258	0.85	80
length	Sub	-1.465 ± 0.223	1.987 ± 0.402	0.59	70
hell weight	Inter	-0.142 ± 0.017	1.002 ± 0.012	0.99	187
vhole weight	Sub	-0.109 ± 0.038	0.992 ± 0.025	0.98	107
hell weight	Inter	-0.803 ± 0.140	2.301 ± 0.148	0.92	80
height	Sub	-0.572 ± 0.197	2.266 ± 0.230	0.85	70
hell weight	Inter	-0.172 ± 0.142	2.682 ± 0.274	0.83	80
hort axes width	Sub	-0.105 ± 0.228	2.635 ± 0.409	0.65	70
vhole weight	Inter	-0.689 ± 0.127	2.329 ± 0.145	0.93	80
height	Sub	-0.451 ± 0.194	2.262 ± 0.231	0.85	70
vhole weight	inter	-0.056 ± 0.139	2,726 ± 0.270	0.84	80
length	Sub	-0.008 ± 0.224	2.645 ± 0.404	0.72	70
eight	Inter	-0.090 ± 0.085	0.689 ± 0.097	0.85	80
ength	Sub	-0.047 ± 0.106	0.594 ± 0.124	0.57	70
vhole body weight	Inter	1.013 ± 0.024	0.973 ± 0.052	0.95	80
oft body weight	Sub	1.038 ± 0.044	1.072 ± 0.097	0.88	70
hell weight	Inter	0.088 ± 0.026	0.957 ± 0.055	0.94	80
oft body weight	Sub	0.092 ± 0.048	1.069 ± 0.099	0.87	70
eight	inter	0.739 ± 0.014	0.391 ± 0.030	0.89	80
oft body weight	Sub	0.681 ± 0.024	0.414 ± 0.052	0.79	70
ength	Inter	0.407 ± 0.014	0.309 ± 0.030	0.85	80
oft body weight	Sub	0.434 ± 0.026	0.290 ± 0.054	0.63	70

TABLE 1.—A comparison of the allometric coefficients for various morphological relationships for intertidal and subtidal oysters utilizing the equation $\log Y = \log a + b \log X$.



FIGURE 2.—The fitted allometric curves for the shell weight/dry body weight and dry body weight/whole weight relationships in intertidal (I) and subtidal (S) oysters.

equations had significantly different log a values (Figure 3). The ratio between dry body weight and soft body weight expresses the percent moisture in the tissues. The fitted expressions show that the percent moisture is almost constant with size since the fitted b values approach 1. The percent moisture is 83.4% in the intertidal oysters and 81.1% in the subtidal oysters.

The height/soft body weight relationships had significantly different log a values, but the b values were not significantly different (Figure 3).

The dry body weight/height relationships were significantly different in respect to their fitted log a values; the b values were not significantly different. Significantly different log a values, but similar b values indicate that the fitted curves are almost parallel (Figure 4).

The dry body weight/length relationships were the only fitted data with both significantly different log a and b values (Figure 4).

No significant differences were found between intertidal and subtidal oysters in the remaining relationships, and no significant differences were found between samples when each sample was calculated separately.

Data for subtidal oysters tended not to fit the allometric relationship as well as the intertidal oyster data. This tendency is indicated by the lower r^2 values for subtidal models, where $r^2 \times 100$ is an estimate of the percent variability of the data explained by a model. The lower r^2 values for subtidal oyster relationships may be partially attributed to the fact that fewer observations were made on this group of oysters.

DISCUSSION AND CONCLUSION

The quantitative relationships between the various parameters of weight and linear size for intertidal and subtidal oysters of different sizes have never been adequately described previously.

All significantly different relationships between intertidal and subtidal oysters involve dry body weight. Since a large proportion of the nutrients and energy available to the secondary consumers in the oyster food web is contained within the body of the oyster, this parameter is important in productivity studies. It is also important that the prediction of dry body weight



FIGURE 3.—The fitted allometric curves for the dry body weight/soft body weight and height/soft body weight relationships in intertidal (I) and subtidal (S) oysters.



FIGURE 4.—The fitted allometric curves for the dry body weight/height and dry body weight/length relationships for intertidal (I) and subtidal (S) oysters.

from different measurements depends on significantly different models for the intertidal- and subtidal-zone oysters.

The shell weight/dry body weight ratio for *Crassostrea virginica* at North Inlet is significantly higher in subtidal oysters than in intertidal oysters. This observation supports the general observation of Galtsoff (1964) that the shells of intertidal oysters are usually thinner than those of subtidal oysters. The higher shell weight/dry body weight ratio for subtidal versus intertidal oysters is substantiated by the findings of Wilbur and Jodrey (1952), who showed that the amount of shell deposited by *C. virginica* was directly proportional to the time exposed to sea water. Rao (1953), observing a similar relationship between intertidal and subtidal Mytilus edulis and M. californianus, believed that the deposition of calcium by molluscs is directly dependent on the amount of time the animal is submerged. Baird and Drinnan (1957), finding a lower ratio of shell weight/dry body weight in subtidal *M. edulis* than in intertidal mussels of the same species, suggested that closed, exposed animals undergo anerobic metabolism which reduces body tissues more rapidly than chemical erosion of the shell. Lent (1957), discovering no differences in the shell weight/dry body weight ratio for the mussel Modiolus de*missus* from different tidal levels, attributed the result to the air-gaping phenomenon exhibited by *Modiolus*, which allows this organism to continue aerobic metabolism in both the submerged and exposed states. At present, it is doubtful if a general statement can be made that will resolve the different hypotheses. Thus, one might speculate that local environmental conditions such as tidal range, wave action, and water chemistry may be important in determining shell weight/dry body weight ratios.

In this study, the percentage water in the tissues, as calculated from the dry body weight/soft body weight relationship, falls within the reported range of 75-88% for *Crassostrea virginica* (Galtsoff, 1964). Intertidal oysters appear to retain a significantly higher proportion of their body water than subtidal oysters. The higher retention of water in intertidal oysters may result from some form of physiological adaptation to the intertidal environment, such as an increased ability to remain closed when they are exposed.

The relationships of dry body weight/whole body weight, dry body weight/height, and dry body weight/length are all different for intertidal and subtidal oysters, but there appears to be no obvious biological reason to explain these differences. It may simply be that any differences in dry body weight for intertidal and subtidal oysters are translated into differences in allometric relationships.

Galtsoff (1964) has noted that the condition index (dry body weight/volume of shell cavity \times 100) varies seasonally with the reproductive status of the adult oyster. The condition index was not measured in the present study, and no significant seasonal variations were found in any of the relationships.

It is interesting that in the present study no significant differences were found in the height/ length relationships for intertidal and subtidal oysters. Glaser (1903), Orton (1936), Gunter (1938), and Galtsoff (1964) have noted differences in the long axis length/short axis width relationship for intertidal and subtidal oysters and have offered various reasons for these differences.

From the practical aspect, height appears to be the most useful parameter to predict other biomass parameters because of high coefficient of determination values in those relationships utilizing height and less time necessary to make each measurement.

In conclusion, quantitative relationships between various parameters of size can be different for oysters from intertidal or subtidal environments. These differences are important functionally in the biology of the organism and practically as predictive tools for ecological investigations.

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