

NOTES

EFFECT OF SEASON AND LOCATION ON THE RELATIONSHIP BETWEEN ZOOPLANKTON DISPLACEMENT VOLUME AND DRY WEIGHT IN THE NORTHWEST ATLANTIC¹

Biomass or "standing stock" is a routinely measured index of abundance for studies of the interactions between trophic levels in the oceanic food web. Zooplankton biomass is usually reported as quantity of zooplankton per unit volume of water. Measures of quantity currently in use include displacement volume (Frolander 1957; Sutcliffe 1957; Yentsch and Hebard 1957; Tranter 1960; Ahlstrom and Thraillkill 1963), wet weight (Nakai and Honjo 1962), dry weight (Lovegrove 1966), and carbon (Curl 1962; Platt et al. 1969). These measures can be applied to a species at a specific developmental stage, to the entire population, or to all members of the community combined. Carbon and dry weight have been considered preferable because variability caused by interstitial and intracellular water is eliminated by either technique (Ahlstrom and Thraillkill 1963). They are not, however, practical measures in some investigations because specialized equipment is required and the techniques' destructive nature prevents further analysis of the sample. Measurement of displacement volume and wet weight are nondestructive, rapid, and use simple techniques which provide indexes of abundance, but do measure total matter, including water.

As an alternative, conversion factors or tables of "equivalents" have been used to transform displacement volume or wet weight into carbon or dry weight (Bsharah 1957; Menzel and Ryther 1961; Platt et al. 1969; Bé et al. 1971; Le Borgne 1975; Wiebe et al. 1975). However, plankton samples represent aggregations of organisms at a particular time and place which change according to season, geographical location, and local environmental conditions. For these reasons, and because many conversion factors were calculated with data produced by outdated techniques, the accuracy of interconversions between biomass measures has been questioned (Lovegrove

1966; Platt et al. 1969; Beers 1974). Recently, Wiebe et al. (1975) provided conversion factors based on data collected from different oceanic areas over several years in order to account for seasonal and geographical variation in samples.

This study explores whether a conversion equation based on data from numerous samples collected in contiguous areas during different seasons can account for sample variability and more accurately convert between biomass measures than equations derived from smaller and smaller subsets of data. Unlike previous studies, an intense sampling strategy provided the means to derive equations to convert between displacement volume and dry weight for samples from both broad and restricted geographic areas and for different seasons. Interconversion accuracy was verified with subsequent samples by comparing estimated values with field measurements. In addition, the relative variability and the values of both measures were compared in order to determine which index is more useful for these types of studies.

Materials and Methods

Plankton samples were collected by the National Marine Fisheries Service Northeast Fisheries Center in conjunction with the Marine Resources Monitoring Assessment and Prediction (MARMAP) program (Sherman 1980). Sampling was conducted six times a year in 1977 and 1978 off the northeast coast of the United States in three adjacent areas: Gulf of Maine (GOM), Georges Bank (GB), and Southern New England (SNE). Sampling locations are shown in Figures 1 and 2. Paired 61 cm diameter bongo samplers fitted with 0.505 mm and 0.333 mm mesh nets were towed obliquely through the water column at a speed of 1.5-2.0 kn. Maximum sampling depth was 200 m or 5 m from the bottom in shallower areas, and tow duration was 5-15 min. A flowmeter was strung inside the bongo frame to measure the volume of water filtered. Plankton samples from the 0.333 mm mesh nets were used in this analysis. Samples were preserved in 5% buffered Formalin² for at least 6 mo before anal-

¹MARMAP Contribution MED/NEFC 81-8.

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

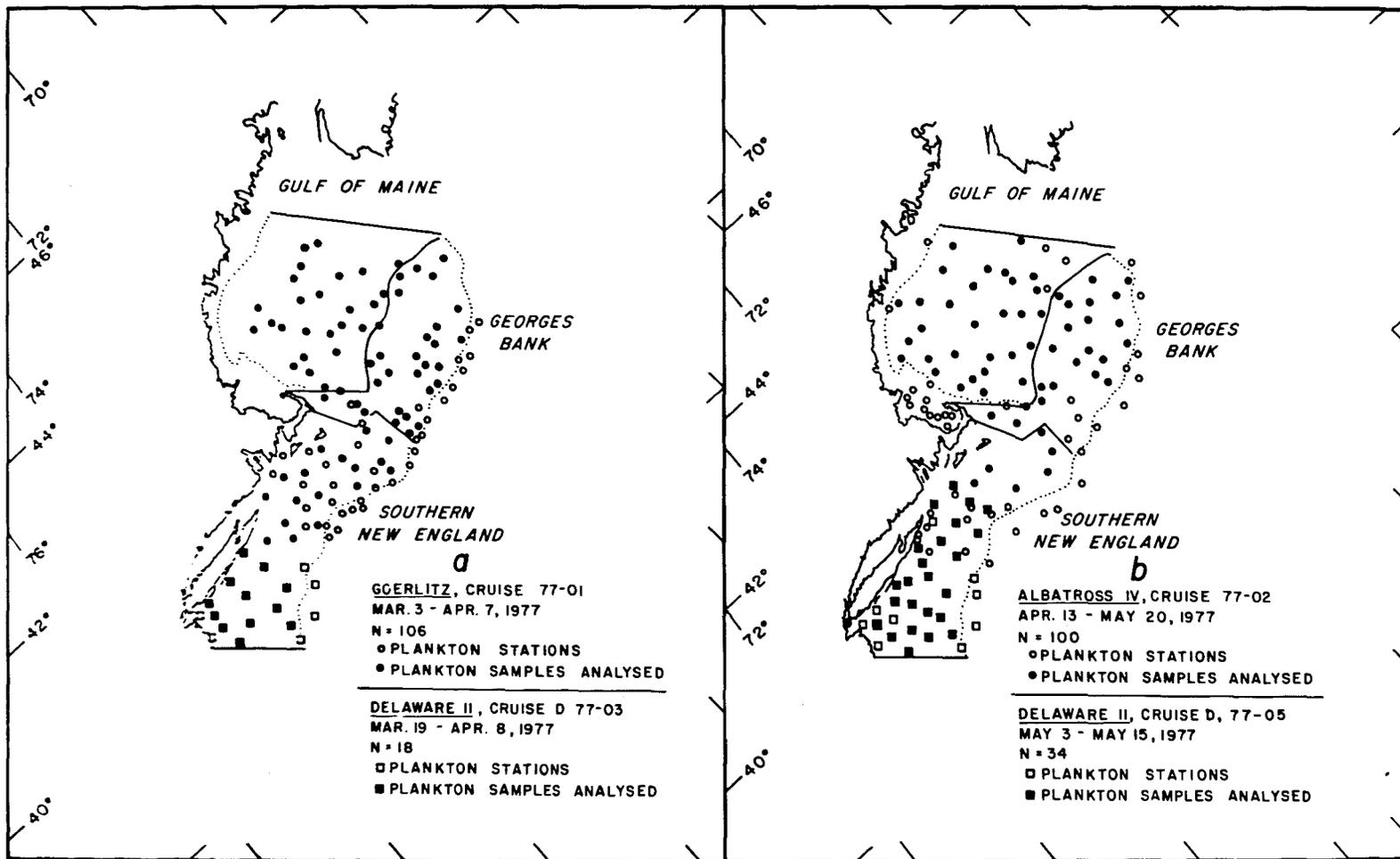


FIGURE 1.—Sampling locations and cruise numbers from the six seasonal MARMAP surveys for 1977.

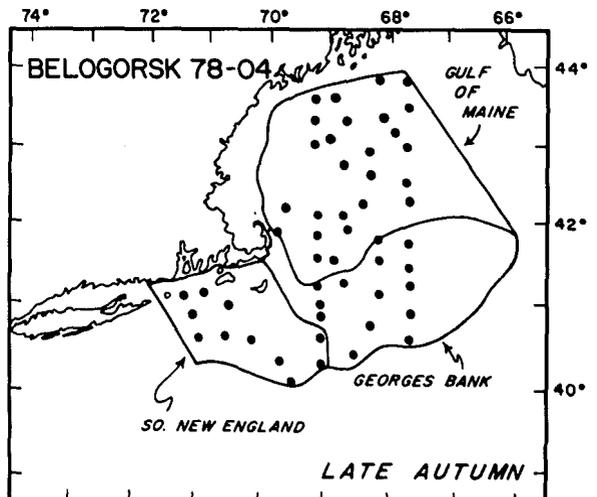
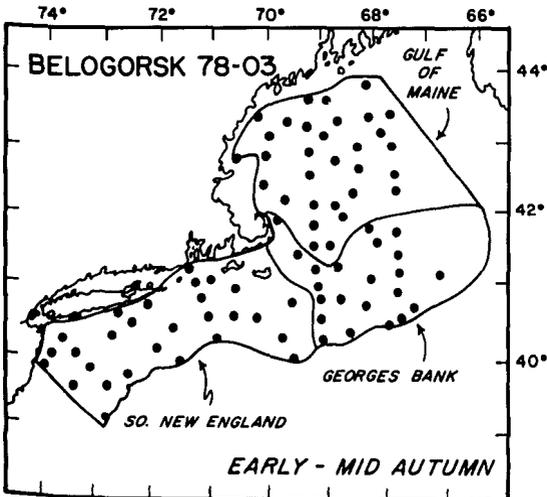
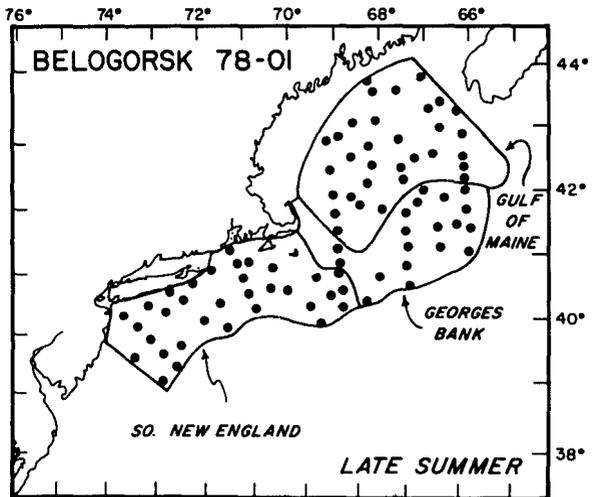
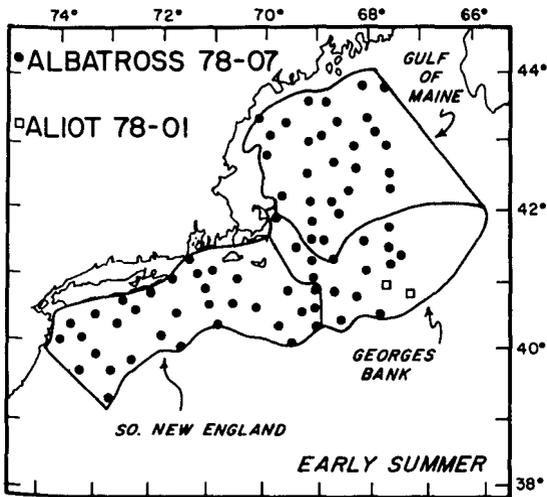
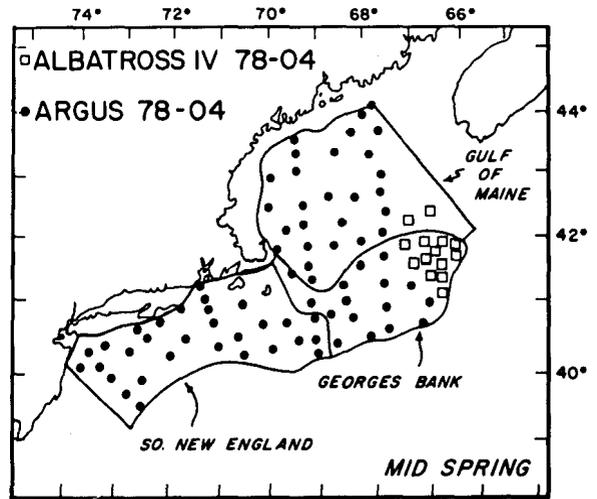
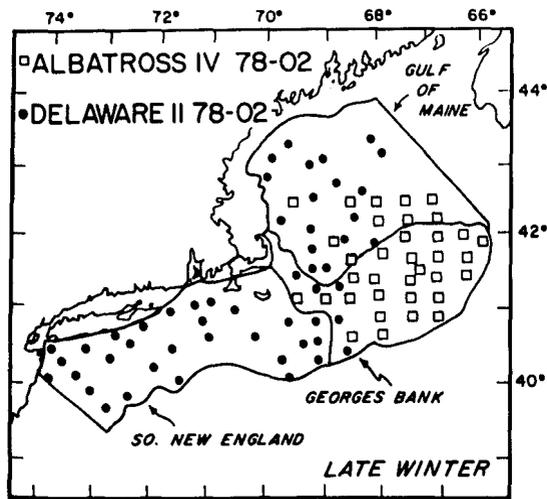


FIGURE 2.—Sampling locations and cruise numbers from the six seasonal MARMAP surveys for 1978.

ysis, sufficient time for the plankton to reach equilibrium volume and weight (Steedman 1976).

In the laboratory, displacement volumes were determined by using the technique outlined by Ahlstrom and Thraillkill (1963), with slight modifications. All organisms larger than 2.5 cm and nonplanktonic matter, i.e., small adult fishes, juvenile fishes, and seaweed, were removed prior to pouring the sample into a 1 l graduated cylinder, with 1 ml increments. After recording the volume, the sample was poured into a cone of 0.253 mm mesh suspended over a second graduated cylinder, and allowed to drain until the interval between drops was 15 s. The water volume was recorded. The difference between readings was recorded as the displacement volume. Dry weight was measured using the procedure outlined by Lovegrove (1966). Samples were dried at 60°C to a constant weight (2-5 d); a weight loss of 1 mg or less was considered constant. Samples were weighed to 0.01 mg on an analytical microbalance. Before analysis, all values were expressed as ml or gm/100 m³ of water filtered and logarithmically transformed (base 10).

The geometric mean (GM) regression was used to express the relationship between displacement volume and dry weight because it is applicable to short series of measurements that have moderate or large variability, where the nature of error sources in the measurements is primarily natural, when compared with measurement error (Ricker 1973). The convention of using the GM regression for relating pairs of biomass measures was introduced by Wiebe et al. (1975), where a more detailed discussion of the theoretical and mathematical considerations of the GM regression as it applies to biomass measures is presented.

Using samples collected in 1977, conversion equations for displacement volume to dry weight were calculated using GM regressions for groups of measurements divided according to station and/or time of sampling as follows:

1) General: All measurements regardless of location or season (1).

2) Area: All measurements from a distinct oceanic region throughout the year (3).

3) Seasonal: Measurements within an area for a particular season (18).

Individual displacement volume readings from 1978 samples were converted to dry weight using

each type of conversion equation. The predictive accuracy of the different equations was calculated by measuring the difference between the estimated and the directly measured dry weight, and expressing this difference as a percentage of the latter. The absolute values of the percent deviations for each conversion factor were then averaged for each group of seasonal and area-specific samples to determine which equation was most accurate. This method for evaluating different conversion factors was used instead of comparing differences between measured and estimated means because of the cancelling effect very high or low estimates would have on each other.

Results

A strong linear relationship exists between zooplankton displacement volume and dry weight (Table 1). Slopes of the GM regression lines were significantly different from zero ($P < 0.001$), and correlation coefficients were high (0.885-0.977) for all lines within each class. The range of slope and elevation values for the 18 seasonal equations was significantly wide ($P < 0.05$) to conclude that the different lines were not expressing the same biomass relationship. It was hypothesized that from among these regression lines there might exist discrete groups of significantly similar lines which could be combined to describe a fourth category of conversion equations. A Neuman-Keuls multiple range test (Zar 1974) pinpointed lines which differed significantly ($P < 0.05$) in slope and/or elevation, but other lines could not be accurately assigned to distinct groups because of overlapping similarities. Increasing the amount of data might yield more acceptable conclusions, but it is more likely that these results reflect a gradient of changing trophic conditions which gradually alter the biomass relationship from season to season.

The seasonal class of conversion equations yielded significantly ($P < 0.05$) more accurate estimates than either the general or areal equations. For the 18 groups of seasonal and areal samples collected in 1978, predicted dry weights on the average deviated 15.98% (range: 2.31-34.4%) from the actual values using the seasonal equations, as opposed to 29.27% (range: 12.62-66.34%) and 31.4% (range: 15.90-53.45%) for the areal and general equations, respectively. However, for certain seasons, the appropriate regression equation did not accurately convert dis-

TABLE 1.—Geometric mean regression equations calculated from 1977 displacement volume (DV) and dry weight (DW) measures for each area by season, each individual area, and for all values combined. Also included is the equation for phytoplankton-dominated stations.

Area/season	Regression equation	N	r	Variance of slope
Southern New England				
I Late winter-early spring	Log (DW) = -1.079 + 0.963 Log (DV)	27	0.951	0.00348
II Midspring	Log (DW) = -1.235 + 1.022 Log (DV)	30	0.900	0.00706
III Late spring	Log (DW) = -1.663 + 1.312 Log (DV)	30	0.956	0.00532
IV Midsummer	Log (DW) = -1.803 + 1.382 Log (DV)	34	0.890	0.0123
V Midautumn	Log (DW) = -1.190 + 0.976 Log (DV)	27	0.907	0.00672
VI Late autumn	Log (DW) = -1.245 + 1.006 Log (DV)	20	0.961	0.00476
All seasons	Log (DW) = -1.226 + 1.138 Log (DV)	168	0.943	0.000106
Georges Bank				
I Late winter-early spring	Log (DW) = -1.182 + 1.045 Log (DV)	28	0.885	0.00902
II Midspring	Log (DW) = -1.328 + 1.114 Log (DV)	23	0.929	0.00811
III Late spring	Log (DW) = -1.405 + 1.184 Log (DV)	27	0.930	0.00757
IV Midsummer	Log (DW) = -1.552 + 1.274 Log (DV)	21	0.898	0.0166
V Early autumn	Log (DW) = -1.622 + 1.296 Log (DV)	18	0.949	0.0104
VI Late autumn	Log (DW) = -1.210 + 1.091 Log (DV)	20	0.914	0.0111
All seasons	Log (DW) = -1.308 + 1.127 Log (DV)	137	0.954	0.000823
Gulf of Maine				
I Early spring	Log (DW) = -1.161 + 1.142 Log (DV)	13	0.960	0.00922
II Midspring	Log (DW) = -1.347 + 1.223 Log (DV)	21	0.954	0.00593
III Late spring	Log (DW) = -1.170 + 1.145 Log (DV)	27	0.947	0.00548
IV Midsummer	Log (DW) = -1.470 + 1.377 Log (DV)	28	0.966	0.00476
V Midautumn	Log (DW) = -1.201 + 1.242 Log (DV)	23	0.977	0.00339
VI Late autumn	Log (DW) = -1.747 + 1.514 Log (DV)	30	0.932	0.0108
All seasons	Log (DW) = -1.311 + 1.257 Log (DV)	142	0.963	0.00290
All areas				
Every season	Log (DW) = -1.383 + 1.207 Log (DV)	447	0.925	0.000484
Phytoplankton stations	Log (DW) = -1.481 + 1.016 Log (DV)	20	0.962	0.00910

placement volume to dry weight. It was found that a change in the biomass relationship occurred between years in the six seasons that predictive accuracy was lowest. This was determined by calculating regressions with 1978 data (Table 2) and comparing them with the corresponding 1977 seasonal equations. Year-to-year differences ($P < 0.05$) in slope and/or elevation were evident for the following: GB early-mid-autumn, GB late autumn, GOM mid-late sum-

mer, GOM midautumn, SNE late winter, and SNE late spring-early summer. After perusal of sample contents, sampling dates, and sample species abundance, it was apparent that year-to-year changes in these factors were correlated with the 1977-78 differences in the regression equations mentioned above (Tables 3-5).

For those areas where no change in the relationship between displacement volume and dry weight occurred between years, data was com-

TABLE 2.—Geometric mean regression equations derived from 1978 displacement volume (DV) and dry weight (DW) values for each area by season and for samples with abundant siphonophore fragments.

Area/season	Regression equation	N	r	Variance of slope
Southern New England				
VII Late winter	Log (DW) = -0.795 + 0.725 Log (DV)	25	0.903	0.00810
VIII Midspring	Log (DW) = -1.287 + 1.088 Log (DV)	25	0.960	0.00620
IX Early summer	Log (DW) = -1.939 + 1.541 Log (DV)	30	0.969	0.00980
X Midsummer	Log (DW) = -1.802 + 1.388 Log (DV)	19	0.939	0.01900
XI Midautumn	Insufficient Data			
XII Late autumn	Log (DW) = -1.266 + 1.045 Log (DV)	10	0.927	0.0219
Georges Bank				
VII Late winter	Log (DW) = -1.229 + 1.095 Log (DV)	23	0.964	0.00941
VIII Midspring	Log (DW) = -1.515 + 1.238 Log (DV)	20	0.990	0.00260
IX Early summer	Log (DW) = -1.416 + 1.186 Log (DV)	16	0.900	0.0123
X Late summer	Log (DW) = -1.079 + 0.956 Log (DV)	18	0.881	0.0156
XI Midautumn	Log (DW) = -1.349 + 1.070 Log (DV)	20	0.945	0.00941
XII Late autumn	Log (DW) = -1.509 + 1.215 Log (DV)	14	0.950	0.0129
Gulf of Maine				
VII Late winter	Log (DW) = -1.158 + 1.148 Log (DV)	21	0.913	0.0219
VIII Midspring	Log (DW) = -1.137 + 1.085 Log (DV)	25	0.947	0.00865
IX Early summer	Log (DW) = -0.949 + 1.042 Log (DV)	27	0.927	0.00846
X Late summer	Log (DW) = -1.079 + 1.089 Log (DV)	22	0.949	0.00846
XI Midautumn	Log (DW) = -1.343 + 1.304 Log (DV)	24	0.957	0.0129
XII Late autumn	Log (DW) = -1.454 + 1.349 Log (DV)	20	0.875	0.0353
Siphonophore samples	Log (DW) = -0.975 + 0.773 Log (DV)	15	0.969	0.00397

TABLE 3.—A) The recommended geometric mean regressions for interconversion between displacement volume (DV) and dry weight (DW) in the Southern New England area; and B) the relative abundance of the major taxa (>1%) associated with the particular equation, expressed as percent of total numbers. Copepods are broken down into major species (>1%) with their abundance expressed as percent of total copepod numbers (in parentheses). Zooplankton data from Sherman et al. (1978, 1979).

A				
Season	Regression equation	N	r	Variance of slope
Late winter	Log (DW) = -0.795 + 0.725 Log (DV)	21	0.903	0.00810
Early spring	Log (DW) = -1.079 + 0.963 Log (DV)	27	0.951	0.00348
Midspring	Log (DW) = -1.103 + 0.929 Log (DV)	55	0.929	0.00348
Late spring	Log (DW) = -1.663 + 1.312 Log (DV)	30	0.956	0.00532
Early summer	Log (DW) = -1.939 + 1.541 Log (DV)	30	0.969	0.00980
Midsummer	Log (DW) = -1.795 + 1.379 Log (DV)	53	0.900	0.00757
Midautumn	Log (DW) = -1.190 + 0.976 Log (DV)	27	0.907	0.00672
Late autumn	Log (DW) = -1.251 + 1.109 Log (DV)	30	0.956	0.00360

B							
Late winter		Early spring		Midspring		Late spring	
Copepoda	88.6	Copepoda	88.2	Copepoda	91.5	Copepoda	88.4
<i>P. minutus</i>	(87.8)	<i>P. minutus</i>	(75.1)	<i>C. finmarchicus</i>	(55.3)	<i>P. minutus</i>	(44.3)
<i>C. finmarchicus</i>	(6.2)	<i>C. finmarchicus</i>	(8.5)	<i>P. minutus</i>	(28.8)	<i>C. finmarchicus</i>	(37.2)
<i>C. typicus</i>	(3.0)	<i>T. longicornus</i>	(6.2)	<i>M. lucens</i>	(3.0)	<i>T. longicornus</i>	(11.7)
Chaetognatha	8.6	<i>C. typicus</i>	(5.4)	<i>A. longiramus</i>	(1.9)	<i>M. lucens</i>	(2.3)
		Cirripedia	9.6	<i>C. typicus</i>	(1.3)	Chaetognatha	6.3
				Chaetognatha	4.2	Cladocera	3.0
				Cladocera	1.4		

Early summer		Midsummer		Midautumn		Late autumn	
Copepoda	91.3	Copepoda	66.2	Copepoda	75.6	Copepoda	91.8
<i>P. minutus</i>	(33.9)	<i>C. typicus</i>	(59.8)	<i>C. typicus</i>	(70.1)	<i>C. typicus</i>	(60.6)
<i>C. finmarchicus</i>	(27.8)	<i>C. finmarchicus</i>	(19.8)	<i>A. clausi</i>	(5.1)	<i>P. parvus</i>	(15.3)
<i>C. typicus</i>	(19.0)	<i>P. minutus</i>	(5.2)	<i>A. tonsa</i>	(4.0)	<i>P. minutus</i>	(11.0)
<i>T. longicornus</i>	(11.6)	<i>M. lucens</i>	(3.1)	<i>P. minutus</i>	(3.4)	Chaetognatha	5.5
<i>M. lucens</i>	(1.2)	Cladocera	23.6	<i>P. parvus</i>	(3.2)		
Chaetognatha	7.8	Chaetognatha	4.5	<i>C. minor</i>	(2.2)		
		Thaliacea	1.7	Cladocera	21.3		
		Amphipoda	1.6	Chaetognatha	1.0		

TABLE 4.—A) The recommended geometric mean regressions for interconversion between displacement volume (DV) and dry weight (DW) in the Georges Bank area; and B) the relative abundance of the major taxa (>1%) associated with the particular equation, expressed as percent of total numbers. Copepods are broken down into major species (>1%) with their abundance expressed as percent of total copepod numbers (in parentheses). Zooplankton data from Sherman et al. (1978, 1979).

A				
Season	Regression equation	N	r	Variance of slope
Late winter-early spring	Log (DW) = -1.195 + 1.059 Log (DV)	39	0.908	0.00518
Midspring	Log (DW) = -1.324 + 1.119 Log (DV)	37	0.989	0.00372
Late spring-early summer	Log (DW) = -1.360 + 1.159 Log (DV)	40	0.954	0.00314
Midsummer-late summer	Log (DW) = -1.403 + 1.176 Log (DV)	36	0.891	0.00828
Early autumn	Log (DW) = -1.662 + 1.296 Log (DV)	18	0.949	0.0104
Midautumn	Log (DW) = -1.349 + 1.070 Log (DV)	20	0.945	0.00941
Late autumn (1977)	Log (DW) = -1.210 + 1.091 Log (DV)	20	0.914	0.0111
Late autumn (1978)	Log (DW) = -1.509 + 1.215 Log (DV)	14	0.950	0.0129

B							
Late winter-early spring		Midspring		Late spring-early summer		Midsummer	
Copepoda	80.7	Copepoda	89.7	Copepoda	76.6	Copepoda	89.3
<i>P. minutus</i>	(55.6)	<i>C. finmarchicus</i>	(79.8)	<i>C. finmarchicus</i>	(42.8)	<i>C. typicus</i>	(53.1)
<i>C. finmarchicus</i>	(37.1)	<i>P. minutus</i>	(16.9)	<i>P. minutus</i>	(36.1)	<i>C. hamatus</i>	(16.6)
<i>C. typicus</i>	(2.6)	<i>M. lucens</i>	(2.5)	<i>C. hamatus</i>	(11.7)	<i>C. finmarchicus</i>	(10.2)
<i>M. lucens</i>	(1.8)	Chaetognatha	2.3	<i>C. typicus</i>	(5.1)	<i>P. minutus</i>	(8.9)
Chaetognatha	6.9	Ostracoda	1.5	<i>M. lucens</i>	(1.5)	<i>P. parvus</i>	(5.6)
Cirripedia	4.9	Cirripedia	1.3	<i>T. longicornus</i>	(1.3)	<i>M. lucens</i>	(3.7)
Amphipoda	4.8	Amphipoda	1.1	Chaetognatha	6.7	Chaetognatha	4.9
Pelecyopoda	1.7			Coelenterata	5.6	Cladocera	1.8
				Cladocera	4.1		
				Decapoda	3.1		

Early autumn		Midautumn		Late autumn (1977)		Late autumn (1978)	
Copepoda	95.1	Copepoda	94.5	Copepoda	86.6	Copepoda	89.8
<i>C. typicus</i>	(50.1)	<i>C. typicus</i>	(64.6)	<i>C. typicus</i>	(57.0)	<i>C. typicus</i>	(51.1)
<i>P. minutus</i>	(19.8)	<i>C. finmarchicus</i>	(10.2)	<i>P. minutus</i>	(28.0)	<i>P. parvus</i>	(19.9)
<i>C. hamatus</i>	(18.4)	<i>C. hamatus</i>	(8.7)	<i>C. finmarchicus</i>	(4.3)	<i>C. finmarchicus</i>	(11.0)
<i>C. finmarchicus</i>	(2.5)	<i>P. parvus</i>	(5.7)	<i>C. hamatus</i>	(3.8)	<i>P. minutus</i>	(7.9)
<i>M. lucens</i>	(2.0)	<i>P. minutus</i>	(5.6)	<i>P. parvus</i>	(2.2)	<i>C. hamatus</i>	(6.1)
<i>P. parvus</i>	(1.9)	<i>M. lucens</i>	(1.3)	<i>M. lucens</i>	(1.7)	Chaetognatha	8.7
Pelecyopoda	1.7	Chaetognatha	2.3	Pelecyopoda	6.9		
Chaetognatha	1.3	Amphipoda	1.4	Chaetognatha	5.5		

TABLE 5.—A) The recommended geometric mean regressions for interconversion between displacement volume (DV) and dry weight (DW) in the Gulf of Maine area; and B) the relative abundance of the major taxa (>1%) associated with the particular equation, expressed as percent of total numbers. Copepods are broken down into major species (>1%) with their abundance expressed as percent of total copepod numbers (in parentheses). Zooplankton data from Sherman et al. (1978, 1979).

A				
Season	Regression equation	N	r	Variance of slope
Late winter-early spring	Log (DW) = -1.168 + 1.156 Log (DV)	25	0.956	0.00504
Midspring	Log (DW) = -1.169 + 1.106 Log (DV)	37	0.954	0.00314
Late spring-early summer	Log (DW) = -1.035 + 1.080 Log (DV)	47	0.949	0.00260
Midsummer	Log (DW) = -1.470 + 1.377 Log (DV)	28	0.966	0.00476
Late summer	Log (DW) = -1.079 + 1.089 Log (DV)	22	0.949	0.00846
Midautumn (1977)	Log (DW) = -1.201 + 1.242 Log (DV)	23	0.977	0.00339
Midautumn (1978)	Log (DW) = -1.343 + 1.304 Log (DV)	24	0.957	0.0129
Late autumn	Log (DW) = -1.576 + 1.419 Log (DV)	44	0.935	0.00608

B							
Late winter-early spring		Midspring		Late spring-early summer		Midsummer	
Copepoda	96.3	Copepoda	93.5	Copepoda	94.0	Copepoda	97.5
<i>C. finmarchicus</i>	(63.7)	<i>C. finmarchicus</i>	(86.7)	<i>C. finmarchicus</i>	(83.5)	<i>C. finmarchicus</i>	(79.9)
<i>M. lucens</i>	(18.9)	<i>P. minutus</i>	(8.0)	<i>P. minutus</i>	(10.3)	<i>P. minutus</i>	(10.0)
<i>P. minutus</i>	(13.6)	<i>M. lucens</i>	(5.0)	<i>M. lucens</i>	(4.6)	<i>M. lucens</i>	(4.2)
<i>Oithona</i> sp.	(1.7)	Amphipoda	5.0	<i>A. longiremis</i>	(1.1)	<i>C. typicus</i>	(4.2)
Amphipoda	1.3			Cladocera	4.8	<i>A. longiremis</i>	(1.3)
						Cladocera	1.1

Late summer		Midautumn (1977)		Midautumn (1978)		Late autumn	
Copepoda	99.2	Copepoda	99.0	Copepoda	98.9	Copepoda	99.1
<i>C. finmarchicus</i>	(47.3)	<i>C. finmarchicus</i>	(51.3)	<i>C. typicus</i>	(39.1)	<i>C. typicus</i>	(37.0)
<i>C. typicus</i>	(42.0)	<i>C. typicus</i>	(29.3)	<i>C. finmarchicus</i>	(34.6)	<i>C. finmarchicus</i>	(28.3)
<i>P. minutus</i>	(7.7)	<i>P. minutus</i>	(11.4)	<i>P. minutus</i>	(17.9)	<i>P. minutus</i>	(21.4)
		<i>M. lucens</i>	(3.5)	<i>A. longiremis</i>	(1.5)	<i>P. parvus</i>	(4.7)
		<i>P. parvus</i>	(2.6)	<i>P. parvus</i>	(1.3)	<i>M. lucens</i>	(4.5)
						<i>A. longiremis</i>	(1.1)

bined and a new regression equation calculated. These equations, and the equations showing significant differences between years, are the recommended equations for conversion between the biomass measures (Tables 3-5). Choice of which regression to use should be based on area, season, and species composition. Confidence limits can be calculated for any predicted dry weight or displacement volume by using the method outlined by Ricker (1973) or Wiebe et al. (1975). A listing of values for predicting dry weights and displacement volumes within 95% confidence limits is given in Table 6.

The limitations of the method for the area under study are as follows. The presence in samples of organisms such as salps, jellyfish, and doliolids, which have a high displacement volume to dry weight ratio due to a greater retention of intracellular water, can significantly affect the accuracy of dry weight estimates (Wiebe et al. 1975). This was also observed in our data, but only on rare occasions were these organisms encountered. Chaetognaths were also mentioned by Wiebe et al. as organisms that could alter the biomass relationship. Since they are common, but not dominant, components of the plankton throughout the year in our sampling areas, the seasonal regressions account for their continuous presence and are therefore appli-

cable to samples where they are present. This study revealed two additional situations in which sample composition caused a deviation in the biomass relationship. Twenty samples collected during late winter 1977 from the GOM and GB contained high concentrations of diatoms, primarily *Rhizosolenia* sp. and *Thalassiosira* sp., and microzooplankton not normally captured by 0.333 mm mesh nets. The samples resembled thick "pea soup" and many hours were required for draining in order to obtain a displacement volume reading. Since their dry weight to displacement volume ratios were very low compared with other samples collected during the same period, the samples were eliminated from the general analysis and a separate regression calculated ($r = 0.962$) for them (Table 1). The second situation was observed in autumn 1978 when the siphonophore population increased dramatically, especially off SNE and in the GOM. Since these delicate colonial aggregations are easily fragmented during collection, their abundance could not be measured quantitatively. For these samples, displacement volume to dry weight ratios were disproportionately high because of the intracellular water retained by their nectophores. The regression line calculated with data only from siphonophore-dominated samples was significantly different ($P < 0.05$) in both

TABLE 6.—Values needed to calculate 95% confidence limits for predicted dry weights (DW) and displacement volumes (DV) from the equations in Tables 3-5. For an explanation of symbols and the methods used, one should consult Ricker (1973) or Wiebe et al. (1975).

Area/season	Prediction of DW				Prediction of DV		
	t_{95}	\bar{X}	ΣX^2	$Sy'x^2$	\bar{Y}	ΣY^2	$Sx'y^2$
Southern New England							
Late winter	2.05	1.329	4.384	0.0156	0.775	4.067	0.0168
Early spring	2.08	0.945	1.894	0.0154	-0.110	0.996	0.0292
Midspring	2.01	1.598	8.156	0.0281	0.478	9.250	0.0248
Late spring	2.04	1.915	2.025	0.0107	0.850	3.484	0.00622
Early summer	2.04	1.683	0.694	0.00671	0.655	1.651	0.00282
Midsummer	2.01	1.706	2.614	0.0205	0.577	4.973	0.0108
Midautumn	2.05	1.334	1.147	0.00780	0.117	1.092	0.0081
Late autumn	2.05	1.347	1.588	0.00568	0.121	1.648	0.00545
Georges Bank							
Late winter-early spring	2.02	0.962	3.363	0.0194	0.122	4.073	0.0173
Midspring	2.03	1.783	3.361	0.00309	0.671	4.918	0.00228
Late spring-early summer	2.02	1.892	5.938	0.0189	0.833	7.972	0.0141
Midsummer-late summer	2.03	1.615	1.730	0.0145	0.497	2.391	0.0105
Early autumn	2.10	1.471	0.652	0.00678	0.284	1.0952	0.00403
Midautumn	2.09	1.150	0.655	0.00615	0.256	0.748	0.00539
Late autumn (1977)	2.09	1.393	1.088	0.0119	0.310	1.2935	0.00997
Late autumn (1978)	2.15	1.492	0.767	0.00949	0.198	1.133	0.00676
Gulf of Maine							
Late winter-early spring	2.06	1.045	1.261	0.00630	0.041	1.685	0.00471
Midspring	2.03	1.571	2.037	0.00641	0.568	2.491	0.00524
Late spring-early summer	2.01	1.695	3.009	0.00772	0.796	3.508	0.00662
Midsummer	2.05	1.675	0.977	0.00470	0.836	1.851	0.00252
Late summer	2.12	1.396	1.738	0.00985	0.423	2.059	0.00832
Midautumn (1977)	2.07	1.708	1.446	0.0049	0.920	2.230	0.00317
Midautumn (1978)	2.16	1.501	0.232	0.00302	0.614	0.395	0.00177
Late autumn	2.01	1.592	2.552	0.0154	0.683	5.147	0.00766

slope and elevation from all other seasonal lines and had a high r value (Table 2). Since the occurrence of siphonophores in large numbers has been reported in our sampling areas (Sumner 1911; Rogers et al. 1978), this predictive equation should be useful for future occurrences of this phenomenon.

A coefficient of variation (cv) was calculated for each group of displacement volume and dry weight measures in order to compare the relative variability between the two indexes. As expected, both indexes were highly variable, with cv's averaging 54.3% (31.6-133.5%) and 65.4% (33.4-147.8%) for displacement volume and dry weight, respectively. Surprisingly, of the 36 data sets, 31 exhibited higher cv's for dry weight than for displacement volume. A two-tailed variance test was used to determine whether this difference was significant (Lewontin 1966) for the paired displacement volume-dry weight values. Only GOM late autumn (1977) displacement volumes had a significantly ($P < 0.05$) lower cv than the corresponding dry weights. When all values were combined, however, and a single cv calculated for each index, displacement volumes were significantly ($P < 0.05$) less variable. This was unexpected, because water retained interstitially and intracellularly should increase variability among displacement volumes. It appears, then,

that displacement volume is a more consistent and more reliable measure of plankton standing stock than dry weight.

Zooplankton standing stock for 1977 and 1978 in each area is plotted in Figure 3A-C. The measures are juxtaposed in order to reveal whether any discrepancies exist between the two patterns. For SNE and GB the two indexes of abundance follow strikingly similar patterns. In the GOM, however, the dramatic midautumn increase in dry weight for 1977 is not equally reflected by the displacement volume curve. *Calanus finmarchicus* dominated these samples (Sherman et al. 1978) and further examination revealed that they were stage V copepodites, the condition in which they overwinter. Comita et al. (1966) showed that *C. finmarchicus* collected from the Bute Channel, England, reach their weight and caloric maxima in autumn and early winter, with stage V individuals having the highest values. The impact these overwintering preadults had on the dry weight measures was confirmed by plotting the seasonal mean dry weight-displacement volume ratios for all three areas (Fig. 4). GOM autumn ratios were highest for both years, 17.4% and 13.4%, respectively. Furthermore, samples dominated by *C. finmarchicus* had higher ratios than samples from shallower stations where the copepods *Pseudo-*

FIGURE 3.—Changes in median displacement volumes and dry weights for A) Southern New England, B) Georges Bank, and C) Gulf of Maine waters. Dashed lines represent intersurvey periods. Similar abundance trends are portrayed by both indexes, but discrepancies in magnitude between measures occur for Georges Bank summer samples and throughout the year in the Gulf of Maine. Displacement volumes are from Sherman et al. (1977, 1978).

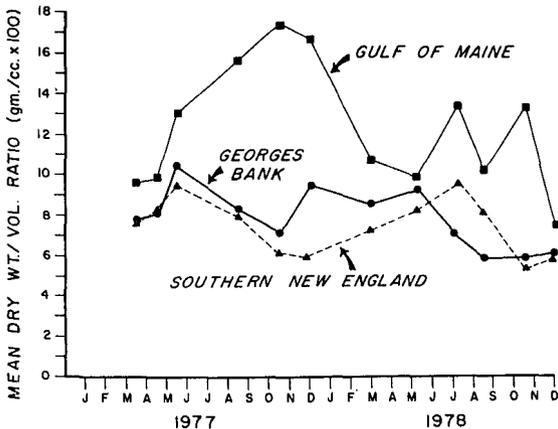
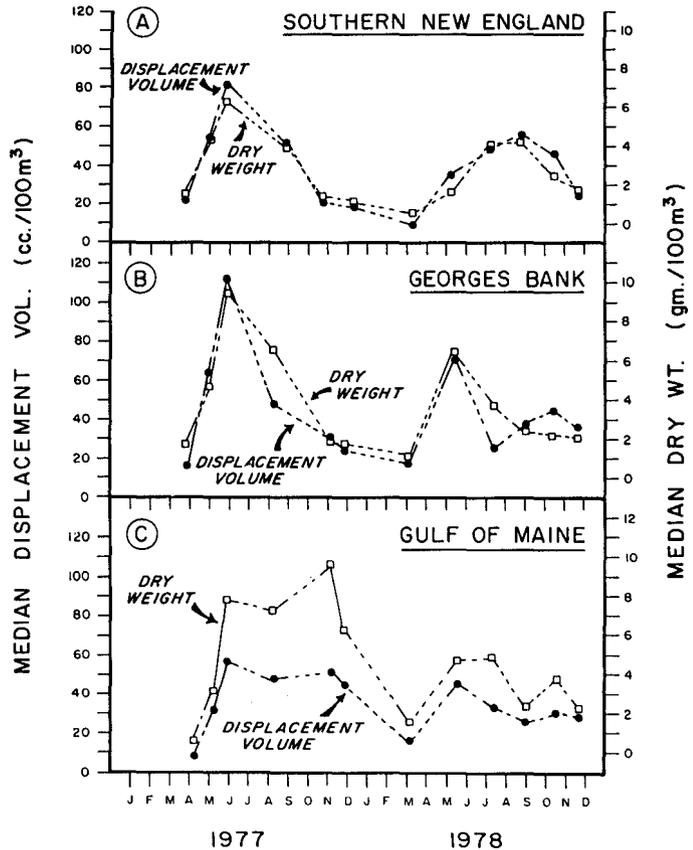


FIGURE 4.—Seasonal changes in dry weight/displacement volume ratios for the three sampling areas. Points are placed at the midpoints of the survey cruises. Gulf of Maine samples have higher values throughout the year.

calanus minutus or *Centropages typicus* were abundant. The preadult *Calanus* apparently store lipid reserves for survival through the

winter and represent a substantial biomass underestimated by displacement volumes.

Autumn increases in dry weight were not observed for GB or SNE, though both areas support large populations of *Calanus* in the spring and summer. In general, overwintering *Calanus* remain in deep water and do not migrate vertically (Marshall and Orr 1955). The only concentrations of preadult *Calanus* found in these areas were at a few stations located near or below the 100 m contour line during late autumn. These samples had higher dry weight-displacement volume ratios than *Calanus* free stations. The GOM is able to support a large population of overwintering *Calanus* in deepwater basins.

Discussion

The linear relationship between displacement volume and dry weight is affected by the seasonal changes in species composition and age structure which occur throughout the year in zooplankton communities. Accurate interconversion between them is possible only with a ser-

ies of seasonal equations that are restricted to a specific area. A single general conversion equation derived from samples from a widespread area cannot provide estimates of abundance with sufficient accuracy to describe the variation in abundance and community composition necessary for detailed studies of trophic structure and community composition. The findings presented here are generally consistent with those of previous investigators (Lovegrove 1966; Platt et al. 1969; Beers 1974), with the exception of Wiebe et al. (1975). It should be recognized that the latter approach (Wiebe et al. 1975) has utility in comparing disparate data sets from different geographical areas and seasons. It is necessary to recognize the limitations of each approach and select according to the intended use of the data.

Previous reports have recommended dry weight determinations over displacement volumes because both interstitial and intracellular water is eliminated from the sample, removing bias caused by gelatinous organisms (Ahlstrom and Thrailkill 1963; Beers 1974). Further, since only organic and inorganic substances remain in the sample, dry weight should provide information regarding the potential food value of the plankton standing stock. However, the high correlation found between displacement volume and dry weight ($r = 0.925$, 442 df) implies that both measures provide equivalent assessments of standing stock and potential food value. In two of the three areas investigated, GB and SNE, both measures portray identical ascending and descending trends in biomass with maximal and minimal points closely correlated (Fig. 3). In addition, variability, though high for both techniques, is higher for dry weight.

Discrepancies between the two measures appear, however, when one examines GOM data. Standing stock is underestimated by displacement volume because samples there have high dry weight to displacement volume ratios (Fig. 4). As a consequence, when biomass is compared between the GOM and GB or SNE, each index gives a different interpretation of between-area differences (Fig. 5). For example, in autumn 1977, mean dry weight for the GOM was five times higher than for SNE, but mean displacement volume was only twice as high. This phenomenon is attributed to the life history of *C. finmarchicus* in the GOM. Dry weight values reported by other investigators from different areas are also more readily comparable than displacement volumes because Lovegrove's tech-

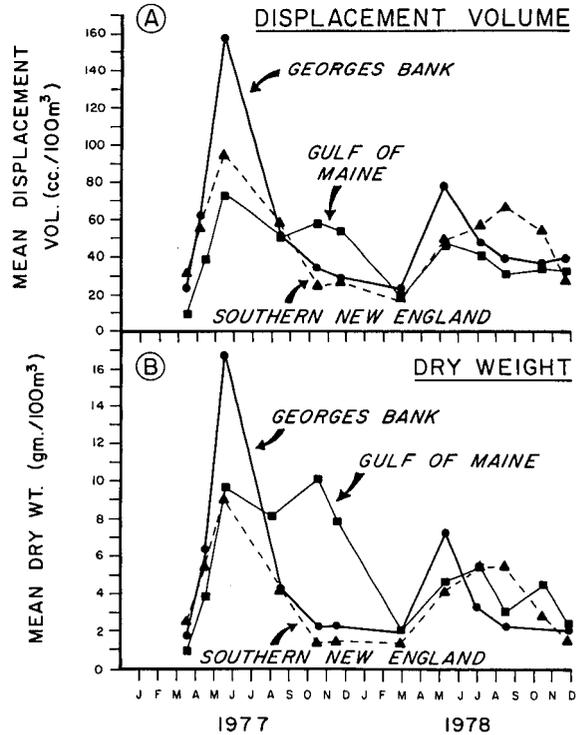


FIGURE 5.—Trends in plankton abundance for the three areas in 1977 and 1978 as measured by A) displacement volume, and B) dry weight. Each measure gives a different interpretation of between-area differences in biomass, especially in the Gulf of Maine.

nique (1966) for measuring them has been widely accepted, while techniques for measuring displacement volumes vary, especially in the attempt to remove interstitial water (Wiebe et al. 1975). Thus, for studies comparing standing stock between different sea areas, and for other advantages previously mentioned, dry weight is the preferred measure.

Summary

This report has provided a series of season- and area-specific equations for the interconversion of zooplankton displacement volume and dry weight. In addition, interconversion equations for samples with large amounts of phytoplankton and siphonophore fragments have been calculated. However, dry weights should be measured directly on samples containing organisms with large amounts of intracellular water because they drastically affect the biomass rela-

tionship. It is our experience, however, that these organisms are abundant only on rare occasions in the MARMAP study area. The predictive equations should assist investigators assessing zooplankton standing stock on the continental shelf of the Northwest Atlantic.

General conversion factors at best yield only gross estimates, thus investigators should be aware of the limitations imposed by these values. A decision must be made by the investigator as to what level of accuracy is acceptable on the basis of what the data is to be used for. Further breakdown of the data into smaller subsets than area and season is possible, but the result would be an unwieldy number of equations sensitive to minute changes in trophic conditions. However, one can conclude from this study that effective displacement volume to dry weight conversion equations must to some extent take into account seasonal and areal variations in community composition. Given these considerations, the data presented here show no increase in variability inherent in displacement volume over dry weight biomass measures. Displacement volume provides a simple, easily routinized, rapid and non-destructive method of representing biomass, which is appropriate for processing the large numbers of samples typical of survey sampling programs.

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JOSEPH KANE

Northeast Fisheries Center Narragansett Laboratory
National Marine Fisheries Service, NOAA
South Ferry Road, Narragansett, RI 02882.

ESTIMATION OF EQUILIBRIUM SETTLEMENT RATES FOR BENTHIC MARINE INVERTEBRATES: ITS APPLICATION TO *MYA ARENARIA* (MOLLUSCA: PELECYPODA)

It is generally agreed that marine invertebrates possessing planktotrophic larval stages experience extremely high mortality during the early stages of their life history. In the settlement of benthic invertebrates, mortality occurs during three critical phases: 1) fertilization, 2) the free-swimming pelagic stage, and 3) the early post-larval attachment period. Since egg loss, larval recruitment, and early postlarval mortality may often be the limiting steps in the development and maintenance of marine benthic communities, it is of interest to ecologists to be able to make direct estimates of settlement rates in such populations.

It is often difficult, however, to obtain reason-

able estimates of early life history stage mortality rates. The earliest attempt to determine such rates was made by Thorson (1966). Based on the standing crop of a population of *Venus* (= *Mercenaria*) *mercenaria*, he estimated that approximately 98.6% of the clams died during the post-larval period (stage 3) and that loss prior to this was probably much heavier. More recently, Muus (1973), in a study of 11 species of bivalves in the Oresund, Denmark, found postlarval mortality rates (stage 3) of 67-100% for all species; whereas Gledhill (1980) calculated larval mortality rates (stage 2) of 99.38% and 99.99% for two populations of *Mya arenaria* in Gloucester, Mass. None of these estimates, however, take into account the heavy mortality that occurs during stage 1, thereby overlooking the substantial loss occurring during the fertilization process itself.

In an attempt to overcome the difficulty in estimating early survival parameters empirically, Vaughan and Sails (1976) developed an indirect method using the Leslie matrix for determining mortality rates during the first year of life for the Atlantic bluefin tuna, *Thunnus thynnus*, assuming an equilibrium population. By expanding their treatment, as suggested by Van Winkle et al. (1978), it is possible to divide age class 1 into particular stages, thereby making the model appropriate for cases dealing with animals possessing more complex life cycles (i.e., those which include egg, larvae, postlarval juveniles, etc.). In the case of benthic invertebrates with free-swimming larval stages, this method can be used to calculate mortality rates during settlement for any species population for which demographic parameters are available. Such theoretical estimates are of special interest for two reasons. First, the equilibrium settlement rate (r_s) value can be compared with field-determined estimates; second, the value may be useful in the prediction of future age structures in natural populations.

This paper describes the indirect method for estimating the settlement rate based on age-specific fecundity and survivorship rates and discusses its application to a commercially important species of bivalve, *Mya arenaria*.

Results

Leslie Matrix

Matrix methods for analyzing age-structured populations were developed by Leslie (1945,