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Energy values of marine benthic invertebrates from the Canadian Arctic

J. W. Wacasey, E. G. Atkinson

Arctic Biological Station, Department of Fisheries and Oceans, 555 St. Pierre Boulevard, Ste-Anne-de-Bellevue, Québec H9X 3R4, Canada

ABSTRACT: Caloric values were determined for 121 species of cold-water benthic invertebrates, 109 of which are representative of a soft bottom community in Frobisher Bay, Northwest Territories (Canada). The mean caloric value for the community was 5.424 kcal g^{-1} ash-free dry weight (SD ± 0.403). This is not significantly different from values from lower latitudes, as has been suggested for planktonic communities. With one exception, the Ascidiacea, there were no significant differences in mean caloric value among major taxa. The interspecific distribution of AFDW caloric value is discussed; present data support the growing evidence that the natural pattern is symmetrical with values concentrated about a mean of 5.4 to 5.7 kcal g^{-1} AFDW for benthic invertebrates. Caloric equivalents for biomass estimates and large-scale community comparisons may be derived from the regression of dry weight caloric value on percent organic content (dry weight): Y (kcal g^{-1} AFDW) = −0.3897 + 0.0605 X (% organic content), when the organic fraction is determined directly. Two problematical taxa, Porifera and Echinodermata, are discussed and separate regressions are presented.

INTRODUCTION

Although energy values of many cold-water marine zoobenthic invertebrates are available (Ellis 1960, Brawn et al. 1968, Cummins & Wuycheck 1971, Tyler 1973, Percy & Fife 1980, 1981, Bamstedt 1981, Norrbin & Bamstedt 1984, Steimle & Terranova 1985), to our knowledge no study has attempted to elucidate the distributional pattern of caloric value in a large number of species occurring in a single natural community in the Arctic.

The use of a variety of methods of expressing biomass estimates (live, whole wet, wet meat, whole dry, dry meat weight) has made comparisons of benthic communities difficult and often misleading. A more suitable expression of standing stock is ash-free dry weight, and caloric equivalents provide basic information for energetic studies.

The present study was undertaken to obtain organic content and caloric equivalents for as many species of benthic invertebrates from Canadian Arctic waters as practicable, and values are presented for 121 species, 114 of which are a representative assemblage from a depth transect in Frobisher Bay. The relevance of the community mean value, taxonomic variations, and interspecific distribution pattern of caloric values is discussed. The relationships between caloric value and organic content gives equations from which fast, reliable estimates of caloric content may be derived from a knowledge of organic content. These may confidently be used for community comparisons where seasonal or intra-specific variation on a variety of parameters is not of primary concern.

MATERIALS AND METHODS

Benthic invertebrates were collected by trawl from stations in the Canadian Arctic during August, between 1968 and 1976. All but 7 species were collected in Frobisher Bay from the intertidal zone to 90 m depth with 109 species being obtained from soft bottoms at depths between 30 and 65 m. The salinity (30 to 34 ‰) and temperature (−1.75 to 0.5 °C) of the water immediately above the substrate at the latter range of depths varies little throughout the year.

Specimens were sorted, identified and dried at 60 to 110 °C, usually within 12 h of capture. Tubes, shells,

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tests and other hard parts were removed where possible, before or after drying. In echinoderms and sponges dry weight includes skeletal material and spicules, because these inorganic structures are difficult to separate mechanically from the organic, and it was considered that acidic decalcification of complex echinoderm skeletons would adversely affect caloric value. Specimens were dried at 100 °C to constant weight. A detailed discussion of the drying technique is given by Atkinson & Wacasey (1983). Dried animals were finely pulverized (0.250 mm, # 60 standard screen) and kept in a desiccator until analysed for ash and caloric content.

A sample consisted of a pool of all individuals of a species collected on a given date. This usually involved a number of animals of variable size, sex and reproductive condition, and believed to be representative of the population of that species *in vivo*. This study did not attempt to examine seasonal or life-cycle variation in caloric value. Infrequently, a sample consisted of only a single individual; this occurred with some large, widely dispersed species, mostly Asteroidea.

Ashing was carried out in a muffle furnace at a temperature of 500 °C. Ashing time varied from 16 h in the early determinations to 4 h in later runs to minimize breakdown of ash (Paine 1966, 1971, Atkinson & Wacasey 1983). Most samples were ashed in duplicate and a mean was determined from the two values when they differed by less than 1 %. The weight loss from ashing is regarded as the organic content, and for convenience, the percent organic content of dry weight (DW) rather than the percent ash weight is presented in Tables 1 & 2 as this was used to express the caloric content in terms of ash-free dry weight (AFDW).

Homogeneous dry samples were formed into pellets and calorimetric determinations were made with both a Parr model 1243 adiabatic bomb calorimeter with automatic temperature control and the 1107 semi-micro bomb. General calorimetric procedures, as given in Parr manuals 142 (1969) and 144 (1973), and ASTM standards for bomb calorimetry (1971) were followed. Each sample was determined in triplicate and a mean was calculated when the 3 values differed by less than 3 % (Golley 1961).

Corrections for fuse wire and heat of formation of acid were determined and applied to all calculations. In samples with an organic content less than 25 %, known amounts of benzoic acid (up to 30 %) were added to promote ignition and ensure complete burning. Additional corrections were made on samples with large amounts of calcareous (echinoderms) and silicious (sponges) material. Correction factors for water of hydration and endothermic dissociation of $CaCO_3$ were used to adjust ash and caloric values for some species (Table 1). The effects of these correction factors are discussed in greater detail by Atkinson & Wacasey (1976, 1983).

RESULTS

The organic content and energy values determined for 121 species of benthic invertebrates are presented in Table 1, and summarized for major taxa in Table 2. The organic content and caloric values represent the mean of all available sample values (each the mean respectively of duplicate or triplicate determinations) for a given species. Column 'n' lists the number of such values. Where n = 1 the percent organic content range is 1 %; caloric value SD and confidence interval are derived from the 3 replicates; where $n > 1$, SD and confidence interval are derived from the total number of sample values summed. Thus the 95 % confidence limits of the caloric values are large when few and significantly different sample values are combined.

The grand mean of AFDW caloric values was 5.424 kcal g^{-1} (SD $\pm$ 0.403). The distribution of values (Fig. 1) was negatively skewed ($g_1 = -1.115$) and leptokurtic ($g_2 = 2.447$).

The regression of AFDW caloric value on percent organic content for the values presented in Table 1, is Y (kcal g^{-1} AFDW) = 0.0149 X (% organic content) + 4.396 ($r = 0.568$, df = 180, $t = 9.26$, $p < 0.001$). This excludes data from Echinodermata and Porifera which have a high ash content due to inclusion of inorganic skeletal material, and which have had caloric estimates corrected for water of hydration and endothermy.

A summary of regressions of caloric value per unit DW on percent organic content for major taxa, and all individual samples is presented in Table 3 and Fig. 2. These regressions represent caloric value as determined in the bomb, with no correction applied for endothermy, and organic content obtained from muffle furnace combustion, with no correction applied for water of hydration. The Echinodermata include only those species from which the skeleton could not be removed. The regressions for Echinodermata and Porifera based on corrected data in Table 3 and depicted in Fig. 3 demonstrate the effect of compensating for inaccuracies which are known to arise, and will be discussed below. The regression equation for all data was Y (kcal g^{-1} DW) = −0.3897 + 0.0605 X (% organic content; $r = 0.986$, df = 211, $t = 87.114$, $p < 0.001$). This may be used to predict accurate caloric values when organic content has been determined directly, except for the Echinodermata and Porifera. For these taxa, adjustments for water of hydration and endothermy have been made to give more accurate predictive equations. For Porifera this was Y = −0.3141 + 0.0588 X; for Echinodermata, Y = −0.4037 + 0.0617 X.

Table 1. Organic content and caloric values of marine benthic invertebrates from the Canadian Arctic

Species	n	Organic % DW	Range	kcal g^{-1} DW	kcal g^{-1} AFDW	± SD	± 95 % CI
ANNELIDA: Polychaeta							
Amphitrite groenlandica	1	71.1	–	4.107	5.777	0.011	0.034
Branchiomma infarcta	1	80.6	–	4.477	5.554	0.049	0.151
Enipo gracilis	2	68.3	60.3–76.3	3.653	5.350	0.034	0.047
Harmothoe nodosa	1	73.4	–	4.036	5.499	0.010	0.131
Harmothoe oerstedi	2	80.2	77.5–82.8	4.314	5.382	0.013	0.161
Lumbrineris fragilis	1	88.4	–	5.035	5.696	0.012	0.036
Myriochele heeri	1	–	–	1.079	5.422	0.046	0.139
Nephtys ciliata	1	72.9	–	3.982	5.462	0.054	0.164
Nephtys paradoxa	1	84.4	–	5.131	6.079	0.067	0.204
Nicomache lumbricalis	3	66.9	62.9–69.0	3.590	5.371	0.015	0.446
Pherusa plumosa	1	42.7	–	2.263	5.299	0.034	0.428
Phyllodoce groenlandica	1	71.6	–	4.010	5.601	0.079	1.009
Pista flexuosa	1	58.6	–	3.382	5.771	0.011	0.136
Pista maculata	1	78.2	–	4.740	6.061	0.017	0.051
Praxillella praetermissa	1	76.2	–	4.171	5.474	0.062	0.188
Sabella crassicornis	1	82.4	–	4.629	5.618	0.019	0.059
Scalibregma inflatum	1	43.3	–	2.186	5.048	–	–
Thelepus cincinnatus	2	79.4	71.6–87.2	4.487	5.627	0.336	4.277
ARTHROPODA: Amphipoda							
Anonys nugax	2	66.1	65.0–67.2	3.960	5.990	0.049	0.629
Gammarus oceanicus/setosus	1	65.2	–	3.610	5.537	0.010	0.032
Paramphithoe hystrix	1	55.9	–	3.076	5.502	0.031	0.095
Stegocephalus inflatus	2	61.5	57.8–65.2	3.737	6.106	0.678	8.616
ARTHROPODA: Cirripedia							
Balanus balanoides	1	79.7	–	4.552	5.712	0.050	0.153
Balanus balanus	3	70.0	66.9–72.8	3.772	5.387	0.059	0.178
Balanus crenatus	1	67.3	–	3.656	5.432	0.048	0.145
ARTHROPODA: Cumacea							
Diastylis goodsiri	1	43.7	–	1.991	4.557	0.028	0.086
ARTHROPODA: Decapoda							
Argis dentata	3	77.3	73.4–79.6	4.402	5.684	0.359	1.091
Eualus gaimardi	1	62.3	–	3.301	5.298	0.025	0.077
Lebbeus groenlandicus	4	69.8	62.3–75.6	3.961	5.668	0.194	0.357
Pagurus pubescens	1	53.6	–	3.033	5.659	0.040	0.122
Sabinea septemcarinata	2	79.7	0.0	4.397	5.517	0.117	1.491
Sclerocrangon boreas	6	75.3	67.1–79.6	4.241	5.633	0.174	0.200
Spirontocaris spinus	7	69.0	62.8–74.1	3.867	5.608	0.101	0.101
ARTHROPODA: Isopoda							
Arcturus baffini	5	49.5	46.1–53.0	2.478	5.012	0.702	0.975
Mesidotea entomon[1]	1	58.2	–	3.388	5.821	0.014	0.042
Mesidotea sabini[1]	1	58.3	–	3.425	5.875	0.015	0.046
ARTHROPODA: Pycnogonida							
Nymphon hirtipes	3	48.3	31.3–68.1	2.506	5.137	0.206	0.626
BRACHIOPODA							
Hemithyris psittacea	3	57.4	50.7–64.8	3.002	5.242	0.312	0.950
CHORDATA: Ascidiacea							
Ascidia callosa	2	32.7	25.4–40.0	1.511	4.533	0.559	7.098
Boltenia echinata	1	11.9	–	0.584	4.908	0.139	0.423
Boltenia ovifera	3	45.4	32.1–46.8	2.300	4.968	0.335	0.616
Ciona intestinalis	2	25.8	22.4–29.1	0.981	3.803	0.073	0.925
Dendrodoa aggregata	1	52.3	–	2.629	5.026	0.070	0.213
Kukenthalia borealis	1	35.9	–	1.650	4.595	0.086	0.260
Pelonaia corrugata	1	42.0	–	1.954	4.653	0.052	0.159
Rhizomolgula globularis[1]	1	37.0	–	1.704	4.605	0.020	0.062
Styela rustica	2	27.3	21.7–32.8	1.300	4.695	0.518	6.582

Table 1 (continued)

Species	n	Organic % DW	Range	kcal g^{-1} DW	kcal g^{-1} AFDW	± SD	± 95 % CI
COELENTERATA: Anthozoa							
Halcampa arctica	1	78.1	–	4.025	5.154	0.021	0.262
COELENTERATA: Hydrozoa							
Tubularia regalis	1	66.0	–	3.361	5.092	0.033	0.100
ECHINODERMATA: Asteroidea							
Henricia eschrichti	1	45.8[2]	–	2.375	5.345	0.055	0.167
Henricia scabrior	2	65.0[2]	55.8–74.2	3.592	5.605	0.158	2.013
Leptasterias polaris	1	48.3[2]	–	2.558	5.475	0.060	0.184
Pteraster pulvillus	1	45.1[2]	–	2.260	5.172	0.027	0.083
Solaster papposus	3	48.7[2]	39.2–61.1	2.755	5.777	0.143	0.436
Solaster syrtensis	1	45.6[2]	–	2.336	5.291	0.009	0.026
ECHINODERMATA: Crinoidea							
Heliometra glacialis	4	24.7[2]	23.7–27.2	1.219	5.124	0.338	0.621
ECHINODERMATA: Echinoidea							
Strongylocentrotus droebachiensis	3	51.8	46.2–58.6	2.968	5.705	0.374	1.056
ECHINODERMATA: Holothuroidea							
Cucumaria frondosa	1	75.3	–	4.293	5.701	0.063	0.191
Myriotrochus rinki	1	25.0	–	1.203	4.811	0.029	0.089
Psolus fabricii	3	58.8	53.5–64.1	3.202	6.042	0.274	0.832
Thyonidium pellucidum	1	68.5	–	3.739	5.459	0.052	0.157
ECHINODERMATA: Ophiuroidea							
Ophiacantha bidentata	3	24.6[2]	24.3–24.8	1.374	5.474	0.464	1.413
Ophiocten sericeum	1	15.9[2]	–	0.790	5.920	0.055	0.166
Ophiopus arcticus	1	20.4[2]	–	0.901	5.013	0.105	0.321
Ophiura sarsi	2	19.7[2]	17.6–21.8	0.925	5.430	0.042	0.557
ECTOPROCTA							
Alcyonidium gelatinosum[1]	1	37.6	–	1.491	3.966	0.039	0.490
MOLLUSCA: Cephalopoda							
Rossia molleri/palpebrosa	2	87.3	87.2–87.3	5.048	5.786	0.023	0.296
MOLLUSCA: Gastropoda							
Boreotrophon fabricii	3	81.8	77.7–84.7	4.656	5.687	0.150	0.457
Buccinum angulosum	1	88.9	–	5.082	5.717	0.025	0.076
Buccinum hydrophanum	2	89.9	89.4–90.4	5.148	5.727	0.141	1.788
Buccinum scalariforme	1	90.9	–	5.324	5.857	0.026	0.080
Capulacmaea radiata	1	88.0	–	5.030	5.716	0.023	0.068
Colus islandicus	2	88.6	88.4–88.8	4.827	5.448	0.153	1.941
Colus pubescens	1	86.5	–	4.769	5.513	0.046	0.140
Colus tortuosus	2	81.5	80.9–82.1	4.718	5.790	0.223	2.839
Cylichna alba	1	77.0	–	3.677	4.775	0.024	0.301
Dendronotus robustus	1	70.5	–	3.932	5.578	0.040	0.121
Lepeta caeca	1	69.5	–	3.949	5.682	0.049	0.626
Littorina saxatilis	1	78.2	–	4.333	5.541	0.023	0.071
Lunatia pallida	1	85.9	–	4.743	5.521	0.034	0.104
Margarites costalis	1	68.4	–	3.868	5.655	0.064	0.193
Margarites groenlandicus	1	74.8	–	3.629	4.852	0.056	0.170
Margarites helicinus	1	70.7	–	3.929	5.557	0.015	0.045
Margarites olivaceus	1	63.3	–	3.647	5.762	0.087	0.265
Margarites umbilicalis	1	81.6	–	3.819	4.680	0.033	0.100
Marsenina glabra	1	90.0	–	5.152	5.724	0.024	0.074
Natica clausa	2	89.7	87.6–91.7	4.697	5.237	0.187	2.381
Neptunea despecta	2	90.4	89.6–91.2	5.001	5.532	0.002	0.027
Onchidiopsis glacialis	2	84.6	83.9–85.2	4.786	5.660	0.006	0.072
Tachyrhynchus reticulatus	1	65.4	–	4.063	6.212	0.082	0.251
Velutina plicatilis	1	83.9	–	5.117	6.099	0.063	0.190
Velutina undata	3	82.2	80.3–84.2	4.487	5.416	0.200	0.609
Velutina velutina	2	80.3	79.3–81.3	4.274	5.322	0.023	0.296

Table 1 (continued)

Species	n	Organic % DW	Range	kcal g^{-1} DW	kcal g^{-1} AFDW	± SD	± 95 % CI
MOLLUSCA: Pelecypoda							
Astarte borealis	3	83.6	81.3–87.5	4.486	5.370	0.254	0.774
Astarte montagui	1	78.5	–	4.120	5.248	0.002	0.025
Chlamys islandica	2	87.0	86.8–87.2	4.634	5.273	0.204	2.597
Clinocardium ciliatum	4	83.6	78.6–86.2	4.539	5.431	0.177	0.325
Hiatella arctica	4	74.9	72.8–77.3	3.956	5.283	0.231	0.424
Macoma calcarea	2	78.8	77.3–80.3	4.293	5.446	0.150	1.905
Macoma moesta	2	76.7	76.3–77.1	4.147	5.406	0.048	0.611
Musculus discors	4	81.8	80.1–82.9	4.595	5.616	0.073	0.134
Musculus niger	3	83.5	77.1–87.3	4.624	5.538	0.016	0.049
Mya truncata	3	64.3	61.8–67.7	3.317	5.161	0.110	0.336
Mytilus edulis[1]	2	86.4	86.3–86.5	4.893	5.664	0.035	0.440
Nucula belloti	1	81.0	–	4.766	5.884	0.011	0.035
Nuculana minuta	2	71.4	69.4–73.4	3.909	5.476	0.065	0.827
Nuculana pernula	2	73.3	71.1–75.4	4.019	5.487	0.047	0.593
Pandora glacialis	1	78.4	–	4.016	5.123	0.064	0.194
Pecten groenlandicus	1	50.5	–	2.780	5.505	0.037	0.112
Periploma abyssorum	1	49.5	–	2.612	5.276	0.050	0.637
Portlandia intermedia[1]	3	82.4	78.9–87.3	5.133	6.219	0.319	0.971
Serripes groenlandicus	2	81.1	77.4–84.8	4.503	5.558	0.201	2.552
Thyasira gouldi	1	78.5	–	4.177	5.321	0.005	0.014
Yoldia hyperborea	1	80.0	–	4.323	5.404	0.019	0.059
NEMERTINA							
Nemerteans	1	80.1	–	4.265	5.325	0.011	0.035
PORIFERA							
Haliclona gracilis	2	26.2[2]	18.2–34.2	1.409	5.262	0.519	6.595
Lissodendoryx indistincta	1	26.0[2]	–	1.421	5.477	0.012	0.036
Mycale lingua	2	26.6[2]	23.7–29.5	1.446	5.447	0.062	0.791
Polymastia mammillaris	2	27.4[2]	24.9–29.8	1.470	5.378	0.076	0.961
Tetilla sibirica	1	18.1[2]	–	1.007	5.541	0.013	0.038
SIPUNCULA							
Golfingia margaritacea	1	58.0	–	3.113	5.367	0.076	0.231

[1] Not collected in Frobisher Bay
[2] Dry weight includes skeletal material. Organic content has been corrected for water of hydration; caloric values for endothermy and/or water of hydration

Table 2. Mean organic content and caloric values of taxa represented by more than 2 species

Taxon	No. of species	Mean org. content % DW	Range	Mean kcal g^{-1} DW	Mean kcal g^{-1} AFDW	±SD	±95 % CI
Polychaeta	18	71.7	42.7–88.4	3.848	5.561	0.257	0.131
Amphipoda	4	62.2	55.9–67.2	3.596	5.784	0.309	0.568
Cirripedia	3	72.3	66.9–79.7	3.993	5.510	0.176	0.536
Decapoda	7	69.6	53.6–79.7	3.886	5.581	0.137	0.136
Isopoda	3	55.3	46.1–53.0	3.097	5.569	0.483	1.471
Ascidiacea	9	34.5	11.9–52.3	1.624	4.648	0.362	0.294
Asteroidea	6	49.8	39.2–74.2	2.646	5.444	0.221	0.254
Holothuroidea	4	56.9	25.0–75.3	3.109	5.503	0.520	0.955
Ophiuroidea	4	20.2	15.9–24.8	0.997	5.459	0.371	0.681
Gastropoda	26	80.9	63.3–91.7	4.487	5.548	0.354	0.146
Pelecypoda	21	76.4	49.5–87.5	4.183	5.461	0.247	0.115
Porifera	5	24.9	18.1–34.2	1.351	5.421	0.106	0.148

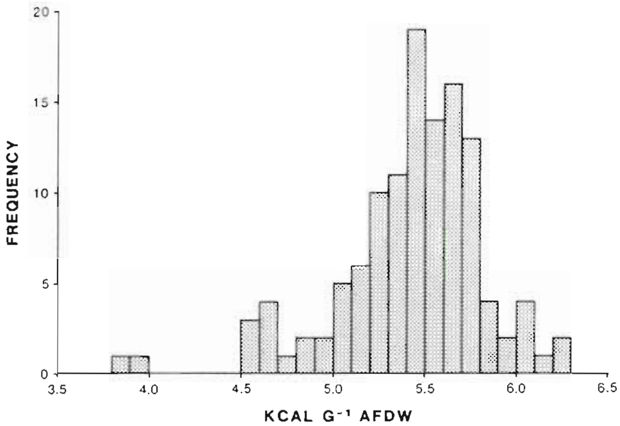

Fig. 1. Frequency distribution of caloric values for 121 benthic invertebrates

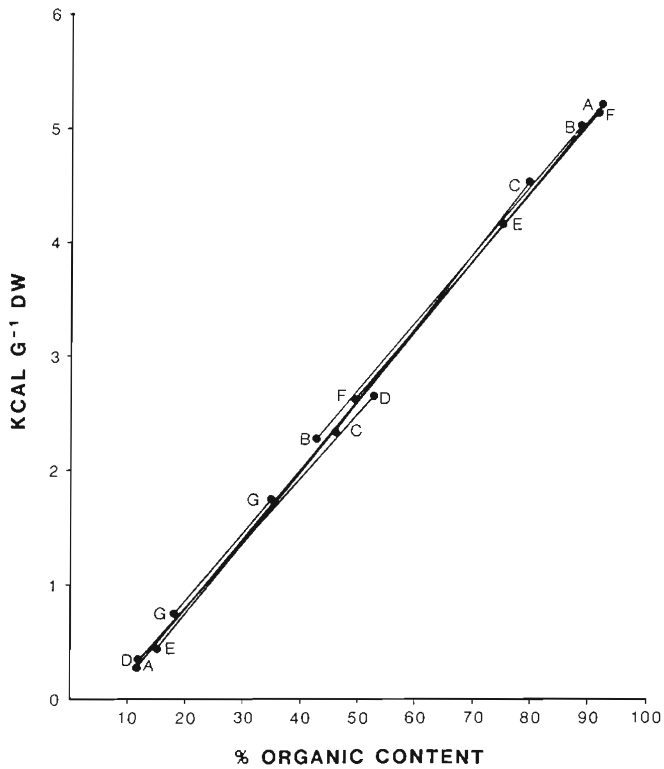

Fig. 2. Regression of DW caloric value on percent organic content. A: all values; B: Polychaeta; C: Crustacea; D: Ascidiacea; E: Echinodermata (with skeleton); F: Mollusca; G: Porifera

DISCUSSION

Examination of AFDW caloric values in Table 2 reveals that with the exception of the Ascidiacea, none of the taxa differ significantly from each other. Prus (1970) demonstrated that caloric values within taxonomic groups are symmetrically distributed about a mean that is similar for most groups. This probably reflects a variety of feeding types within most higher taxa which would tend to minimize caloric differences at this level and casts doubt on the validity of treating members of a taxon as energetic equivalents in general community comparisons. The Ascidiacea, all filter feeders, are thought to have a low caloric value due to high ash content, a relationship to be discussed presently. The grand mean for all species, 5.424 kcal g^{-1} AFDW, is similar to the value for proteinaceous material (5.7 kcal) and agrees with 5.470 kcal g^{-1} AFDW for aquatic invertebrates (Cummins & Wuycheck 1971) and with 5.429 kcal g^{-1} AFDW calculated from the invertebrate values of Thayer et al. (1973). It is slightly lower than community means (5.6 to 5.7 kcal g^{-1} AFDW) determined by other investigators (Ostapenya & Sergeev 1963, Paine 1964, Griffiths 1977, Norrbin & Bamstedt 1984).

Griffiths (1977) postulated that in response to

Table 3. Regression of dry weight caloric value on percent organic content for major taxa

Taxon	% Org. content interval	n	y intercept	Regression slope	r	t	$t_{0.05}$	Probability
Polychaeta	42.7–88.4	23	−0.2693	0.0595	0.985	26.557	2.080	$p < 0.001$
Crustacea	46.1–79.7	43	−0.5766	0.0644	0.952	20.919	2.021	$p < 0.001$
Ascidiacea	11.9–52.3	15	−0.3454	0.0573	0.990	25.559	2.160	$p < 0.001$
Echinodermata[1]	15.9–74.2	21	−0.4794	0.0619	0.994	39.851	2.093	$p < 0.001$
Echinodermata[2]	15.9–74.2	21	−0.1204	0.0584	0.993	36.904	2.093	$p < 0.001$
Mollusca	49.5–91.7	84	−0.3698	0.0598	0.904	21.181	1.993	$p < 0.001$
Porifera[3]	18.1–34.2	8	−0.3141	0.0588	0.980	12.309	2.365	$p < 0.001$
Porifera[4]	18.1–34.2	8	−0.1088	0.0585	0.992	19.404	2.365	$p < 0.001$
All values[5]	11.9–91.7	213	−0.3897	0.0605	0.986	87.114	1.960	$p < 0.001$

[1] With skeleton. Organic content uncorrected for water of hydration; caloric value uncorrected for endothermy
[2] With skeleton. Appropriate corrections applied to organic content and caloric values
[3] Organic content uncorrected for water of hydration
[4] Organic content corrected for water of hydration
[5] Uncorrected for water of hydration or endothermy

decreasing environmental predictability with increasing latitude, organisms should tend to store increasing amounts of energy and have higher caloric values. Bamstedt (1981) summarized some data on lipid and energy content of several zooplankton species which support this hypothesis. It is unclear, however, to what extent the data are seasonal, or what proportion of a community is represented. The mean value for the Frobisher Bay benthic community, when compared with those from lower latitudes, does not support this premise. Since samples for this study were collected in August at the time of peak reproductive activity in arctic waters, the mean is likely near the high end of the range of annual variation; however, it is at the low end of the range of estimates discussed above. Other studies reported by Clarke (1983) indicate no increase in lipid storage with increasing latitude in benthic invertebrates.

Frequency distributions of AFDW caloric value have been presented and discussed by various investigators (Slobodkin & Richman 1961, Prus 1970, Cummins & Wuycheck 1971, Thayer et al. 1973, Norrbin & Bamstedt 1984). Although not always representative of natural communities, the available data strongly indicate a natural pattern symmetrical about a mean in the range of 5.4 to 5.7 kcal g^{-1} AFDW. Most values in a community are grouped close to this, reflecting an optimal and consistent biochemical composition. According to Slobodkin & Richman (1961) this pattern implies a selection against caloric values that deviate in either direction from the mean. The slight negative skewness of the distribution presented in Fig. 1 is attributable to a lack of representative fish values. If the observed leptokurtosis is not a similar artifact, it further supports the idea of selection toward an optimal biochemical composition which is reflected in the caloric value.

The relationship reported above between AFDW caloric value and percent organic content ($Y = 0.0149\,X + 4.396$) is similar to the one obtained by Thayer et al. (1973) for estuarine benthic invertebrates near Beaufort, North Carolina (USA), which took the form K (kcal g^{-1} AFDW) = 0.0183 X (% organic content) + 3.991. The relationship shown in this study, as with Thayer's, is significant but not particularly strong. The implication is that increasing ash content is associated with organic material of decreasing caloric value, assuming there is no systematic effect of ash on caloric value as determined in bomb calorimeters. Although this was not noted in the present research, it is reasonable to suspect any value for animal material below 4.2 kcal g^{-1} AFDW (the value for carbohydrate). This includes the values reported in Table 1 for the ascidian *Ciona intestinalis* and the ectoproct *Alcyonidium gelatinosum*.

The positive correlation between organic content and caloric value per unit DW has been discussed by a number of authors (Ostapenya & Sergeev 1963, Platt et al. 1969, Prus 1970, Thayer et al. 1973, Norrbin & Bamstedt 1984). The differences among the regressions presented by these authors and that reported here are slight. However, the variation between taxa in both slope and intercept value (Table 3, Fig. 2) is much less in the present study than reported by Norrbin & Bamstedt (1984) for their benthic data. This can be accounted for mainly by larger sample size for all taxa in this study.

Ostapenya & Sergeev (1963) demonstrated that regressions of DW caloric value on percent organic content more closely approach the origin with increasing accuracy of the caloric determination technique. This was noted in the present work and is depicted in Fig. 3 where the regressions for the Porifera and Echinodermata (Table 3) are compared prior to and following application of appropriate corrections for water of hydration and endothermy. It will be noted

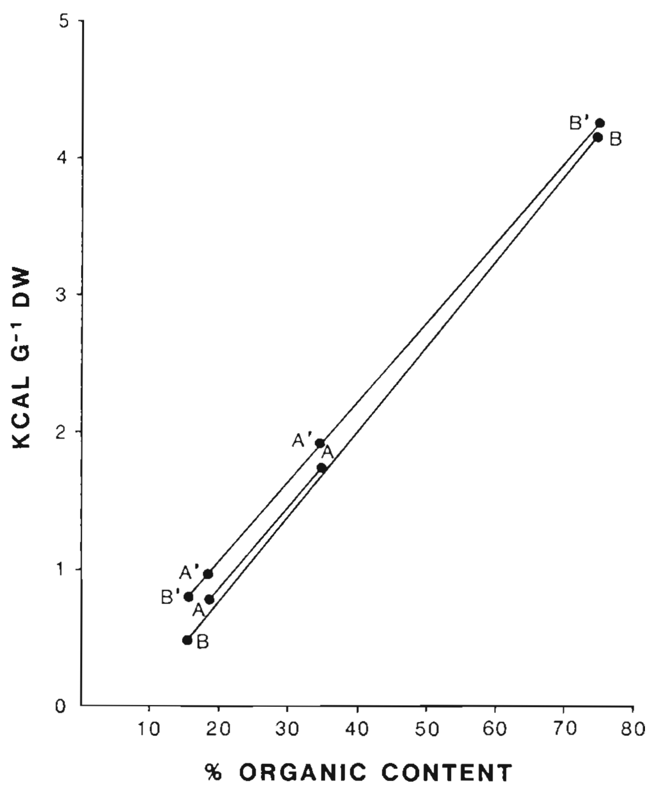

Fig. 3. Regression of DW caloric value on percent organic content. A: Porifera, organic content uncorrected for water of hydration; A': Porifera, organic content corrected for water of hydration. B: Echinodermata (with skeleton), organic content uncorrected for water of hydration, caloric value uncorrected for endothermy; B': Echinodermata (with skeleton), organic content corrected for water of hydration, caloric value corrected for endothermy

that the regressions for corrected data, A'-A' and B'-B' for Porifera and Echinodermata, respectively, become coincident with a Y-intercept value of approximately -0.11 kcal g^{-1} DW. Thus these 2 groups, adjusted for errors, have 2 of the highest correlations and their regression lines pass closest to the origin.

Thus a rigorous technique combined with large sample size can yield highly reliable equations to predict caloric value if percent organic content is determined directly. This is highly variable both intra- and interspecifically (Table 1) and is the single most important factor in the calculation, especially if AFDW values are desired. A simpler but less accurate approximation can be obtained by applying mean AFDW caloric values for taxa (Table 2), or a grand mean of invertebrate values which in the case of this study is 5.424 kcal g^{-1} AFDW.

These techniques are suitable for estimating standing stocks and making large scale comparisons of communities. However, detailed studies of energy partitioning and flow within populations and communities require detailed and accurate determinations of all variables.

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LITERATURE CITED

American Society for Testing Materials (ASTM) (1971). Standards for bomb calorimetry. Authorized reprint from Annual Book of ASTM Standards, Philadelphia

Atkinson, E. G., Wacasey, J. W (1976). Caloric values of zoobenthos and phytobenthos from the Canadian Arctic. Fish. Mar Serv. Res. Dev. Tech. Rep. 632: 1–24

Atkinson, E. G., Wacasey, J. W. (1983). Caloric equivalents for benthic marine organisms from the Canadian Arctic. Can. Tech. Rep. Fish. Aquat. Sci. 1216: 1–31

Bamstedt, U. (1981). Water and organic content of boreal macrozooplankton and their significance for the energy content. Sarsia 66: 59–66

Brawn, V. M., Peer, D. L., Bentley, R. J. (1968). Caloric content of the standing crop of benthic and epibenthic invertebrates of St. Margaret's Bay, Nova Scotia. J. Fish. Res. Bd Can. 25 (9): 1803–1811

Clarke, A. (1983). Life in cold water. In: Barnes, M. (ed.) Oceanography and marine biology, Vol. 21. Aberdeen Univ. Press, Aberdeen, p. 341–453

Cummins, K. W., Wuycheck, J. C. (1971). Caloric equivalents for investigations in ecological energetics. Mitt. int. Verein. theor. angew. Limnol. 18: 1–158

Ellis, D. V (1960). Marine infaunal benthos in Arctic North America. Arctic Institute of North America, Tech. Paper No. 5

Golley, F. F. (1961). Energy values of ecological materials. Ecology 42 (3): 581–584

Griffiths, D. (1977). Caloric variation in Crustacea and other animals. J. Anim. Ecol. 46: 593–605

Norrbin, F., Bamstedt, U. (1984). Energy contents in benthic and planktonic invertebrates of Kosterfjorden, Sweden. A comparison of energetic strategies in marine organism groups. Ophelia 23 (1): 47–64

Ostapenya, A. P., Sergeev, A. I. (1963). The caloric content of the dry substance of aquatic invertebrates used as food by fish. Vopr. Ikhtiol. 3: 177–183 (Russian; transl. by Fish. Res. Bd Can. Trans. Ser. 874)

Paine, R. T. (1964). Ash and caloric determinations of sponge and opisthobranch tissues. Ecology 45: 384–387

Paine, R. T. (1966). Endothermy in bomb calorimetry. Limnol. Oceanogr. 11: 126–129

Paine, R. T (1971). The measurement and application of the calorie to ecological problems. Ann. Rev. Ecol. Syst 2: 145–164

Parr Instrument Company (1969). Instructions for 1241 and 1242 Adiabatic Calorimeters. Manual No. 142. Moline, Illinois

Parr Instrument Company (1973). Instructions for the 1411 Semimicro Oxygen Bomb Calorimeter. Manual No. 144. Moline, Illinois

Percy, J. A., Fife, F. J. (1980). The proximate composition and caloric content of arctic marine invertebrates from Frobisher Bay. Can. Data Rep. Fish. Aquat. Sci. 214: 1–35

Percy, J. A., Fife, F. J. (1981). The biochemical composition and energy content of arctic marine macrozooplankton. Arctic 34 (4): 307–313

Platt, T., Brawn, V M., Irwin, B. (1969). Caloric and carbon equivalents of zooplankton biomass. J. Fish. Res. Bd Can. 26: 2345–2349

Prus, T. (1970). Caloric values as an element of bioenergetical investigations. Polskie Arch. Hydrobiol. 17: 183–199

Slobodkin, L. B., Richman, S. (1961). Calories/gm in species of animals. Nature, Lond. 191. 299

Steimle, F. W., Terranova, R. J. (1985). Energy equivalents of marine organisms from the continental shelf of the temperate northwest Atlantic. J. Northw. Atl. Fish. Sci. 6: 117–124

Thayer, G. W., Schaaf, W. E., Angelovic, J. W., LaCroix, M. W (1973). Caloric measurements of some estuarine organisms. Fish. Bull. U.S. 71 (1): 289–296

Tyler, A. V (1973). Caloric values of some North Atlantic invertebrates. Mar. Biol. 19: 258–261

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