RELATIONSHIPS BETWEEN ZOOPLANKTON DISPLACEMENT VOLUME, WET WEIGHT, DRY WEIGHT, AND CARBON[1]

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ABSTRACT

Interconversion of various measures of zooplankton biomass have great utility in studies requiring nondestructive techniques, or for interpretation of past data. In establishing predictive relationships between such measures, the appropriate regression to use is the geometric mean estimate, which provides a regression line in which the regressions of X on Y and Y on X are identical. We have employed this type of analysis in determinations on samples from diverse sea areas in different seasons and have determined that statistically significant relationships exist between carbon, wet weight, displacement volume, and dry weight when a constant technique is used. The slope of the regression line for log transformed values for carbon vs. dry weight and wet weight vs. displacement volume was sufficiently close to unity to assume a straight percentage conversion between these values. Carbon was 31-33% of dry weight and wet weight was 72-73% of displacement volume, according to our techniques. Comparability of different techniques for a biomass measurement may be poor, especially in the case of displacement volume and wet weight measurements due to variations in the interstitial water content. Moreover, interstitial water content varies inversely with total biomass density, which accounts for the absence of a simple percentage relationship between wet weight or displacement volume and other measures of zooplankton biomass.

Biomass is a classic and useful measure of the zooplankton standing crop. A number of techniques exist to measure it. Four commonly used techniques involve measurement of displacement volume (Yentsch and Hebard 1957; Frolander 1957; Sutcliffe 1957; Tranter 1960; Ahlstrom and Thrailkill 1963), wet weight (Nakai and Honjo 1962), dry weight (Lovegrove 1966), and carbon (Curl 1962; Platt et al. 1969). For most studies, especially those determining energy flow through food chains, carbon is the most fundamental of these gross measures. Many zooplankton collections frequently serve several purposes and the destructive techniques required to determine carbon or dry weight frequently cannot be employed. An alternative is to measure displacement volume or wet weight, and convert the data into either dry weight or carbon. These latter techniques, if done properly, are nondestructive since the organisms can still be identified when re-suspended in liquid. There is an obvious need for conversion factors that reliably define the relationship between the various biomass measures. This need also arises when data based on different techniques are compared. Although conversion factors exist in the literature, they often are based on data from restricted sea areas. Further, in some cases, biomass determinations were made by techniques which are no longer recommended (see Lovegrove 1966). The objective of this paper is to more satisfactorily define the relationships between the biomass measures mentioned above. Using both data derived from samples collected from diverse oceanic areas over the past 6 yr and data selected from the literature, we have empirically determined linear regression equations relating pairs of biomass measures.

THEORETICAL CONSIDERATIONS

Ideally, any two biomass measures, X and Y should be related by a constant of proportionality, a, such that

$$Y = a\, X^{\beta}, \tag{1}$$

where $\beta = 1.0$. A measurement error or bias which occurs as a constant fraction of the biomass results only in a change in the value of a. When natural variability or an error factor(s) in X or Y is disproportionate or inversely proportional to the amount of biomass, β cannot be assumed to equal

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1.0 and Y is not a simple percentage of X. If β is a constant, then the $\log_{10}$ of the two measures will be linearly related:

$$\text{Log}_{10}(Y) = \text{Log}_{10}(a) + \beta \, \text{Log}_{10}(X). \quad (2)$$

In the sections which follow, we will show that in most cases $\beta \neq 1.0$ and equation (2) is adequate for describing the linear relationship between log transformed measures of biomass.

METHODS

The station locations where samples were collected are shown in Figure 1 (symbol key given in Table 1). At many of these stations, more than one sample was collected. A single symbol may represent a number of collections as indicated in Table 1. Not shown are the stations of *Gosnold* 140, a cruise to the coastal upwelling region off Peru.

Collections were made with 70-cm or 100-cm diameter ring nets, 70-cm diameter Bongo nets (McGowan and Brown 1966), or the 50 × 50 cm net (Bé et al. 1971), all equipped with a flowmeter (Table 1). In shallow regions, Buzzards Bay, *Atlantis II* 52 (continental Atlantic shelf), *Gosnold* 140 (Peru Current), *Gosnold* 166 (New York Bight), tows were made to near the bottom. In deeper waters, oblique tows were generally made to below 300 m.

Ring net collections were generally split with a plankton splitter (McEwen et al. 1954). One-half was preserved in 10% buffered Formalin[4] for displacement volume analysis and the other half was frozen in a chest freezer for wet weight, dry weight, and carbon analyses (re Bermuda Table 1: Menzel and Ryther (1961) do not state how this half was stored prior to analysis). A similar procedure was carried out for Bongo net collections; one of the paired samples was preserved in Formalin while the other was frozen.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

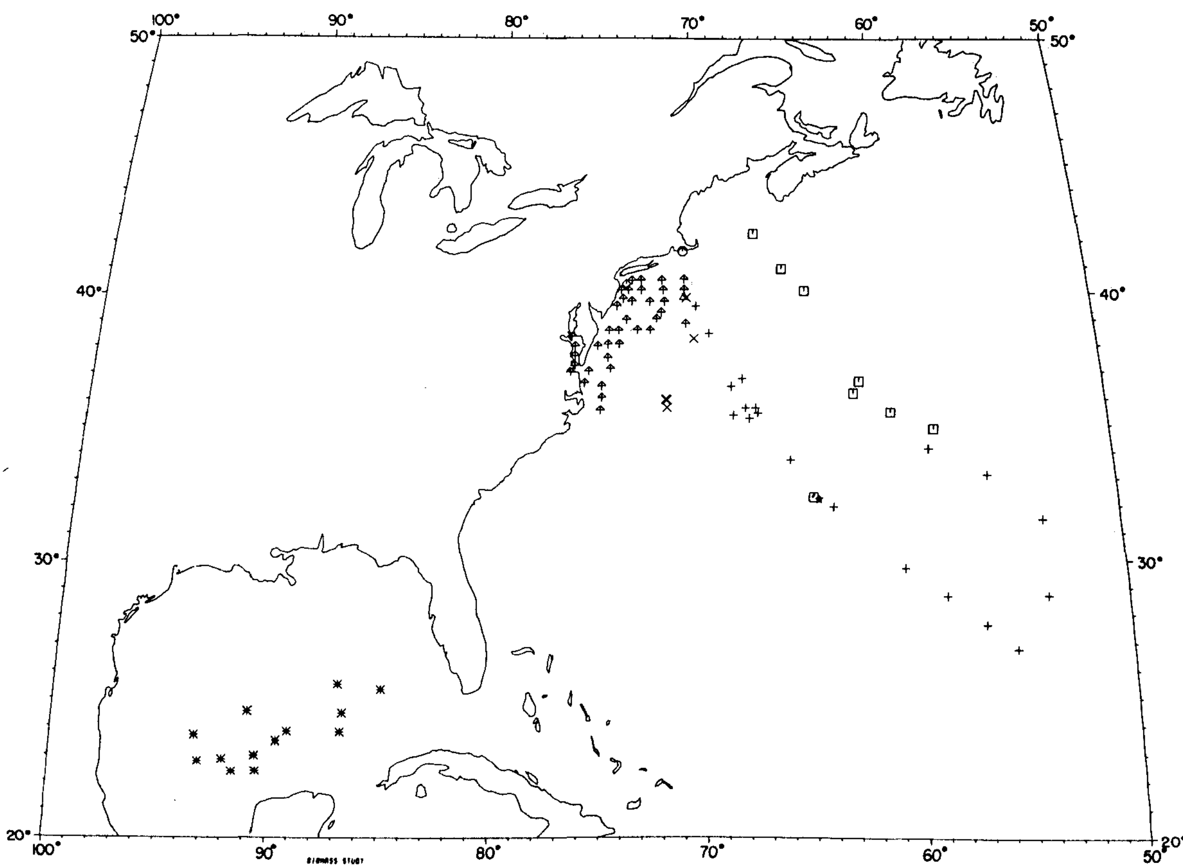


FIGURE 1.–Location of zooplankton collection sites. For symbols, see Table 1.

TABLE 1.—Number of observations and symbol designation for each cruise or area from which zooplankton samples were collected. The symbols are used in Figures 1 and 3-5.

Cruise or area	Symbol	Date(s)	Number of observations: Displacement volume	Wet weight	Dry weight	Carbon	Type of net (mesh)
Buzzards Bay	○	Jan.-June 1972	15	16	16	16	70 cm (240 µm) diam.
Slope	△	June-Aug. 1972	14	12	14	14	100 cm (333 µm) diam.
Bermuda[1]	☆	1957-59	52	0	52	0	100 cm (366 µm) diam.
Gosnold 140	⌑	May 1969	[2]0	0	33	33	70 cm (240 µm) diam.
Gosnold 166	◇	June 1970	32	0	33	33	70 cm (240 µm) diam.
Atlantis II 48	✳	Nov. 1968	0	0	20	20	70 cm (240 µm) diam.
Atlantis II 52	✢	Sept. 1969	0	0	37	37	70-cm (240 µm) diam. Bongos
Atlantis II 71	+	Sept. 1972	27	43	43	42	100 cm (333 µm) diam.
Chain 111	□	Feb. 1973	13	13	13	0	100 cm (333 µm) 70-cm Bongos
Knorr 35 II	×	Nov. 1973	10	11	11	0	100 cm (333 µm) 70-cm Bongos
Bé North Atlantic	◇	—[3]	229	229	229	0	50 × 50 cm (202 µm)
Bé South Atlantic	+	—[4]	176	192	193	0	50 × 50 cm (202 µm)

[1]Data from Menzel and Ryther (1961).
[2]Omitted, bad data.
[3]See Bé et al (1971) for geographical and seasonal coverage.
[4]Data from Bé (footnote 5).

Displacement volumes were measured by one of two techniques. The Mercury Immersion method of Yentsch and Hebard (1957) was used to determine the values given by Menzel and Ryther (1961-Bermuda), by Bé et al. (1971-North Atlantic) and Bé (1973-unpubl. data for the South Atlantic).[5] A modified version of the Mercury Immersion technique was used to measure displacement volumes on *Gosnold* 140, but further work has shown that the method has significant variable errors and is unreliable (Grice and Wiebe unpubl. data). We have not, therefore, used the *Gosnold* 140 displacement volume data. All other displacement volumes were measured by the method described by Ahlstrom and Thrailkill (1963) after removal of all organisms larger than 5 cc. For split samples, organisms larger than 5 cc were removed prior to the split. On *Gosnold* 166, displacement volumes were run prior to sample preservation (see Vaccaro et al. 1972 for data) and again 2 yr after preservation. Contrary to the findings of Ahlstrom and Thrailkill (1963), shrinkage did not occur (Figure 2). These samples were, however, heavily dominated by copepods (Wiebe et al. 1973) which are least likely to undergo shrinking.

Wet weight was measured by straining the plankton through a 333-µm plankton gauze, rinsing with freshwater, and blotting the remaining mass on absorbant paper towels until water was no longer absorbed onto the towel. The biomass was then transferred to a pre-weighed glass jar with a stainless steel spatula. The jar was weighed on a Mettler balance to ± 2.5 mg and the wet weight of plankton determined by subtracting the jar weight from the total. Each jar was then dried to constant weight in an oven at 60°C. This

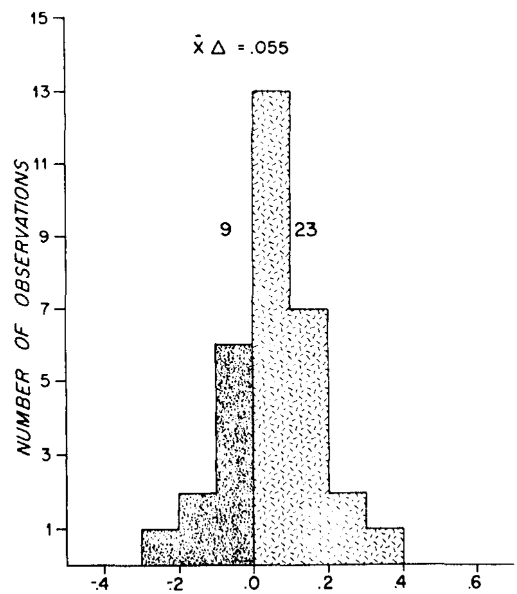


FIGURE 2.—Distribution of differences between displacement volumes measured 2 yr after preservation and the live displacement volume. The live displacement volumes ranged from 30 to 321 cc (0.57 to 2.53 cc/m³) and the 2-yr values ranged from 38 to 340 cc (0.58-2.40 cc/m³).

[5]Bé, A. W. H. 1973. Studies of zooplankton standing stock in the South Atlantic. Unpubl. final tech. rep. to Natl. Sci. Found., 14 p.

frequently took 2 wk or longer owing to the large volumes of plankton collected. Dried samples were pulverized and an aliquot(s) of the powder used to determined carbon in either a Perkin-Elmer No. 240 or a Hewlett Packard No. 185 B carbon, hydrogen, nitrogen analyzer. A number of exceptions to this procedure are evident in Table 1. In some cases, wet weight was not measured; in others, carbon was not determined.

All data presented below were standardized to biomass per cubic meter and then logarithmically transformed (base 10) before use in the regression analyses.

RESULTS

Several regression lines can be used to express the relationship between pairs of variables (Ricker 1973). The appropriate one is determined by the frequency distribution of the parent population as well as the nature of the error sources in the measurements (natural or measurement error). Since the biomass measures are all subject to natural variability and measurement error and since the observations presented cannot be assumed to be a random sample from a bivariate normal population, the "geometric mean (GM) estimate of the functional regression of Y on X" (Ricker 1973:412) is appropriate. As Ricker points out, this regression line minimizes the sum of the products of the vertical and horizontal distance of each point from the line. Thus, the GM regression lines of Y on X and X on Y are identical. Given the GM regression equation:

$$Y' = u + vX', \tag{3}$$

where $Y' = \log(Y)$ and $X' = \log(X)$, one can determine both an X given Y or Y given X. Although Ricker's (1973) paper should be consulted for an in depth discussion of the assumptions and computations, we note that the slope, v, is given by:

$$v = \pm \frac{b}{r} = \pm \sqrt{\frac{\Sigma(y_i' - \overline{Y}')^2}{\Sigma(x_i' - \overline{X}')^2}}, \tag{4}$$

where b is the slope of the predictive regression of Y' on X' and r is the correlation coefficient. The Y'-axis intercept, u, is easily determined by:

$$u = \overline{Y}' - v\overline{X}'. \tag{5}$$

Plots of the values used in the GM regressions are given in Figures 3-5. The equations are listed in Table 2. All equations have slopes significantly different from zero ($P<0.001$). As indicated above, in the case where β of Equation (1) (v of Equation (3)) is equal to 1.0, one biomass measure is a straight percentage of another. The only regressions with a v approaching 1.0 compare dry weight to carbon and displacement volume to wet weight. In these cases, predicted carbon varies from 31 to 33% of zooplankton dry weight and predicted wet weight varies from 72 to 73% of displacement volume. In all other regressions, a variable bias is present which causes v to deviate from 1.0. We believe that a large portion of the bias is caused by the interstitial water present in displacement volumes and wet weights. This bias is inversely proportional to the sample size; i.e., a small sample

TABLE 2.–Functional (geometric mean) regression equations for pairs of biomass measures. Carbon: C; dry weight: DW; wet weight: WW; displacement volume: DV; Bé et al. (1971) and Bé (footnote 5) wet weight: BWW; Bé et al. (1971) and Bé (footnote 5) displacement volume: BDV; Bé et al. (1971) and Bé (footnote 5) dry weight: BDW; Platt et al. (1969) dry weight: PDW; Platt et al. (1969) carbon: PC. Logarithms to the base 10.

Equation	Regression equation	N	Variance of slope	r^2
1	Log (DV) = −1.429 + 0.808 Log(C)	87	0.0003187	0.96
2	Log(WW) = −1.537 + 0.822 Log(C)	70	0.0008303	0.92
3	Log(DW) = 0.508 + 0.977 Log(C)	193	0.0001438	0.97
4	Log(DV) = −1.828 + 0.848 Log(DW)	161	0.0001814	0.96
5	Log(WW) = −1.983 + 0.922 Log(DW)	93	0.0005800	0.94
6	Log(DV) = 0.670 + 0.950 Log(WW)	77	0.0013729	0.90
7	Log(BWW) = −1.897 + 0.835 Log(BDW)	420	0.0009725	0.63
8	Log(BDV) = −1.826 + 0.754 Log(BDW)	404	0.0011106	0.56
9	Log(BDV) = −0.219 + 0.848 Log(BWW)	403	0.0006079	0.75
10	Log(PDW) = 0.558 + 1.024 Log(PC)	45	0.0148049	0.39
11	Log(DV)[1] = 1.048 + 0.821 Log(DW)	110	0.0010510	0.83
12	Log(WW)[1] = 0.975 + 0.946 Log(DW)	94	0.0010173	0.90
13	Log(DV)[1] = 0.078 + 1.026 Log(WW)	75	0.0022271	0.85

[1]Note that biomass data used to determine equations 1-10 were standardized to per cubic meter while the data used to determine equations 11-13 were not standardized.

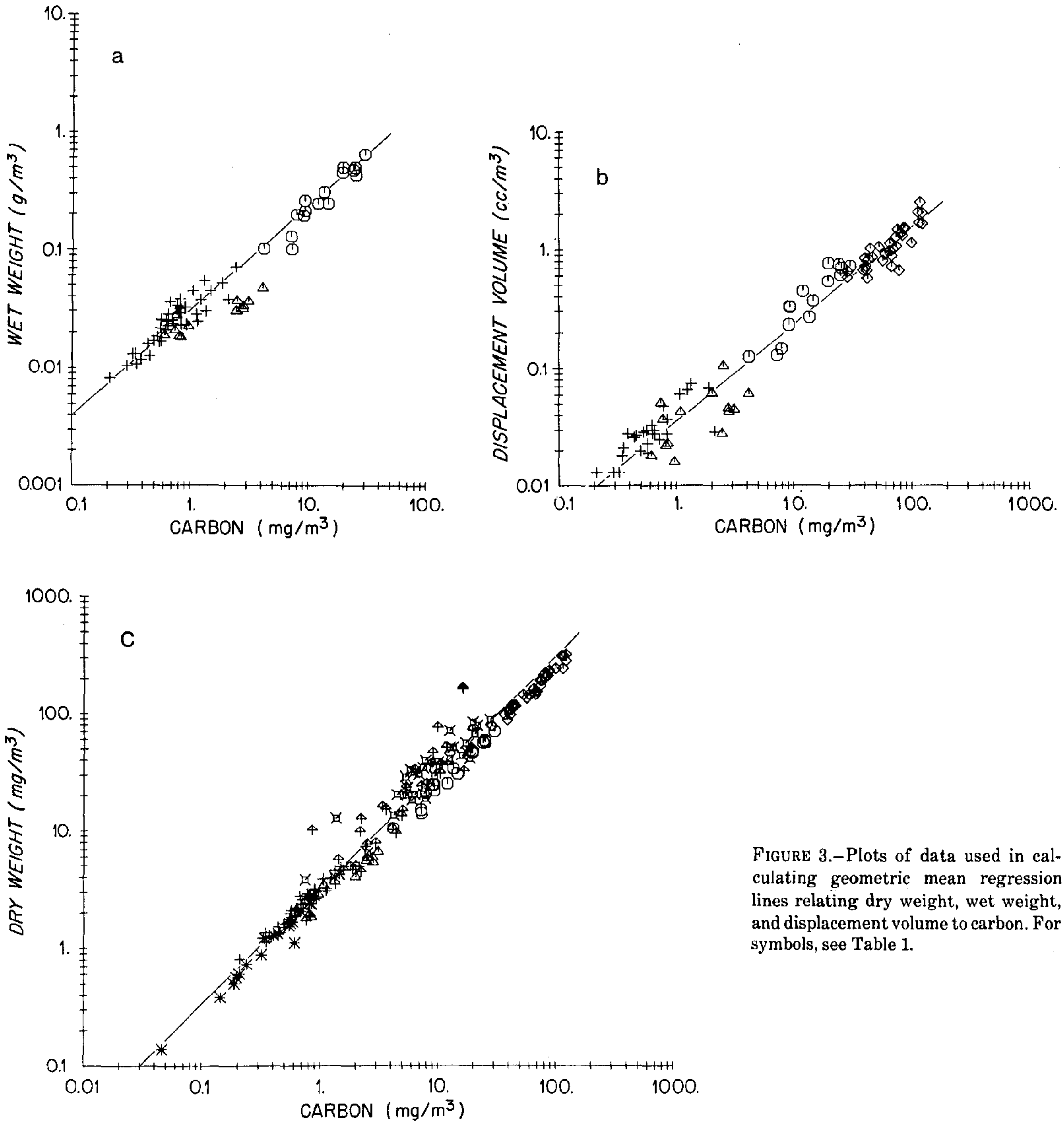
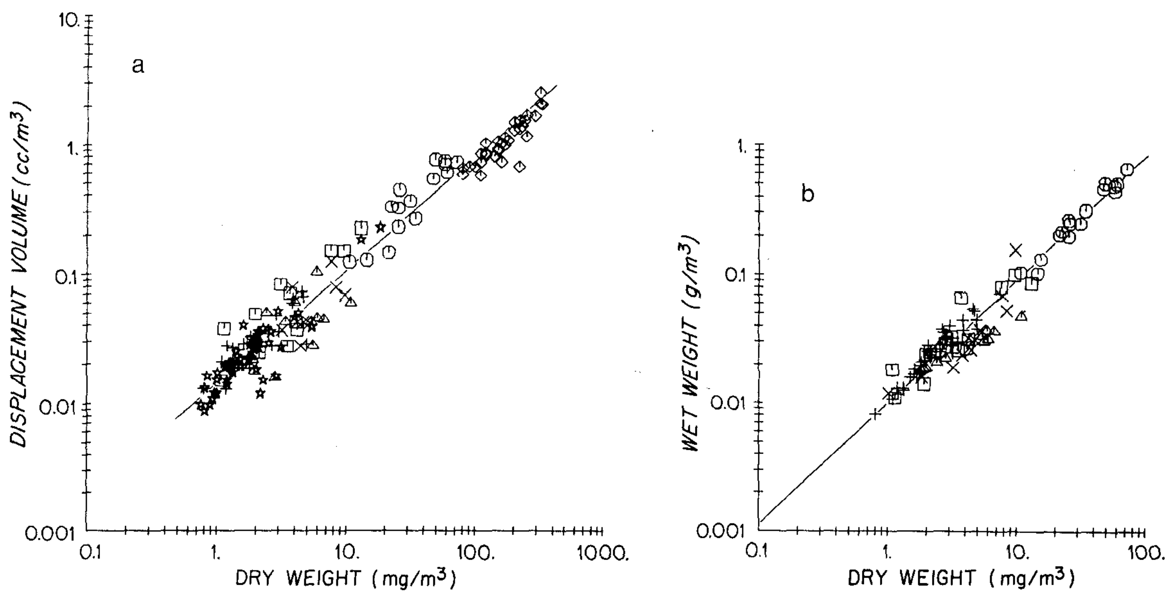


FIGURE 3.—Plots of data used in calculating geometric mean regression lines relating dry weight, wet weight, and displacement volume to carbon. For symbols, see Table 1.

appears to have a larger percentage of interstitial water than a large sample. It is evident in our log transformed raw data as well as the data standardized to biomass per cubic meter and then log transformed (see Table 4). The reason why the bias is not significantly influenced by the standardization to biomass per cubic meter results from the fact that the volume of water filtered in collecting most samples was quite similar, between 100 and 1,000 m^3, while the biomass per cubic meter varied by as much as four orders of magnitude. As a result of the variable bias, it is not valid to assume a simple percentage relationship between the other pairs of biomass estimators. For example, dry weight is approximately 5% of displacement volume for low biomass per cubic meter and approximately 13% for high biomass per cubic meter.



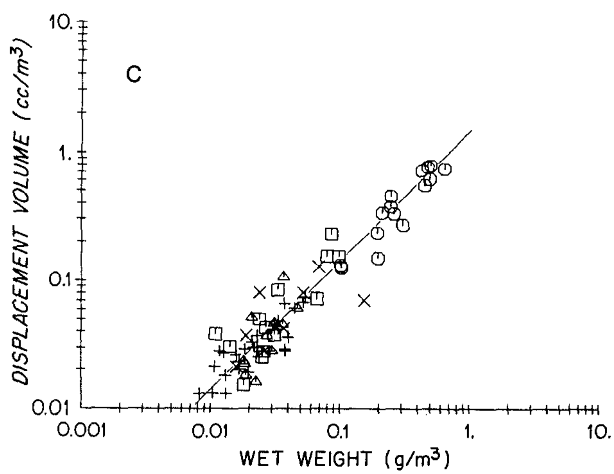


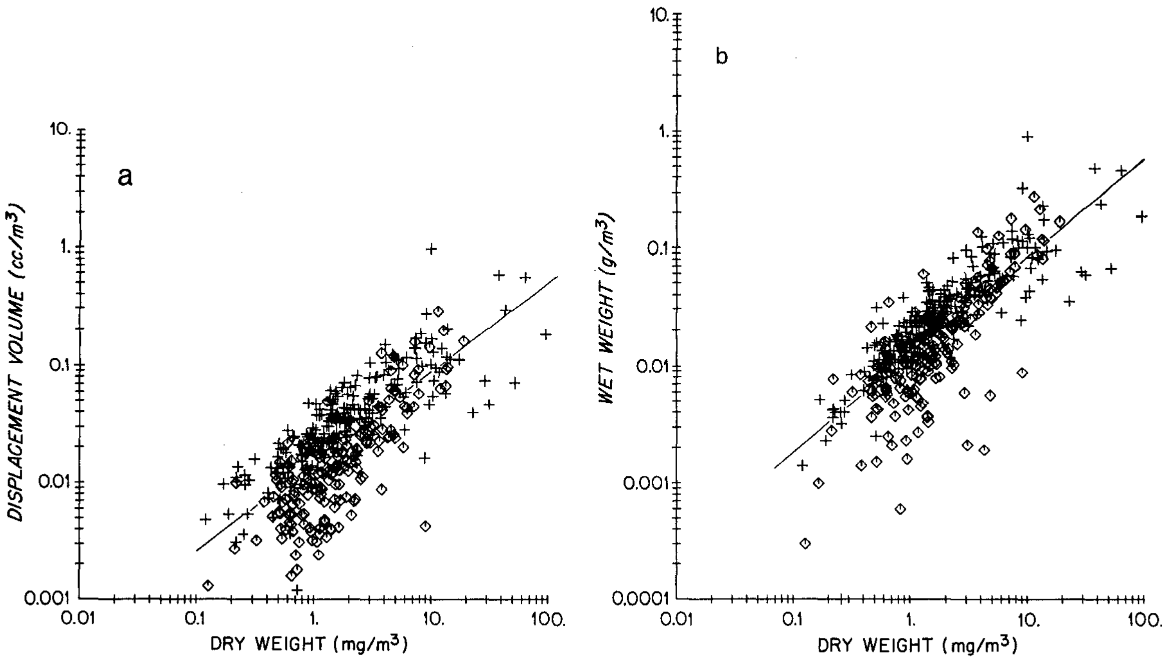
FIGURE 4.—Plots of data used in calculating geometric mean regression lines relating wet weight and displacement volume to dry weight and displacement volume to wet weight. For symbols, see Table 1.

Confidence limits can be calculated for predicted values of X or Y. Following Ricker (1973:411), the general form of the variance estimate for a single estimate of Y' given X' is:

$$S_{y'x'}^2\left(1+\frac{1}{N}+\frac{(P_{x'}-\overline{X}')^2}{SSX'}\right), \qquad (6)$$

where $S_{y'x'}^2$ is the variance of observations from the regression line in the vertical direction, N is the number of observation pairs in the regression, and $P_{x'}$ is the value of X' used to estimate Y'. In the reverse case where X' is being predicted, $S_{x'y'}^2$, SSY', $P_{y'}$, and $\overline{Y}'$ are substituted for $S_{y'x'}^2$, SSX', $P_{x'}$, and $\overline{X}'$. Because we have used GM regression equations rather than predictive regression equations, the use of Expression (6) is not strictly legitimate. However, Ricker (1973:413) finds the error involved is small and concludes that "... it is possible to recommend using ordinary symmetrical confidence limits for the GM regression. They are a reasonable approximation to the true limits and will rarely lead to incorrect conclusions."

The values required to use Expression (6) to calculate confidence limits for predicted X's or Y's are given in Table 3. This variance and the t_{95} value are used to construct confidence limits for the logarithms:



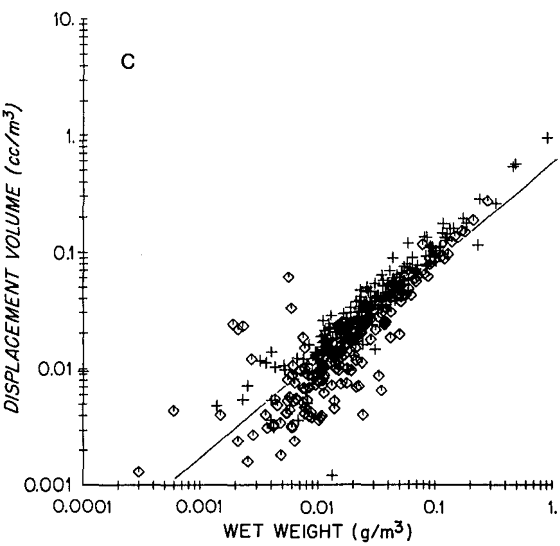


FIGURE 5.—Plots of Bé et al. (1971) and Bé (footnote 5) data used in calculating geometric mean regression lines relating wet weight and displacement volume to dry weight, and displacement volume to wet weight. For symbols, see Table 1.

$$Y' \pm t_{95}\sqrt{\hat{V}\text{ar}\, Y'} \text{ or } X' \pm t_{95}\sqrt{\hat{V}\text{ar}\, X'}.$$

Antilogging provides multiplicative limits for the untransformed data. For example, suppose an estimate of carbon is desired having measured a displacement volume (Y) of 0.1 cc/m³. Using Equation 1 in Table 2 and Expression (6) the following values result:

Log (Y)	*Log* (X)	X(*mg*/m³)	*Log (upper limit)*	*Upper limit*	*Log (lower limit)*	*Lower limit*
-1.0	0.557	3.61	0.916	8.25	0.198	1.58

Thus, the antilogged estimate of carbon is 3.6% of the displacement volume with upper and lower 95% limits of 8.3% and 1.6%.

Comparison of the regressions based upon the data of Bé et al. (1971) and Bé (footnote 5) with the

TABLE 3.–Values required to calculate 95% limits for values of X or Y predicted from regression equations in Table 2. The t_{95} value is based on the number of observations for each regression. For comparison abbreviations see Table 2 caption.

Comparison	t_{95}	Prediction of Y			Prediction of X		
		$\bar{X}$	SSX	S^2_{yx}	$\bar{Y}$	SSY	S^2_{xy}
DV vs. C	1.98	0.8310	69.3796	0.022095	−0.7573	47.1915	0.032483
WW vs. C	2.00	0.2076	22.0394	0.018282	−1.3663	16.1224	0.024992
DW vs. C	1.96	0.6456	117.7726	0.016987	1.1383	115.5700	0.017311
DV vs. DW	1.96	0.8369	106.4068	0.019299	−1.1181	79.6486	0.025782
WW vs. DW	1.98	0.6473	19.9736	0.011558	−1.3868	18.0252	0.012808
DV vs. WW	1.99	−1.3706	17.3509	0.023822	−1.2347	17.4390	0.023701
BDV vs. BDW	1.96	0.2408	85.9032	0.093843	−1.6446	63.8768	0.092518
BWW vs. BDW	1.96	0.2343	87.7505	0.085121	−1.7010	73.2612	0.077210
BDV vs. BWW	1.96	−1.6813	89.1699	0.054240	−1.6439	85.8228	0.056355
PDW vs. PC	2.02	0.6992	1.9394	0.028706	1.5742	2.0334	0.027378
DV vs. DW[1]	1.99	0.3918	25.6916	0.026995	1.3693	17.3094	0.040067
WW vs. DW[1]	1.99	0.1432	10.9063	0.011083	1.1101	9.7621	0.012383
WW vs. DV[1]	1.99	1.0998	7.1279	0.015876	1.2063	7.5091	0.015070

[1]Calculated values based on biomass data which was not standardized to per cubic meter.

regressions based solely on our data reveals two notable features. First, the slopes of the regressions based on the same biomass estimators; i.e., displacement volume versus dry weight, wet weight versus dry weight, and displacement volume versus wet weight, are significantly different ($P<0.05$). This was tested by calculating approximately 95% limits for the difference in slopes using standard normal distribution theory: $(v_w - v_{Bé}) \pm 1.96\sqrt{\hat{V}ar\, v_w + \hat{V}ar\, v_{Bé}}$. As was true in our cases, if $\Delta v \pm$ 95% limit does not cross 0, the slopes are significantly different. In all cases, slopes of the regressions derived from our data are closer to 1.0.

The second feature is that there is a significant difference ($P<0.005$) in the variance of observations from the regression lines. The Bé et al. (1971) and Bé (footnote 5) variance for displacement volume versus dry weight is 4.9 times larger than that calculated for our data; for wet weight versus dry weight, it is 7.4 times larger; for displacement volume versus wet weight it is 2.3 times larger.

These differences are probably due in large part to the differences in methods used to determine displacement volume and wet weight. The mercury immersion method Bé et al. (1971) and Bé (footnote 5) used to measure displacement volume provides estimates substantially more variable than the technique used by us (Grice and Wiebe unpubl. data). The increased variability of their wet weights may have resulted from their use of a vacuum to remove some of the interstitial water.

One implication of the lower slopes for the Bé et al. (1971) and Bé (footnote 5) data is that it appears the percentage of interstitial water in their samples may change more radically with increasing biomass than in our samples. This inference is drawn from the calculated values relating dry weight to wet weight and displacement volume in percent (Table 4). The alternate explanation is that as biomass per cubic meter increases, the percentage of wet weight or displacement volume that constitutes dry weight increases as a result of a decrease in intracellular water. It seems unlikely that this accounts for the differences between the two sets of data. Seasonal effects have been minimized by collection of samples at various times of the year and geographical effects should be similar since both studies covered wide geographical ranges.

TABLE 4.–Regression equation prediction of the percentage of displacement volume (DV) or wet weight (WW) that is dry weight (DW) for selected dry weight concentrations.

DW (mg/m³)	Bé et al. (1971) and Bé (footnote 5)		This study		DW[1] (g)	This study	
	% DV	% WW	% DV	% WW		% DV	% WW
0.1	3.80	5.39	5.10	8.95	0.1	5.9	9.4
1.0	6.70	7.89	6.95	10.95	1.0	9.0	10.6
10.0	11.80	11.53	9.48	11.27	10.0	13.5	12.0
100.0	20.80	16.87	12.94	12.65	100.0	20.5	13.6

[1]Calculated values based on biomass data which were not standardized to per cubic meter.

DISCUSSION

Platt et al. (1969), in a comparison of the seasonal changes in dry weight, carbon, and caloric values of zooplankton collected from St. Margaret's Bay, Nova Scotia, found a fivefold variation in caloric content per unit dry weight. As a result they concluded ". . . that there is no single conversion factor that will serve to convert biomass of zooplankton, expressed as dry weight, to its energy equivalent." A similar conclusion was inferred for the conversion of dry weight to carbon. They found, however, that the carbon content of zooplankton could be used to predict the energy equivalent. These results appear to contradict our finding that a statistically significant relationship does exist between pairs of the different measures of biomass including dry weight and carbon. The explanation for this discrepancy lies in the fact that the data of Platt et al. represents a small segment of the extensive range of biomass per cubic meter which occurs in marine waters. This fact, coupled with high variation of the dry weight to carbon ratios, appeared to them to provide a nonsignificant relationship. We have used their data (as tabulated by Platt and Irwin 1968, table 4) to examine the fit of their data to our regression line. After transformation to logarithms (base 10), a linear GM regression line was calculated for their 45 pairs of dry weight and carbon values. While the slope of this line was significantly different from zero ($P<0.001$), it was nonsignificantly different ($P>0.05$) from ours (Table 2). However, the intercept was substantially different. This is a reflection of the fact that their carbon values average 14% of dry weight, whereas in our data the average is 32%. The wet-combustion method (described by Strickland and Parsons 1965) which they used to determine carbon apparently provides lower estimates (an average here of 58% lower) than the high temperature combustion technique we used. Sharp (1973) found that persulfate oxidation yields an average 22% lower values than high temperature combustion when these methods are used to measure total organic carbon in seawater.

In terms of variability, the observations of Platt et al. (1969) have a variance from the regression line significantly ($P<0.01$) larger than ours by a factor of 1.6.

It is clear from the comparisons of biomass measures we have carried out, and from other unpublished work performed at this laboratory, that the techniques used by various investigators in determining a particular biomass measure (such as displacement volume) provide substantially different answers which are not readily comparable. This is particularly true of displacement volume and wet weight and to a lessor degree, carbon. A similar conclusion was reached by Nakai and Honjo (1962). Only the procedure for measuring dry weight described by Lovegrove (1966) seems to have been widely adopted and values presented by various investigators using this technique seem to be intercomparable. With displacement volume and wet weight, the problem stems largely from the differing amounts of interstitial water adhering to the zooplankton at the time of measurement. We have found. as did Nakai and Honjo (1962), that for a given technique, the amount of interstitial water varies inversely with the amount of biomass being measured. The amount, however, varies from technique to technique. Efforts to significantly reduce the amount of interstitial water present appear to create additional error. Rather than simply concentrating on the reduction of interstitial water, it is more important to establish a reproduceable procedure that generates values which can be directly related to a more absolute standard such as carbon as we have tried to do. The data on which Equations 1 to 6 and 11 to 13 in Table 2 are based were developed using methods which appeared to us to involve the least amount of technique-derived error and which required little complex instrumentation.

The zooplankton biomass values used in this study encompass a significant part of the range of values an investigator is likely to encounter working in either coastal waters or the open ocean. Thus, the equations we have presented should be useful in a wide variety of situations providing the same techniques to measure biomass are employed. It is important to bear in mind, however, that situations do occur in which these equations may not apply. One example is where marine populations are dominated by salps, doliolids, jellyfish, or chaetognaths. The very high percentage of intracellular water in these organisms may cause the relationships between displacement volume or wet weight and dry weight or carbon to deviate strongly from our predicted relationships. In such cases, which in our experience occur infrequently, we recommend that dry weight or carbon be measured directly.

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