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Energy content of macrobenthic invertebrates: general conversion factors from weight to energy

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Abstract: In ecological studies, especially in those dealing with energy circulation in nature, determinations of the energy content of organisms are inevitable. Energy determinations are, however, laborious and time-consuming. Average conversion factors based on different species form various areas and seasons may often be a shortcut for overcoming this problem. To establish general energy conversion factors for aquatic invertebrate groups, we used 376 values of $J \cdot mg^{-1}$ DW and 255 values of $J \cdot mg^{-1}$ AFDW, representing 308 and 229 species, respectively. The dry-weight-to-energy factors were highly variable both within and between taxonomic groups, e.g.: Porifera, 6.1 $J \cdot mg^{-1}$ DW; insect larvae, 22.4 $J \cdot mg^{-1}$ DW (median values). The energy-conversion factors related to AFDW showed a much smaller dispersion with a minimum median value of 19.7 $J \cdot mg^{-1}$ AFDW (Ascidiacea) and a maximum of 23.8 $J \cdot mg^{-1}$ AFDW (insect larvae). Within taxonomic groups, the 95% confidence intervals (AFDW) were only a few percent of the median values. The use of energy-conversion factors based on AFDW is preferable due to their lower dispersion. For aquatic macrobenthic invertebrates, a general conversion factor of 23 $J \cdot mg^{-1}$ AFDW can be used.

Key words: Energy content; Invertebrate; Macrobenthos

INTRODUCTION

Energy transformation between organisms and circuits of energy in nature are of fundamental interest in ecological studies of terrestrial, limnic, marine, and global ecosystems (e.g., Odum, 1971).

Energy content determinations of living and dead organic matter are, however, time-consuming and often also difficult to perform. Variations in the energy content due to season, taxonomic groups, developmental and reproductive stages, food conditions, environmental differences, and other factors strongly influence the results of the measurements, see, e.g., Slobodkin & Richman (1961), Prus (1970), Griffiths (1977), Norrbin & Bamstedt (1984).

Many data on energy content have been published especially during the last decades, and several compilations of these data have been produced in the 1970s. The most extensive one is by Cummins & Wuycheck (1971), which also includes terrestrial plants and animals. Such compilations are very valuable because they often reduce the need for laborious energy determinations.

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TABLE I

Average energy content ($J \cdot mg^{-1}$) of main taxonomic groups. Median and 95% confidence limits of energy content. 1 J = 0.239 cal,, 1 cal = 4.187 J. [1] These values are significantly ($P < 0.05$) different. [2] Except Balanomorpha, large Decapoda and juvenile stages. [3] Except large Decapoda and juvenile stages. [4] This value is significantly ($P < 0.05$) smaller than all other $J \cdot mg^{-1}$ AFDW median values.

Taxon	Weight type	Median ($J \cdot mg^{-1}$)	95% Confidence limits		Lowest value	Highest value	Number	
			Lower	Upper			Values	Species
Porifera	DW	6.10	3.65	11.38	3.65	15.61	8	8
Bivalvia	SFDW	18.85	18.35	19.33	10.94	25.57	55	43
Gastropoda	SFDW	18.24	17.01	19.06	9.17	22.51	61	59
Polychaeta	DW	16.79	15.29	17.50	4.52	23.25	51	43
P. errantia	DW[1]	17.50	16.67	20.34	11.05	23.25	28	20
P. sedentaria	DW[1]	14.19	11.14	17.20	4.52	19.85	23	18
Oligochaeta	DW	22.36	21.51	22.79	21.27	23.00	9	5
Crustacea	DW[2]	15.31	14.63	16.55	8.34	25.26	73	53
Insect larvae	DW	22.44	21.99	22.88	14.82	24.66	28	23
Echinodermata	DW	9.46	6.74	10.76	3.31	17.97	29	25
Ascidiacea	DW	7.13	4.11	10.23	2.45	12.57	11	11
Porifera	AFDW	22.87	21.94	27.11	21.94	27.92	8	8
Bivalvia	AFDW	22.79	22.18	23.27	16.95	29.10	43	38
Gastropoda	AFDW	23.27	22.68	23.79	18.75	30.64	57	57
Polychaeta	AFDW	23.33	22.70	24.16	19.68	27.43	34	27
Crustacea	AFDW[3]	22.74	21.95	23.44	17.95	26.77	55	46
Insect larvae	AFDW	23.81	23.29	24.34	21.67	26.69	25	22
Echinodermata	AFDW	22.74	21.66	23.87	18.59	26.86	22	20
Ascidiacea	AFDW[4]	19.66	18.98	21.04	15.92	25.29	11	11
All taxa	AFDW	23.09	22.79	23.36	15.92	30.64	255	229

This paper is the spin-off of the work of the Baltic Marine Biologists Working Group 11 (Secondary Production), which recently published a compilation of conversion factors on length-to-weight, weight-to-weight, and weight-to-energy content for Baltic macrobenthic invertebrates (Rumohr *et al.*, 1987).

Here, we present an extended compilation of energy content data limited to the main taxonomic groups of macrozoobenthos. Our aim is to give valid conversion factors from weight to energy, useful for general estimations of energy content and energy flow in aquatic ecosystems.

Methods

We searched through the literature available and excerpted most of the energy content data. If a single reference included more than one value per species (e.g., according to different seasons), we calculated a mean value for our compilation. Caloric values were transformed to J.

The following types of energy content data were excluded. (1) Data based on WW and DW of shelled molluscs, because these data were scarce and very scattered. (2) Data based on AFDW, which were not determined by combustion in a muffle furnace, but by subtracting the weight of the residual of bomb calorimetry from DW. (3) Data from taxonomic groups with less than five values available.

Deviation from normal distribution was analysed by means of the Kolmogoroff–Smirnoff test, differences between data sets were analyzed by means of the non-parametric *U* test (Wilcoxon, Mann–Whitney), both quoted from Sachs (1978).

Results

The results are presented in Table 1 at the level of main taxonomic groups. The median is given instead of the arithmetic mean, because some data sets do not show a normal distribution. 376 values of energy-conversion factors based on DW, representing 308 species, and 255 values based on AFDW, representing 229 species are included in the compilation. Approx. 20% of the species are limnic and the rest is of marine and brackish water origin. The areas of investigation and the methods applied by various authors are listed in Table II.

It is obvious from Table I that there is a much wider range of values both within and between taxonomic groups associated with $J \cdot mg^{-1}$ DW than with $J \cdot mg^{-1}$ AFDW. Even within the taxon Polychaeta, we detected significant differences. The conversion factor for the total taxa was, therefore, only calculated on AFDW to energy.

The groups Porifera and Ascidiacea show the lowest energy content values for DW, median values of 6.1 and 7.1 $J \cdot mg^{-1}$ DW, the group Ascidiacea shows the lowest value for AFDW, 19.7 $J \cdot mg^{-1}$ AFDW. Insect larvae show the highest values, 22.4 $J \cdot mg^{-1}$ DW and 23.1 $J \cdot mg^{-1}$ AFDW.

TABLE II

Applied methods. – > c, to constant weight; f-d, freeze-dried.

Reference	DW (°C·h^{-1})	AFDW (°C·h^{-1})	Calorimeter type	Area of investigation
Ankar & Elmgren (1978)	60/24	–	–	Baltic, Askö
Arntz & Brunswig (1975)	80/24	250/1 + 500/1	Phillipson	Baltic, Kiel Bay
Atkinson & Wacasey (1976)	100/12–24	500/16	Parr	Canadian Arctic
Atkinson & Wacasey (1983)	100/12–24	500/16	Parr	Canadian Arctic
Bast & von Oertzen (1976)	60/24	500/ 6	MBC-3	Baltic
Brawn *et al.* (1968)	75/– > c	–	Parr	Nova Scotia
Brunswig (1973)	80/24	250/1 + 500/1	Phillipson	Baltic, Kiel Bay
Caspers (1975)	80/24	550/ 4	Janke & Kunkel	European rivers
Chambers & Milne (1979)	f-d	–	Gallenkamp	North Sea, Scotland
Cummins & Wuycheck (1971)	–	–	–	Compilation
Davis & Wilson (1983)	f-d	–	–	Irish Sea, Dublin Bay
Foberg (1976)	60/ > 24	525/ 4.3	–	Baltic, Luleå
Gilbert (1973)	70/24	–	Phillipson	Atlantic, Massachusetts
Griffiths (1977)	–	–	–	Compilation
Gründel (1976)	80/24	550/24	Phillipson	Baltic, Kiel Bay
Hakala (1979)	60/12	505/6–8	Org. C analysis	Baltic, southern Finland
Hughes (1970)	50/48	500/ 2	Gallenkamp	Irish Sea, northern Wales
Kautsky (1981)	60/ > 24	–	–	Baltic, Askö
Kay & Brafield (1973)	65/– > c	–	Phillipson	Thames estuary, U.K.
Kreutzberg & von Oertzen (1973)	–	–	–	Compilation
Norrbin & Båmstedt (1984)	60/48	500/?	Phillipson	Koster Fjord, Sweden
Paine (1964)	100/– > c	500/2–4	Parr	Pacific, California
Paine (1965)	100/– > c	500/2–4	Parr	Pacific, California
Pruus (1970)	–	–	–	Compilation
Rachor *et al.* (1982)	?	?	Phillipson	Baltic and North Sea
Rumohr *et al.* (1987)	–	–	–	Compilation
Salonen *et al.* (1976)	60/24	500/ > 12	Phillipson	Finland, lakes
Slobodkin & Richman (1961)	?	?	?	?
Sutherland (1972)	?	500/ 3	Parr	Pacific, California
Thayer *et al.* (1973)	60/? or f-d	–	Phillipson	Atlantic, North Carolina
Tyler (1973)	60/ 5	–	Parr	Atlantic, New Brunswick
Wacasey & Atkinson (1987)	100/12–24	500/16	Parr	Canadian Arctic

The general median conversion factor from AFDW to energy content is 23.09 $J \cdot mg^{-1}$. The distribution of the 255 values included is shown in Fig. 1. This distribution is just significantly different from a normal distribution with mean = 22.99 $J \cdot mg^{-1}$ AFDW and variance = 4.42 (Kolmogoroff–Smirnoff test, $D_{test} = 0.059 > D_{tab} = 0.050$, $\alpha = 0.10$).

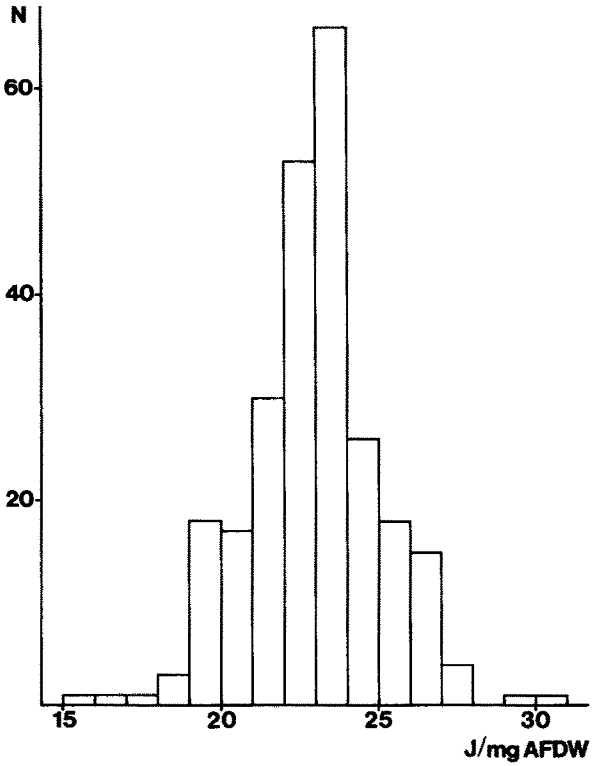

Fig. 1. Distribution of energy content values ($J \cdot mg^{-1}$ AFDW); 255 values referring to 229 macrobenthic invertebrate species.

Discussion

The total energetic content of an animal depends on the amount of carbohydrates, proteins, and lipids contained in its body. The energy values of these compounds are 17.16 $J \cdot mg^{-1}$ DW, 23.65 $J \cdot mg^{-1}$ DW, and 39.55 $J \cdot mg^{-1}$ DW (Crisp, 1984). The ratio of these organic components determines the energy content per unit of body mass if inorganic matter is ignored.

The most precise way to determine the energy content of a certain animal is to measure it, e.g., by means of bomb calorimetry or wet oxidation. However, these procedures require time and money, and it is quite impossible to perform such measurements frequently during larger ecological surveys.

To simplify the laborious energy determinations, we are looking for an ecologically significant quantity related to animals that should meet at least three certain conditions. (1) The measurement should be simple and fast. (2) There should be a strong correlation between this quantity and the energy content of the animal. (3) This correlation should be independent of season, area and species.

A quantity which meets the first condition, is the body mass of an animal, hence, the aim is to establish an empirical relationship between this body mass and energy content. The most common ways to determine body mass are by wet weight (WW), dry weight (DW), shell-free dry weight (SFDW), ash-free dry weight (AFDW), and organic-carbon weight (C_{org}). The methods are ranked according to the increasing effort needed for the determination (first condition above).

With respect to the second condition, the ranking is reversed because of the decreasing amount of inorganic compounds included in the measurement of weight. The energy content is correlated best to carbon weight (e.g., Salonen *et al.*, 1976), even better than to AFDW.

The narrower range of the AFDW to energy values (both within and between taxa) compared with those of DW to energy and SFDW to energy values indicate a closer correlation between energy content and AFDW than SFDW and DW (Table I).

The third condition is the most troublesome. It is well-known that seasonal changes in the lipid, protein, and carbohydrate content cause great variation in the energy content of benthic species, at least from temperate latitudes (e.g., Hakala, 1979; Davis & Wilson, 1983). These seasonal variations are often related to different reproductive stages of the animal.

It is quite clear that interspecific differences in energy content do exist (Table I), but they are much smaller when based on C_{org} or AFDW. One reason for the greater variation in the energy content related to WW, DW, and SFDW could be due to highly differing amounts of inorganic material in the guts of species of various feeding habits (e.g., filter-feeder vs. nonselective deposit-feeder) or in shells and exoskeletons.

Differences in energy content depend also on general life strategies and environment, e.g., planktonic species have been shown to have a higher average energy content ($J \cdot mg^{-1}$ AFDW) than benthic species (Griffiths, 1977; Norrbin & Bamstedt, 1984).

Geographically different races or variants account also for the dispersion in conversion factors. In our compilation, values from wide geographical areas (Atlantic regions of North America and Europe, Pacific regions of North America, brackish and freshwaters of Europe and North America) are included.

As mentioned above, the most accurate empirical relation to energy content is that based on organic carbon mass. However, such determinations are time-consuming and require expensive laboratory equipment (ignition furnace connected to IR analyser for CO_2 detection). Furthermore, there are not many literature data available referring to $J \cdot mg^{-1}$ C_{org}.

Determinations of energy content related to AFDW are less time-consuming and the equipment needed is simpler and cheaper. Additionally, there is a bulk of AFDW based energy content data in the literature (e.g., see Rumohr *et al.*, 1987, and references therein). Therefore, we think that AFDW provides the best compromise in serving as a reference unit of body mass in relation to energy content.

The conversion factors ($J \cdot AFDW^{-1}$) presented in Table I include seasonal, geographical, species-, and method-related deviations. They show a wide range with a maximum value (30.6 $J \cdot mg^{-1}$ AFDW), which is twice the minimum value (15.9 $J \cdot mg^{-1}$ AFDW) of all taxa. However, with respect to all taxa, the 95% confidence interval is only $\approx \pm 1.5\%$ of the median. The confidence intervals for the different taxonomic groups are also small. Thus, these factors can be used as general factors when estimating the energy contents and flows in aquatic ecosystems.

The median value of all taxa included (23.09 + 0.27, −0.30 $J \cdot mg^{-1}$ AFDW) and the corresponding mean (22.99 ± 0.26 $J \cdot mg^{-1}$ AFDW) are practically identical. Hence, the average value for all taxa of macrobenthic invertebrates is 23 $J \cdot mg^{-1}$ AFDW.

This value is in the range of average energy content values given by other authors: 24.4 $J \cdot mg^{-1}$ AFDW (Slobodkin & Richman, 1961), 23.2 $J \cdot mg^{-1}$ AFDW (Prus, 1970), 23.7 $J \cdot mg^{-1}$ AFDW (Salonen *et al.*, 1976), 23.9 $J \cdot mg^{-1}$ AFDW (Norrbin & Bãmstedt, 1984), and 22.7 $J \cdot mg^{-1}$ AFDW (Wacasey & Atkinson, 1987). With the exception of the latter, these factors are based also on pelagic or terrestrial animals. Therefore, they are slightly higher than our average value of 23 $J \cdot mg^{-1}$ AFDW, which refers only to macrobenthic invertebrates.

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