CALORIC MEASUREMENTS OF SOME ESTUARINE ORGANISMS[1]

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ABSTRACT

The caloric content per gram dry weight, per gram ash-free dry weight, and per gram live weight was determined for 51 species of organisms, representing the Ctenophora, Mollusca, Annelida, Arthropoda, Echinodermata, and Chordata, collected from the shallow estuarine system near Beaufort, N.C. Least squares regression analysis showed a highly significant correlation between caloric content per gram dry weight and the percentage organic matter. Decalcification of molluscan tissues did not significantly lower caloric values. We observed significant differences for caloric values of species grouped by phylum, and an evolutionary trend toward increasing energy content per gram live weight. We also observed a frequency distribution of energy which was skewed toward lower values.

Existing publications on the caloric content of organisms (Golley, 1961; Slobodkin and Richman, 1961; Paine, 1964; Cummins, 1967; Brawn, Peer, and Bentley, 1968; Cummins and Wuycheck, 1970) list few species which spend all of or part of their life histories in estuaries. In 1968 we began a survey of the caloric content of estuarine organisms. With knowledge of the caloric content of these species-populations our data on biomass in the shallow system of estuaries near Beaufort, N.C., could be converted to standing crop energy to facilitate the analysis of energy flow in this system. The means for these populations are presented as calories per gram dry weight, per gram ash-free dry weight, and per gram live weight to permit investigators who do not have access to a calorimeter to estimate energy units for their estuarine biomass data.

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METHODS

Organisms were collected in the Newport River estuary and surrounding estuaries near Beaufort. Detailed descriptions of the hydrography of this shallow estuarine system are presented by Williams (1966), Williams and Murdoch (1966), and Thayer (1969). The Newport River has a mean depth of 1.2 m, and the water column generally lacks vertical stratification. Salinity and temperature range from 13 to 35‰ and 7° to 32°C. The sediments of this estuary are primarily of shell and sand near the ocean with finer sands, clays, and silts predominating toward the mouth of the river.

Organisms were processed promptly after collection. All organisms, except ctenophores, were rinsed with distilled water, blotted, and weighed. Ctenophores were rinsed with distilled water and weighed intact without blotting. Gut contents of all organisms were included in the analyses, and this may have accounted, especially in the case of ctenophores, for some of the variability in caloric measurements. Meats were removed from the larger molluscs by shucking and from the smaller molluscs by decalcification with 20% HCl. Decalcification normally required 2-4 min, after which the meat and shell matrix were removed, rinsed with distilled water, blotted, and dried. The majority of organisms and molluscs meats were dried in a lyophilizer and ground to pass through a 40-mesh sieve. Samples collected during 1968 were dried at 60°C in an oven; no attempt was made to compare the results of caloric measurements on freeze-dried and oven-dried samples.

Caloric determinations were made with a Phillipson type oxygen microbomb calorimeter (Gentry Wiegert Instruments).[4] Three to eight pellet replicates, weighing from 5 to 25 mg dry weight each, were run for each sample. After each combustion a nitric acid determination and correction was made (Parr Instrument Co., 1960). In addition, sulfur content of each sample was determined (American Public Health Association, 1965) and a sulfur correction was made on each replicate. Subsamples of each material were ashed in a muffle furnace at 500°C for 36 hr. Caloric content on a dry weight and an ash-free dry weight basis were calculated according to the Parr Manual (Parr Instrument Co., 1960) and Phillipson (1964).

RESULTS AND DISCUSSION

We combusted 425 pellets of 93 samples representing 51 species-populations collected from the estuarine system near Beaufort. The values we obtained for ash content, percent dry weight, and caloric content based on dry weight, ash-free dry weight, and live weight are presented in Appendix Table 1. Some general conclusions have emerged from calorimetric studies, with which our data agree, but specific values and relations for an estuarine system have not been presented before.

We observed a statistically significant relation between energy content per gram dry weight and the percent of organic matter in the sample ($r = 0.857$; $d.f. = 91$) (Figure 1). The least squares regression equation was

$$Y = 0.0604X - 0.420,$$

where Y is kilocalorie per gram dry weight and X is the percent organic matter (ash-free dry weight) in the sample. This equation is similar to those obtained by chemical composition techniques (Ostaypenya and Sergeev, 1963) for marine and freshwater organisms:

$$Y = 0.0616X - 0.286$$

and for marine crustaceans and molluscs:

$$Y = 0.0617X - 0.531.$$

The similarity of the three regression equations suggests a general relation between the caloric content and the percent dry matter of all aquatic organisms. We are continuing to collect and analyze samples, however, to determine whether there are seasonal differences.

The linear regression suggests that if there are changes in chemical composition of the organic matter, primarily differences in the percent lipid material, they are obscured in this relation by relatively large amounts of inorganic substances in the dry tissues of the organisms. We therefore analyzed the correlation between energy content per gram organic matter and the percent organic matter in the samples. Where applicable, corrections for endothermy (Paine, 1964, 1966) were applied. The resulting correlation, although significant, was low ($r = 0.333$; $d.f. = 91$) indicating great scatter about the regression line. The least squares regression equation was:

$$K = 0.0183X + 3.991,$$

where K is kilocalorie per gram organic matter and X is the percent organic matter. The slope of this line is significantly greater than zero, indicating that the organic matter of the species tested did not have a constant proportion of lipid, protein, and carbohydrate materials. These chemical differences were not obvious from the regression analysis of energy per gram dry weight because they were masked by inorganic substances.

It is possible that acid digestion of molluscs may have altered their caloric content. Paine

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

(1966) stated that acid digestion would reduce the ash content and the endothermal effect but that the influence of this treatment on the caloric content of the treated samples is not known. Richards and Richards (1965) found small amounts of organic carbon were lost from *Nassarius trivitattus* during decalcification, and this would cause some loss of energy from the samples. Since the majority of gastropods and some of the pelecypods analyzed were decalcified prior to analysis (Appendix Table 1), we analyzed the effect of decalcification on the caloric content of eight sets of mollusc tissues, including three sets of *Modiolus demissus* from Virginia, North Carolina, and Georgia (Table 1).

To determine the maximum effect of decalcification larger organisms were decalcified for a longer period of time than in the routine analysis. Twelve organisms of each set were shucked and one-half of each group was placed in 20% HCl for 15 min (3-8 times longer than for routine analysis of small molluscs). All samples were then dried in a lyophilyzer, and the ash content of the dried material was measured after combustion for 36 hr in a muffle furnace at 500°C. Although decalcification generally tended to reduce the caloric values, in two cases, *Modiolus demissus* (from Virginia) and *Tagelus plebeius,* differences between untreated and decalcified tissue caloric values were significantly different at the 5% level (Table 1). These data suggest that although the shorter decalcification time employed in routine analysis may have lowered the caloric content of the molluscs through protein hydrolysis and extraction of carbon, the decrease probably was insignificant and would not have appreciably affected the regression equation.

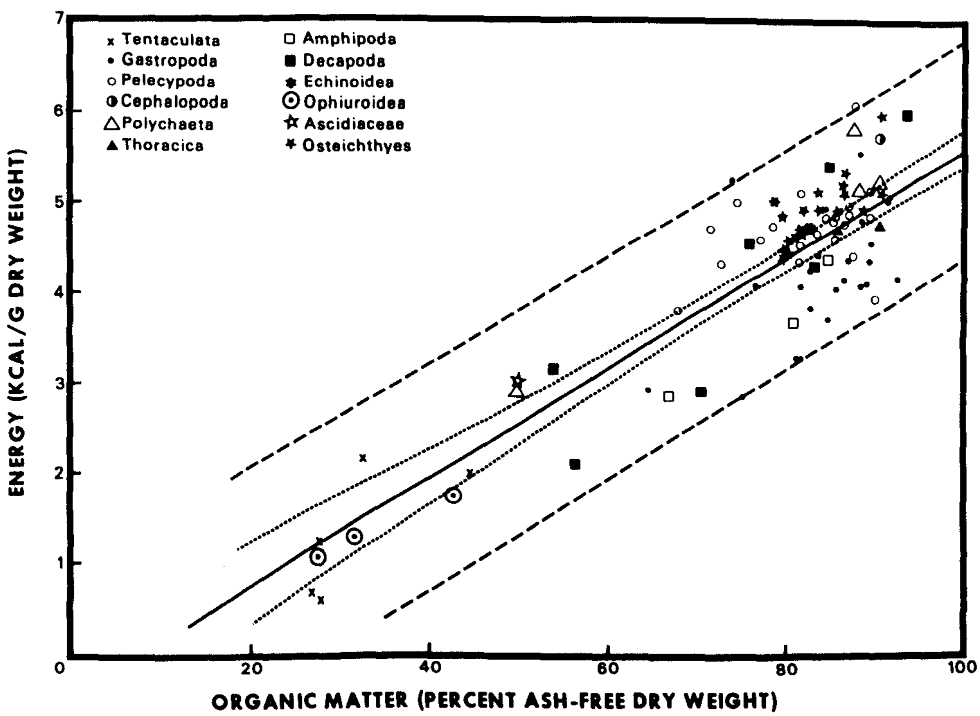

FIGURE 1.—Relation between the caloric and organic content of estuarine organisms. Solid line is the linear regression line; dashed line represents the 95% confidence limits for the prediction equation; dotted line represents the 95% confidence limits for the regression line.

TABLE 1.—Summary of changes in ash and caloric content of decalcified and nontreated tissues of some estuarine molluscs. In each case, six organisms were combined and six caloric measurements made for each combined sample. HCl treatments were for 15 min.

Organism	Collection area	Treatment	Ash %	kcal/g ash-free dry weight	± Standard deviation
Brachidontes recurvus	Florida	None	11.8	5.232	0.056
		HCl	2.5	5.034	0.081
Chione cancellata	North Carolina	None	10.5	5.817	0.096
		HCl	3.7	5.754	0.081
Mercenaria mercenaria	North Carolina	None	18.3	5.235	0.185
		HCl	11.1	5.282	0.045
Modiolus demissus	Virginia	None	11.9	5.036*	0.010
		HCl	3.6	4.783*	0.085
Modiolus demissus	North Carolina	None	15.7	5.118	0.046
		HCl	6.3	4.998	0.087
Modiolus demissus	Georgia	None	5.4	5.102	0.051
		HCl	4.8	5.053	0.095
Mytilus edulis	Virginia	None	13.5	5.006	0.046
		HCl	3.3	5.068	0.045
Tagelus plebeius	North Carolina	None	16.5	5.471*	0.104
		HCl	12.6	4.751*	0.166

*Significantly different at the 0.05 level.

Significant differences in energy content between phyla were observed on the basis of ash-free dry weights and live weights. The phyla show an orderly phylogenetic progression of energy content only on the basis of live weight (Table 2). This is partially the result of decreasing water content of more structurally advanced phyla; we observed significant differences among phylum means for water content which followed a similar trend. Not all phylum means were significantly different, however. The significant overall phylum effect can be attributed to ctenophores' having a significantly lower energy content than the annelids, arthropods, and chordates, but there are no significant differences among the foregoing three phyla nor among the ctenophores, echinoderms, and molluscs (Table 2). Also, within the phylum Mollusca and the class Crustacea the more advanced or more specialized groups (Cephalopoda and Decapoda) had significantly higher caloric contents per gram live weight than the less advanced groups. Although the values we obtained in this study may have resulted from a fortuitous selection of organisms, we feel that the species analyzed are representative of their phyla and that the relation between caloric content, percent dry weight, and percent organic matter, and the phylogenetic position reflects an evolutionary trend for increased caloric content per gram live weight as a result of increased proportion of living tissue with increasing phylogenetic position.

TABLE 2.—Analysis of variance of energy content, in kilocalorie per gram live weight, for all species examined, and listed in Appendix Table 1, and the mean kilocalorie per gram live weight for each taxon.

Source of variation	Degrees of freedom	Mean square	*F* ratio
Among phyla	5	2.494	34.01**
Within phyla	87	0.073	
Total	92	2.567	

Phylum	Mean kcal/g live weight
Ctenophora	0.049
Mollusca	0.373
Echinodermata	0.393
Annelida	0.850
Arthropoda	1.027
Chordata	1.156

**Significant at the 0.01 level.

The differences in caloric content may have arisen from variation in the growth or reproductive stage, or the energy content of the food source. The ctenophores and gastropods showed differences of as much as 1 kcal/g between sampling periods (Appendix Table 1, columns C and D). The variation in the gastropods may have been the result of increased lipid content prior to spring spawning. We feel that the large variation observed for the ctenophores was partially the result of high energy food in the gut contents. February and March are periods of high zooplankton abundance in the Newport River estuary, and ctenophores may exert heavy predation pressure on zooplankton (Hyman, 1940; Herman, Mihursky, and McErlean, 1968). Consequently, high energy zooplankton (Comita and Schindler, 1963) in the gut may have caused the high caloric values obtained during this period.

The Osteichthyes showed trends in their caloric content which were associated with life history stages and feeding habits. Adult fishes did not show the temporal variation in caloric values which was observed for many of the other taxonomic groups (Appendix Table 1). Postlarval and juvenile stages generally had higher caloric (per unit dry weight and per unit ash-free dry weight) and lower ash contents than their adult stage. The higher caloric content per unit dry weight is of course partly due to the lower ash content. The higher caloric content per unit ash-free dry weight is probably the result of consumption of high energy food such as zooplankton (Comita and Schindler, 1963) by postlarval and juvenile fishes. Adult *Brevoortia tyrannus*, a planktonic feeder, tended to have have higher (but not significant) caloric values (mean 6.018 kcal/g ash-free dry weight) than adult carnivore-omnivore feeding types (mean 5.748 kcal/g ash-free dry weight). The higher values obtained for menhaden are not surprising since up to 28.7% of the wet weight of these fishes may be fats (Perkins and Dahlberg, 1971).

On the basis of limited data Slobodkin and Richman (1961) argued that the frequency distribution of energy (per gram ash-free dry weight) in a "haphazard collection of species" is skewed right, i.e., the modal frequency is at the lower end of the energy range. They explain this distribution by stating that ". . . there has always been selection for maximum number of reproducing progeny, but only sporadic selection for high energy content/gm." Even if there always has been selection for maximum number of reproducing progeny, the analysis of energy content relative to spawning time will affect the results. The argument also ignores the evolution of other life history strategies resulting in fewer offspring with higher survival rates (Mac Arthur and Wilson, 1967; Gadgil and Bossert, 1970) where there may be long-term storage of energy in individual organisms. Cummins and Wuycheck (1970) presented a frequency distribution similar to that of Slobodkin and Richman (1961) and stated that the distribution resulted from the predominance of plant values in their data. We suggest, with Paine (1964), that it may have been premature for Slobodkin and Richman to recognize a particular type of distribution. By combining the results of 15 species of invertebrates with Slobodkin and Richman's data on 17 species, Paine observed a more symmetrical distribution.

If, as indicated by our samples, there is an evolutionary trend toward increased energy content, the predominance of structurally more advanced species in our sample would result in a frequency distribution skewed left as shown in Figure 2. The predominance of advanced species in our samples is consistent with available check lists for the Beaufort area (Duke University Marine Laboratory, 1953; Turner and

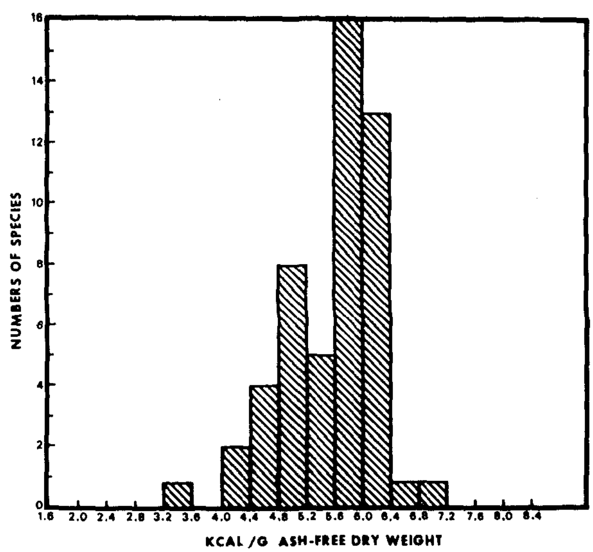

FIGURE 2.—Frequency distribution of energy in a system of shallow estuaries. The values are means for the 51 species presented in Appendix Table 1.

Johnson).[5] The mean of the distribution is 5.57 kcal/g ash-free dry weight, the median is 5.74 and the mode is 5.80. We are continuing to obtain caloric data on these and other species throughout the year to determine whether the frequency distribution of energy in organisms from the Newport River estuary is continually skewed left (Figure 2) or because of seasonal variations follows some other pattern, such as the normal distribution suggested by Paine (1964).

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APPENDIX TABLE 1.—Summary of data collected during caloric analysis of estuarine organisms.

Classification	Collection date	Combustions	(Col. A) Ash	(Col. B) Dry/ live wt	(Col. C)	(Col. D) Energy content	(Col. E)
		Number	%	%	*kcal/g dry wt*	*kcal/g ash-free dry wt*	*kcal/g live wt*
Ctenophora							
Class Tentaculata							
Mixed ctenophores	12-10-69	4	73.2	2.3	[1]0.652 ± 0.419	2.428 ± 1.563	0.014
Mixed ctenophores	1-10-70	6	72.5	2.7	0.579 ± 0.188	1.934 ± 0.546	0.016
Mixed ctenophores	1-22-70	4	72.7	2.8	1.210 ± 0.102	4.439 ± 0.373	0.082
Mixed ctenophores	2-5-70	4	55.5	3.9	2.000 ± 0.103	4.490 ± 0.224	0.079
Mixed ctenophores	3-17-70	4	67.6	2.4	2.178 ± 0.344	6.725 ± 1.062	0.054
Mean			68.3	2.8	1.324	4.003	0.049
Mollusca							
Class Gastropoda[2]							
Bittium varium	11-20-69	6	15.3	10.2	3.696 ± 0.111	4.357 ± 0.119	0.377
B. varium	12-17-69	5	16.4	9.1	4.414 ± 0.199	5.279 ± 0.236	0.402
B. varium	2-11-69	4	23.5	12.2	4.087 ± 0.129	5.334 ± 0.177	0.499
Mitrella lunata	11-20-69	5	18.3	14.8	3.274 ± 0.105	4.005 ± 0.127	0.485
M. lunata	1-14-70	5	7.7	16.1	4.139 ± 0.156	4.483 ± 0.169	0.666
M. lunata	2-11-70	4	10.6	12.5	4.533 ± 0.248	5.060 ± 0.286	0.567
Nassarius obsoletus	11-7-69	4	10.9	9.7	4.096 ± 0.098	4.595 ± 0.111	0.397
N. vibex	8-21-69	4	14.3	6.2	4.027 ± 0.123	4.698 ± 0.145	0.250
N. vibex	11-20-69	3	23.9	6.3	2.855 ± 0.110	3.752 ± 0.144	0.180
N. vibex	2-11-70	3	11.4	5.5	4.805 ± 0.091	5.425 ± 0.098	0.264
N. vibex	3-19-70	4	11.8	4.6	5.575 ± 0.123	6.319 ± 0.139	0.258
Anachis avara	10-29-69	3	18.9	7.3	3.288 ± 0.042	4.108 ± 0.147	0.240
A. avara	12-17-69	4	17.2	7.5	3.816 ± 0.175	4.583 ± 0.214	0.286
A. avara	1-14-70	4	13.8	6.5	4.158 ± 0.153	4.816 ± 0.200	0.270
A. avara	2-11-70	4	17.7	7.8	4.208 ± 0.222	5.099 ± 0.275	0.328
Crepidula convexa	12-17-69	3	35.7	8.8	2.908 ± 4.263	4.553 ± 0.410	0.256
C. fornicata	12-17-69	5	18.4	7.3	4.066 ± 0.132	4.981 ± 0.161	0.297
C. fornicata	4-15-70	4	15.4	6.0	4.957 ± 0.213	5.858 ± 0.252	0.272
C. fornicata (eggs)	4-15-70	4	36.5	7.8	5.248 ± 0.142	8.269 ± 0.223	0.408
Pyramidella fusca	1-14-70	3	11.7	8.6	4.081 ± 0.382	4.621 ± 0.432	0.351
P. fusca	2-11-70	4	26.1	4.0	5.287 ± 0.249	7.158 ± 0.339	0.211
Retusa canaliculata	1-14-70	3	10.7	7.8	4.357 ± 0.281	4.880 ± 0.314	0.340
R. canaliculata	2-11-70	4	8.8	6.2	5.014 ± 0.128	5.491 ± 0.147	0.311
R. canaliculata	3-19-70	4	8.8	5.9	5.072 ± 0.041	5.514 ± 0.044	0.314
Urosalpinx cinerea	2-11-70	3	13.0	4.6	4.369 ± 0.057	5.623 ± 0.060	0.201
Mean			16.7	[3]8.1	4.253	5.154	0.337
Class Pelecypoda							
Pecten irradians	1-14-70	4	12.1	6.0	6.106 ± 0.050	6.949 ± 0.052	0.366
Mercenaria mercenaria	1-2-69	7	25.4	3.1	5.040 ± 0.279	6.757 ± 0.374	0.156
M. mercenaria	12-17-69	5	13.4	3.8	4.793 ± 0.229	5.535 ± 0.264	0.182
Chione cancellata	1-2-69	5	14.4	4.4	4.886 ± 0.150	5.668 ± 0.216	0.215
C. cancellata	12-17-69	3	16.4	4.5	4.699 ± 0.141	5.623 ± 0.169	0.211
C. cancellata	2-11-70	4	18.8	7.7	4.369 ± 0.176	5.381 ± 0.221	0.336
C. cancellata[2]	3-19-70	3	10.5	[3]3.3	5.152 ± 0.072	5.754 ± 0.081	0.170
Tagelus divisus	4-25-69	6	12.2	12.3	4.414 ± 0.442	5.027 ± 0.504	0.543
Modiolus demissus	1-10-69	6	13.0	12.0	5.014 ± 0.342	5.765 ± 0.393	0.601
Crassostrea virginica	12-30-68	6	21.9	3.7	4.756 ± 0.235	6.090 ± 0.301	0.176
C. virginica	4-3-69	6	22.9	3.2	4.605 ± 0.308	5.973 ± 0.400	0.147
Anomia simplex	1-14-70	2	13.0	5.8	4.922	5.660	0.285
Teredo navalis	12-24-69	3	14.4	24.4	4.826 ± 0.079	5.639 ± 0.093	1.178
T. navalis	1-14-70	4	14.8	22.7	4.859 ± 0.165	5.703 ± 0.192	1.069
Macoma balthica[2]	1-14-70	3	10.0	[3]9.9	3.955 ± 0.146	4.391 ± 0.168	0.392
M. balthica[2]	2-11-70	4	18.2	[3]9.0	4.558 ± 0.119	5.776 ± 0.151	0.410
M. tenta[2]	2-11-70	4	27.2	[3]9.2	4.320 ± 0.020	5.935 ± 0.039	0.397
M. tenta[2]	3-19-70	4	28.3	[3]8.2	4.738 ± 0.085	6.611 ± 0.119	0.389
Pinna serrata	3-19-70	4	18.9	8.9	5.129 ± 0.200	6.322 ± 0.247	0.456
Anadara transversa	2-11-70	4	14.9	4.2	4.612 ± 0.134	5.425 ± 0.157	0.194
A. transversa	3-19-70	4	10.3	3.5	4.884 ± 0.088	5.462 ± 0.098	0.171
Mean			16.7	8.1	4.792	5.783	0.383
Class Cephalopoda							
Loligo brevis	12-31-68	5	9.4	18.3	5.743 ± 0.359	6.342 ± 0.398	1.051

See footnote at end of table.

APPENDIX TABLE 1.—Summary of data collected during caloric analysis of estuarine organisms.—Continued.

Classification	Collection date	Combustions	(Col. A) Ash	(Col. B) Dry/live wt	(Col. C)	(Col. D) Energy content	(Col. E)
		Number	%	%	*kcal/g dry wt*	*kcal/g ash-free dry wt*	*kcal/g live wt*
Annelida							
Class Polychaeta							
Amphitrite ornata	1- 2-69	7	50.7	25.4	2.912 ± 0.311	5.906 ± 0.616	0.303
Diopatra cuprea	4-28-69	6	11.9	25.4	5.176 ± 0.433	5.878 ± 0.492	1.315
Nereis pelagica	11-20-69	3	12.2	16.6	5.854 ± 0.128	6.671 ± 0.144	0.972
N. pelagica	2-11-70	3	9.5	15.4	5.252 ± 0.184	5.827 ± 0.204	0.808
Mean			21.1	20.7	4.798	6.070	0.849
Arthropoda							
Order Thoracica[2]							
Balanus balanoides	12-24-69	6	14.1	10.2	4.715 ± 0.235	5.326 ± 0.275	0.481
B. balanoides	1-14-70	5	9.6	10.4	4.777 ± 0.242	5.273 ± 0.278	0.497
Mean			11.8	[3]10.3	4.746	5.299	0.489
Order Amphipoda							
Carinogammarus mucronatus	10-29-69	4	19.4	26.7	3.694 ± 0.322	4.582 ± 0.400	0.986
C. mucronatus	2-11-70	4	15.5	24.7	4.397 ± 0.054	5.202 ± 0.057	1.086
Amphithoe longimana	11-20-69	4	33.3	31.4	2.909 ± 0.188	4.358 ± 0.281	0.913
A. longimana	1-14-70	6	32.3	31.6	3.820 ± 0.209	5.647 ± 0.309	1.207
Mean			25.1	[4]28.6	3.705	4.947	1.048
Order Decapoda							
Paleomonetes pugio	12-31-68	6	15.3	27.4	5.416 ± 0.424	6.393 ± 0.501	1.484
Callinectes sapidus—adult	1-22-69	6	46.4	32.6	3.202 ± 0.375	5.974 ± 0.693	1.044
C. sapidus—immature	11-20-69	5	29.9	27.2	2.945 ± 0.251	4.204 ± 0.358	0.801
Pinnotheres ostreum	4- 8-69	6	6.5	18.5	6.034 ± 0.277	6.357 ± 0.303	1.116
Peneus setiferus	11- 4-69	6	17.7	23.3	4.735 ± 0.163	5.751 ± 0.197	1.103
Callianassa stimpsoni	11-20-69	6	17.1	26.3	4.249 ± 0.113	5.128 ± 0.135	1.117
Upogebia affinis	3-27-69	6	24.4	26.7	4.597 ± 0.376	6.080 ± 0.488	1.227
Libinia dubia	1-14-70	5	44.0	61.9	2.123 ± 0.200	3.215 ± 0.302	1.314
Mean			25.2	[4]30.5	4.163	5.388	1.151
Echinodermata							
Class Echinoidea							
Arbacia punctulata—meat	1-20-69	6	21.6	1.0	5.031 ± 0.467	6.416 ± 0.597	0.050
Class Ophiuroidea							
Ophioderma brevispina	11-20-69	1	72.5	52.3	1.043	3.797	0.551
O. brevispina	1-14-70	4	57.3	32.5	1.763 ± 0.255	4.601 ± 0.667	0.573
O. brevispina	3-19-70	4	68.7	30.7	1.289 ± 0.155	4.438 ± 0.532	0.397
Mean			66.2	38.5	1.365	4.279	0.507
Chordata							
Class Ascidiacea							
Mogula manhattensis	1- 3-69	6	50.3	7.3	3.002 ± 0.332	6.039 ± 0.668	0.219
Class Osteichthyes							
Lagodon rhomboides—adult	12-17-68	7	18.3	26.7	4.665 ± 0.126	5.709 ± 0.153	1.245
L. rhomboides—adult	11-25-69	7	20.6	24.5	4.399 ± 0.308	5.543 ± 0.388	1.078
L. rhomboides—post larval	1-14-70	4	9.2	11.2	6.001 ± 0.420	6.418 ± 0.422	0.672
Brevoortia tyrannus—adult	1-14-70	5	13.7	30.9	5.376 ± 0.210	6.112 ± 0.238	1.661
B. tyrannus—adult	1-22-70	5	13.9	30.2	5.202 ± 0.094	5.925 ± 0.107	1.571
B. tyrannus—post larval	4-22-69	6	9.2	18.5	5.128 ± 0.365	5.694 ± 0.454	0.949
Fundulus heteroclitus—adult	12-24-68	5	19.8	28.5	4.589 ± 0.109	5.722 ± 0.135	1.308
F. majalis—adult	12-17-69	5	20.7	30.2	4.880 ± 0.102	6.155 ± 0.132	1.474
Paralichthys dentatus—adult	8-21-69	7	16.3	23.3	4.927 ± 0.295	5.427 ± 0.345	1.148
P. dentatus—immature	1-14-70	4	11.3	20.7	4.953 ± 0.130	5.588 ± 0.144	1.025
Leiostomus xanthurus—adult	11-25-69	5	16.5	23.9	5.139 ± 0.126	6.152 ± 0.150	1.228
L. xanthurus—adult	5-28-69	5	18.0	22.1	4.948 ± 0.192	6.035 ± 0.234	1.094
Micropogon undulatus—adult	5-28-69	6	19.3	23.7	4.638 ± 0.184	5.744 ± 0.226	1.099
Mugil cephalus—adult	2-27-69	4	20.2	28.3	4.487 ± 0.196	5.393 ± 0.237	1.270
M. cephalus—post larval	1-22-70	2	13.7	24.8	5.142	5.959	1.275
Gobiosoma bosci—adult	10-29-69	4	19.4	32.1	4.758 ± 0.207	5.900 ± 0.256	1.527
Symphurus plagiusa—adult	11- 6-69	6	20.5	22.6	4.492 ± 0.120	5.650 ± 0.138	1.015
S. plagiusa—post larval	11- 6-69	6	14.5	22.5	4.904 ± 0.143	5.735 ± 0.171	1.103
Mean			16.4	24.7	4.924	5.826	1.208

[1] Mean ± 1 standard deviation.
[2] Decalcified with 20% HCl.
[3] Dry weight from dry weight of meat plus protein matrix of shell.
[4] Includes carapace.