http://journal.nafo.int
J. Northw. Atl. Fish. Sci., Vol. 6: 117-124

Energy Equivalents of Marine Organisms from the Continental Shelf of the Temperate Northwest Atlantic

Frank W. Steimle Jr. and Russell J. Terranova
National Marine Fisheries Service, Northeast Fisheries Center
Sandy Hook Laboratory, Highlands, N. J. 07732, USA

Abstract

The availability of appropriate energy equivalents is one of the needs in species or community bioenergetic models. Energy-equivalent data for 151 common invertebrate and vertebrate species on the continental shelf of the temperate Northwest Atlantic from Nova Scotia to North Carolina are presented and compared with the more limited results of other studies. Energy equivalents were found to be variable among major taxonomic or trophic groups and general trends were not evident. A review of equivalents from some recent ecosystem models for the Northwest Atlnatic indicates that the models can be substantially improved.

Introduction

Energy budgets or trophodynamic models are being developed and used for the Northwest Atlantic region and elsewhere to examine theoretical functions and linkages of ecosystem components and the structure of ecosystems or communities (e.g. Walsh, 1981; Pace *et al.*, 1984). Particular interest has been shown in models that are related to fish production, especially in the Northwest Atlantic (Mills and Fournier, 1979; Cohen *et al.*, 1982; Sissenwine *et al.*, 1984). Most of these models or budgets are still quite crude and are based on limited data and assumptions of unknown validity. Often these assumptions are borrowed from earlier models without much evaluation and they vary significantly among the models for various reasons. Common assumptions in many models relate to the energy-equivalent values that are applied to the standing stocks (biomass) of major trophic groups or communities. Usually, the equivalents are based on data for a limited number of species, phyla or samples (Brawn *et al.*, 1968; Tyler, 1973), or for areas that may not be representative of the region being studied (Thayer *et al.*, 1973; Wissing *et al.*, 1973; Atkinson and Wacasey, 1976, 1983).

Despite the problems that are associated with ecosystem modelling, the availability of specific energy equivalents from replicate sampling for a wide range of taxa should be of benefit, especially for comparing different ecosystems. The purpose of this paper is twofold. The first provides an extensive set of original energy-equivalents data, based on bomb calorimetry for 151 species representing 11 phyla, which in concert with data from other relevant studies, cover almost all major groups (with emphasis on larger nektonic and benthic species) that are common in temperate waters of the Northwest Atlantic. The second objective is to reexamine (a) several trends that have been suggested by previous studies of equivalents relating to evolution or habitat, and (b) many of the assumed energy equivalents that have been used in recently-published energy-based ecosystem models.

Materials and Methods

Organisms for this study were collected by various means from the continental shelf between Nova Scotia and North Carolina. Species were selected for analysis on the basis of their relative contribution to energy pools and budgets of the shelf, i.e. they comprise significant standing stocks (Wigley and Theroux, ;1981), or because they are food for many fishery resource species (Edwards and Bowman, 1979). For each species, the most common sizes of animals in the collections or in the stomachs of predators were selected for analysis. Whole bodies were analyzed except in the case of larger predators (i.e. sharks) where samples were represented by vertical sections (slices) when it was impractical to process the entire animals. The data for these sections were not mixed with data for whole bodies in computing mean values. The gastrointestinal tract contents were not purged or removed from the animals before processing, fully understanding the potential variability that this could cause. Most molluscs were removed from their shells and only the meats analyzed, in which cases the mean shell weights were used to estimate whole body values. However, some small species of molluscs were analyzed with their shells. Taxonomic nomenclature and organization of species and groups are based on Gosner (1971) for invertebrates and Robins *et al.* (1980) for fish.

Samples for analysis (usually a minimum of five similar-sized individuals per species per sample) were frozen immediately after collection. Within 60 days, the individual samples were either homogenized and aliquots removed or placed whole (in the case of small organisms) in a vacuum dryer and dried at room temperature to constant weight. These homogenized or dried samples were pulverized in a mill to fine powder and compressed into 1.0 or 0.1 g pellets. The pellets were combusted in a Parr Model 1241 Adiabatic Calorimeter with the use of 1108 standard or 1107 semimicro oxygen bombs, depending on the size of the sample. The recommended procedures of Parr Instrument Company (Anon, 1981a, 1982) were followed closely. Usually, five replicate pellet combustions were made for each species, but additional combustions were made when the variability around the mean of five values exceeded 5% and sample material was still available. Acid corrections were not determined because the anticipated error due to this factor is usually less than 2% (Paine, 1964, 1971).

To calculate wet-weight values of equivalents, duplicate fresh subsamples were weighed, dried at 100°C for 12 hr, and reweighed to determine moisture content. To calculate ash-free dry weights, vacuum-dried material was weighed, burned in a muffle oven at 500°C for 4–5 hr, and reweighed to determine ash content. These ash samples were replaced in the oven and reburned at 900°C for an additional 4 hr to estimate $CaCO_3$ content by weight loss through degradation to CO_2.

Calculations to determine energy equivalents were based on Parr Instrument Company and American Society for Testing and Materials (ASTM) standards (Anon., 1970, 1981b). Benzoic acid (<5%) was added to some samples with high ash content to insure complete combustion. Samples, which were found to contain 25% or more of $CaCO_3$ (total dry weight), were corrected for endothermic $CaCO_3$ breakdown during combustion on the basis of ash-loss corrections that were suggested by Atkinson and Wacasey (1976, 1983).

Results and Discussion

The mean energy equivalents (wet weight and ash-free dry weight) for all major animal phyla or trophic groups are presented separately for pelagic and benthic types (Table 1), together with summary data from other available studies pertinent to the western North Atlantic for comparison. Data on seasonal variability in the ash-free dry-weight energy equivalents for 21 selected species are listed in Table 2. The basic data, representing more than 1400 combustions for 151 species, are listed in the Appendix to this paper.

The results from this study of energy equivalents indicate significant differences in mean values among major taxa (Table 1), especially with regard to the wet-weight values (range 0.25–6.30 KJ/g). Ash-free dry weights, with two exceptions (octocorals and cetaceans), exhibit a relatively narrow range (18.2–26.5 KJ/g). This range and the distribution of values are comparable to ranges and distributions that were reported by Cummins and Wuycheck (1971), Thayer *et al*. (1973) and Griffiths (1977).

The variability of equivalents among major taxa has been ascribed to evolutionary differences (Thayer *et al*., 1973), but this is not evident from Table 1 on a wet-weight or ash-free dry-weight basis. Some of the variability has been linked to species habitat preference, such as benthic *versus* pelagic (Wissing *et al*., 1973), but this is also not fully supported by the data in Table 1. For example, on a wet-weight basis, their idea is probably true for molluscs and fish but not for cnidarians, crustaceans and tunicates. However, Wissing *et al*. (1973) examined many larval or planktonic forms that were not included in the present study. For the ash-free dry-weight values, there is little within-phyla difference between pelagic and benthic taxa, especially when the high standard deviations from the means are considered. However, crustaceans are an exception, as was found also by Griffiths (1977).

The relatively large standard deviations (SD) that are associated with much of the summarized data (Table 1) and some of the specific data (Appendix) may be attributable to a variety of factors. There were significant seasonal differences in the energy equivalents for some species in this study, usually related to gonadal development, but not for all (Table 2). According to Griffiths (1977) and Schroeder (1977), other factors that may influence energy equivalents are life-history stage, size range, molting stage, temporal scales other than season, climatic zone, ash content, and human error. The factors which are applicable to particular groups vary and are not always consistent in the direction of influence. More information is needed about the influences of these factors on specific taxonomic groups to make the best use of data on energy equivalents when very accurate values are required. Most researchers appear to be satisfied with the current level of accuracy, but, as the variables become better defined, the accuracy of energy data will become more important.

Significant improvement in ecosystem modelling may be achieved with the use of group-specific or species-specific energy equivalents. For example, energy budgets have been postulated for western North Atlantic regions on the basis of a general macrofauna biomass-conversion of 0.6 Kcal (2.5 KJ/g) wet weight (Mills and Fournier, 1979; Walsh, 1981). With the use of results of the extensive benthic study of the Middle Atlantic by Wigley and Theroux (1981), conversion of the biomass composition of the major taxa (71% molluscs, 12% echinoderms, 7% polychaetes, 5% crustaceans, and 5% others) to energy from the data in Table 1 yields an average value of about 3.2 KJ/g wet weight or about 0.8 Kcal, a 30% increase. This value may still be conservative because it is based on an 83% contribution of molluscs (99% shelled) and echino-

TABLE 1. Mean energy equivalences (with standard deviations, SD) for major taxonomic or trophic groups on the continental shelf from Nova Scotia to North Carolina, with comparable wet-weight and ash-free dried-weight values from other studies.

Group	No. of species	Wet weight (KJ/g) Mean (SD)	Wet weight (KJ/g) Comparable	Ash-free dried weight (KJ/g) Mean (SD)	Ash-free dried weight (KJ/g) Comparable
Porifera	1	1.51	—	24.20	22.21[a] 25.27[b]
Cnidarià					
Hydrozoids	1	1.85	—	18.97	21.30[a]
Octocorals	1	2.70	2.07[c]	10.70	21.56[a]
Anemones	2	3.43 (1.27)	1.33[d]	20.80 (0.71)	24.72[c]
Medusae	2	0.25 (0.21)	—	18.90 (3.68)	17.13[e]
Ctenophores	—	—	0.21[f]	—	15.73[e] 16.73[f]
Platyhelmenthes	—	—	5.56[c]	—	11.15–26.69[c]
Rhynchocoels	1	4.60	—	23.25	22.28[a]
Chaetognaths	—	—	—	—	24.32[g]
Bryozoans	1	2.30	—	26.50	16.61[a]
Brachiopods	1	2.50	—	—	18.40[c] 21.23[a]
Molluscs					
Bivalves	10	1.54 (0.77)[l]	1.32[h]	21.69 (1.71)	22.88[f] 23.04[a]
Gastropods	7	2.28 (0.88)[l]	1.97[h]	21.17 (1.03)	24.27[a] 19.10[h]
Cephalopods	4	5.50 (1.65)	4.39[f]	22.90 (1.47)	23.26[e] 26.53[f]
Polychaetes	11	4.58 (1.58)	2.68[c] 2.82[h] 3.56[f]	21.85 (3.45)	19.66[c] 23.04[a]
Sipunculids	—	—	2.49[c]	—	22.96[a]
Crustaceans					
Zooplankton	—	—	1.64[c]	—	23.08[c] 27.60[e]
Benthic malacostraca	20	5.40 (2.49)	4.30[c,f]	20.74 (5.17)	17.37[e] 22.63[a] 21.60[c,f]
Pelagic malacostraca	3	3.50 (0.14)	4.06[h]	24.80 (0.14)	23.01[h] 31.52[e]
Echinoderms					
Holothuroids	3	4.77 (3.37)	0.81[c]	20.30 (3.46)	14.85[j] 25.50[a]
Echinoids	4	1.32 (0.78)	0.20[f] 1.20[c]	25.82 (2.53)	23.64[a] 26.84[c]
Stelleroids	6	2.57 (0.63)	2.13[f] 2.42[c]	19.10 (3.19)	17.91[c] 23.68[a]
Tunicata					
Benthic	4	2.25 (1.34)	0.92[f]	19.38 (7.02)	18.44–21.00[a] 25.27[f]
Pelagic	1	0.40	0.29[j]	18.20	22.97[e]
Pisces					
Demersal	32	4.77	4.42[c] 5.13[f]	22.96 (2.30)	22.16[c] 24.06[f] 25.94[a]
Pelagic	27	6.30	6.11[b] 6.76[f] 8.06[c]	24.22 (2.15)[m]	23.56[i] 25.13[f]
Cetacea	1	—	4.8–26.4[o]	33.65[n]	12.7–32.3[o]

[a] Atkinson and Wacasey (1976). [b] Griffiths (1977). [c] Cummins and Wuycheck (1971).
[d] Atkinson and Wacasey (1983). [e] Wissing *et al.* (1973). [f] Thayer *et al.* (1973).
[g] Hopkins *et al.* (1978). [h] Tyler (1973). [i] Kitchell *et al.* (1977).
[j] Lawrence and Kafri (1979). [k] Musaeva and Sokolova (1979).
[l] Means calculated from whole animals and meat values with appropriate shell weight added.
[m] Equivalences for sections of large predators, not included in the mean for whole pelagic fish are about 24.1 KJ/g.
[n] Sample not representative of whole animal.
[o] Slice from anterior ventral groove area and posterior dorsal area of fin whale (Lockyer *et al.*, 1984).

derms (60% echinoid) with relatively low energy equivalents. Another example is that for fish by Sissenwine *et al.* (1984), who used conversion of 1 g (wet weight) = 1 Kcal (4.2 KJ/g) for all fish in their budget. The results in Table 1 indicate a mean value of about 4.8 KJ/g for demersal species and about 6.3 KJ/g for pelagics. The resultant average (5.6 KJ/g), based on almost equal contributions of demersal and pelagic species from the estimates of Sissenwine *et al.* (1984), indicates that the amount of energy in the fish pool of their Georges Bank budget was underestimated by as much as 30%.

Most energy budgets are still crude, and the variables are often inaccurate by a factor of 2 or more. The use of a more accurate value for biomass conversion to energy may not make much of a difference until the accuracy of related variables are also improved. Attempts were made to substitute the present energy data in several published models to see if the conclusions might be altered, but the information in those papers was not sufficiently specific. At present, the types of studies that would benefit most from the availability of more accurate energy equivalents for specific

TABLE 2. Mean seasonal energy equivalences and spawning period for selected species on the continental shelf from Nova Scotia to North Carolina. (* indicates differences significant at the P = 0.05 level.)

Species	Ash-free dry-weight (KJ/g)				Spawning period
	Winter	Spring	Summer	Autumn	
Anthozoa					
Cerianthiopsis americanus	21.1	—	21.7	—	?
Polychaeta					
Aphrodita hastata	—	18.9	19.2	21.1*	?
Nephtys incisa	—	23.5	18.2	21.0*	Spring and autumn
Pherusa affinus	24.0	27.3	21.8	21.7*	Primarily spring
Mollusca					
Illex illecebrosus	24.6	—	22.6	—	Winter
Loligo pealei	20.9	23.2	21.5	21.9*	Late spring
Placopecten magellanicus	—	22.1	20.8	22.6	Autumn
Crustacea					
Hyas areneus	—	13.9	—	20.5	Winter
Libinia emarginata	—	17.1	—	21.5	Summer-early autumn
Meganyctiphanes norvegica	—	24.2	26.6	24.0*	Winter and spring
Echinodermata					
Echinarachnius parma	—	15.3	25.5	31.9*	Autumn
Ophiopholis aculeata	—	10.9	—	16.9	?
Pisces					
Alosa aestivalis	—	21.5	25.7	24.3–29.3*	Late spring-early summer
Alosa pseudoharengus	26.6	—	24.0	23.9*	Spring
Ammodytes americanus	—	25.5	20.4	26.5*	Autumn-winter
Anchoa hepsetus	—	22.8	22.2	25.5	Late spring
Limanda ferruginea	—	21.8	23.9	18.2	Spring-summer
Macrozoarces americanus	—	21.5	22.7	22.4	Autumn
Peprilus triacanthus	—	28.6	29.7	26.3	Summer-autumn
Sebastes sp.	23.1	20.4	25.8	—	Summer
Stenotomus chrysops	—	24.2	25.7	28.1	Spring-summer

components of communities are those which use crude wet or dry weight biomass as the basic unit in estimates of production (Rowe, 1971) or for comparing different ecosystems (Walsh, 1981; Petersen, 1984). The energy equivalents in this paper, although probably requiring further study to fully assess the specific causes and the significance of data variability, should enable more realistic assessments and conclusions in studies that require energy equivalents, especially in the western North Atlantic.

Energy equivalents are presented in this paper for most of the taxonomic or trophic groups which are common on the continental shelf from Nova Scotia to North Carolina. These data show that variability among groups is important and should be included in any conversion of biomass to energy to avoid potentially significant errors. The use of energy equivalents for specific taxa or trophic groups can improve the realism of many energy budgets, production estimates, and comparisons of different ecosystems. However, there is still a high degree of variability in the available equivalents. This is probably a function of the condition (age, reproductive stage, health, etc.) of the species being analyzed, environmental conditions, variation in methodology for different animals, and number of samples.

Acknowledgements

We thank John B. Pearce and Marvin Grosslein for their support and encouragement during this study; Thomas Wilhelm, Charles Idleburger and Al Witik for their invaluable assistance in the Laboratory; Donald Flescher and Charles Stillwell for providing many of the samples; Maureen Montone, Alicia Gruber and Kathe Melkers for typing the various drafts and the tables; and the late David Frame for introducing the senior author to energy studies. The many comments of Anthony Pacheco, unidentified reviewers and the editors greatly improved this paper.

References

ANON. 1970. Oxygen bomb calorimetry and combustion methods. Parr Instrument Co., Moline, Ill., Manual No. 130, 56 p.

1981a. Instructions for 1241 adibatic calorimeters. Parr Instrument Co., Moline, Ill., Manual No. 160, 26 p.

1981b. ASTM standards for bomb calorimetry and combustion methods. American Society for Testing and Materials, Philadelphia, Penn., 56 p.

1982. Instructions for semimicro operation of series 1240 oxygen bomb calorimeters. Parr Instrument Co., Moline, Ill., 19 p.

ATKINSON, E. G., and J. W. WACASEY. 1976. Caloric values of zoobenthos and phytobenthos from the Canadian Arctic. *Can. Fish. Mar. Serv. Tech. Rep.*, **632**: 24 p.

1983. Caloric equivalents for benthic marine organisms from the Canadian Arctic. *Can. Tech. Rep. Fish. Aquat. Sci.*, **1216**: 31 p.

BRAWN, V. M., D. L. PEER, and R. J. BENTLEY. 1968. Caloric content of the standing crop of benthic and epibenthic invertebrates of St. Margaret's Bay, Nova Scotia. *J. Fish. Res. Board Can.*, **25**: 1803-1811.

COHEN, E. B., M. D. GROSSLEIN, M. P. SISSENWINE, F. W. STEIMLE, and W. R. WRIGHT. 1982. Energy budget of Georges Bank. *Can. Spec. Publ. Fish. Aquat. Sci.*, **59**: 95-107.

CUMMINS, K. W., and J. C. WUYCHECK. 1971. Caloric equivalents for investigations in ecological energetics. *Int. Ver. Theor. Angew. Limno. Verh.*, **18**: 1-158.

EDWARDS, R. L., and R. E. BOWMAN. 1979. Food consumed by continental shelf fishes. *In* Predator-prey systems in fishery management (p. 387-406), H. Clepper (ed.), Sport. Fish. Inst., Washington, D.C., 504 p.

GOSNER, K. L. 1971. Guide to identification of marine and estuarine invertebrates, Cape Hatteras to the Bay of Fundy. Wiley-Interscience, New York, N.Y., 693 p.

GRIFFITHS, D. 1977. Caloric variation in Crustacea and other animals. *J. Anim. Ecol.*, **46**: 593-605.

HOPKINS, C. C. E., S. FALK-PETERSEN, and K. TANDE. 1978. A preliminary study of zooplankton sound scattering layers in Balsfjorden: structure, energetics and migrations. *Sarsia*, **63**: 255-264.

KITCHELL, J. F., J. J. MAGNUSON, and W. H. NEILL. 1977. Estimation of caloric content for fish biomass. *Environ. Biol. Fish.*, **2**: 185-188.

LAWRENCE, J. M., and J. KAFRI. 1979. Numbers, biomass and caloric content of the echinoderm fauna of the rocky shores of Barbados. *Mar. Biol.*, **52**: 87-91.

LOCKYER, C. H., L. C. McCONNELL, and T. D. WATERS. 1984. The biochemical composition of fin whale blubber. *Can. J. Zool.*, **62**: 2553-2562.

MILLS, E. L., and R. O. FOURNIER. 1979. Fish production and the marine ecosystem of the Scotian Shelf, eastern Canada. *Mar. Biol.*, **54**: 101-108.

MUSAEVA, E. I., and I. A. SOKOLOVA. 1979. Caloricity of planktonic animals from the Pacific Ocean. Okenologia, **19**(1): 146-149.

PACE, M. L., J. E. GLASSER, and L. R. POMEROY. 1984. A simulation analysis of continental shelf food webs. *Mar. Biol.*, **82**: 47-63.

PAINE, R. T. 1964. Ash and caloric determinations of sponge and opisthobranch tissue, *Ecology*, **45**: 384-387.

1971. The measurement and application of the calorie to ecological problems. *Annu. Rev. Ecol. Syst.*, **2**: 145-164.

PETERSEN, G. H. 1984. Energy flow in comparable aquatic ecosystems from different climatic zones. *ICES Rapp. Proc.-Verb.*, **183**: 119-125.

ROBINS, C. R., R. M. BAILEY, C. E. BOND, J. R. BROOKER, E. A. LACHNER, R. N. LEAR, and W. B. SCOTT. 1980. A list of common and scientific names of fishes from the United States and Canada. *Spec. Publ. Amer. Fish. Soc.*, No. 12 (4th edition), 174 p.

ROWE, G. T. 1971. Benthic biomass and surface productivity. *In* Fertility of the sea (p. 441-454), J. D. Costlow (ed.), Gordon and Breach, New York, N. Y., Vol. 2, p. 309-622.

SCHROEDER, L. A. 1977. Caloric equivalents of some plant and animal material. *Oecologia*, **28**: 261-267.

SISSENWINE, M. P., E. B. COHEN, and M. D. GROSSLEIN. 1984. Structure of the Georges Bank ecosystem. *ICES Rapp. Proc.-Verb.*, **183**: 243-254.

THAYER, G. W., W. E. SCHAFF, J. W. ANGELOVIC, and M. W. LaCROIX. 1973. Caloric measurements of some estuarine organisms. *Fish. Bull. U.S.*, **71**: 289-296.

TYLER, A. V. 1973. Caloric values of some North Atlantic invertebrates. *Mar. Biol.*, **19**: 258-261.

WALSH, J. J. 1981. Shelf-sea ecosystems. *In* Analysis of marine ecosystems (p. 159-196), A. R. Longhurst (ed.), Academic Press, New York, N. Y., 741 p.

WIGLEY, R. L., and R. B. THEROUX. 1981. Atlantic continental shelf and slope of the United States — macrobenthic invertebrate fauna of the Middle Atlantic Bight region — faunal composition and quantitative distribution. *U.S. Geol. Surv. Prof. Pap.*, No. 529-N, 198 p.

WISSING, T. E., R. M. DARNELL, M. A. IBRAHIM, and L. BERNER Jr. 1973. Caloric values of marine animals from the Gulf of Mexico. *Contrib. Mar. Sci.*, **17**: 1-7.

Appendix

Energy equivalents of 151 marine organisms from the continental shelf of the Northwest Atlantic from Nova Scotia to North Carolina. Values are for whole bodies except where specified by footnotes. Shell weight as percentage of total body weight is given for each species analyzed with shells removed.

Taxa	No. of combus- tions	Dry weight % ash	%H_2O	Dry weight KJ/g Mean	Dry weight KJ/g SD	Dry weight ash free KJ/g	Wet weight KJ/g	% shell weight
Porifera								
Suberites ficus	3	52	87	11.6	0.4	23.9	1.5	
Cnidaria								
Hydrozoa								
Syncoryne sp.	3	61	75	7.4	0.4	19.0	1.9	
Scyphozoa								
Cyanea cappilata	5	45	99	11.8	0.7	21.5	0.1	
Aurelia aurita	6	48	95	8.8	0.7	16.3	0.4	
Anthozoa								
Renilla reniformis	3	40	58	6.4	0.1	10.7	2.7	
Metridium senile	3	11	84	18.0	0.1	20.3	2.9	
Ceriantheopsis americanus	12	14	75	18.4	0.6	21.3	4.7	
Rhynchocoela								
Cerebratulus sp.	7	10	78	23.2	0.4	23.3	4.6	
Bryozoa								
Bugula flabellata	5	69	72	8.2	0.7	26.5	2.3	
Brachiopoda								
Terebratulina septentrionalis	4	91	67	7.6	0.7	...	2.5	(24)
Mollusca								
Gastropoda								
Polinices heros	8[a]	10	67	19.9	0.7	22.0	5.9	(46)
Buccinum undatum	8[a]	10	57	18.7	0.9	19.9	7.7	(60)
Colus stimpsoni	4[a]	13	72	18.5	0.5	20.6	5.2	(61)
Colus pygmaeus	4	88	73	3.5	0.2	22.7	0.9	
Neptunea lyrata	7[a]	13		18.2	0.3	21.0	...	
Busycon carica	3[a]	10	73	18.3	0.01	20.2	4.9	(64)
Busycon canaliculatum	5[a]	9	73	19.9	0.3	21.9	5.4	(50)
Lamelledorididae	3	21	78	19.4	0.04	24.6	4.3	
Bivalvia								
Nucula proxima	3[a]	15	84	20.4	0.2	24.0	3.3	(43)
Nucula proxima	4	84	40	3.7	0.3	23.1	2.2	
Modiolus modiolus	8[a]	12	78	19.8	0.7	22.6	4.3	(52)
Chlamys islandicus	3[a]	16	73	19.5	0.4	23.2	5.3	(50)
Placopecten magellanicus	15[a]	15	78	18.5	0.4	21.8	3.0	(44)
Astarte undata	14[a]	12	67	18.0	0.8	21.3	6.2	(80)
Cyclocardia borealis	8[a]	27	90	14.0	0.8	19.2	1.3	(74)
Arctica islandica	294[a]	20	88	15.4	0.2	19.7	1.6	(48)
Spisula solidissima	21[a]	18	81	16.5	0.3	20.2	2.9	(42)
Ensis directus	3[a]	...	83	16.8	0.1	...	2.9	(30)
Periploma leanum	2	...	74	4.8	0.2	...	0.3	
Cephalopoda								
Illex illecebrosus	10	7	69	22.0	0.7	23.6	7.1	
Loligo pealei	14	8	72	20.4	0.5	21.4	5.6	
Lolliguncula brevis	3	14	82	21.3	0.1	24.5	3.8	
Octopus vulgaris	11	19	...	17.9	1.6	20.0	...	
Annelida								
Polychaeta								
Aphrodita hastata	18	34	81	13.4	0.6	20.1	2.4	
Glycera americana	3	12	79	18.8	0.2	21.8	4.0	
Ophioglycera gigantea	3	12	83	19.6	0.5	23.3	3.3	
Nephtys incisa	13	16	74	17.9	1.0	22.3	4.4	
Aglaophamus igalis	5	21	76	15.9	6.3	20.2	3.8	
Ophelia bicornis	5	64	...	7.5	0.6	21.1	...	
Ophelia denticulata	5	56	64	13.5	0.8	30.3	4.9	
Lumbrineris fragilis	2	—	65	21.3	0.1	...	4.7	
Terebellides stroemis	3	12	58	16.4	0.1	18.6	6.9	
Pherusa affinis	21	43	39	14.4	0.9	23.7	7.6	
Chone infundibuliformis	5	11	76	16.0	0.4	18.0	3.8	

Appendix (continued)

Taxa	No. of combus-tions	Dry weight % ash	% H_2O	Dry weight KJ/g Mean	Dry weight KJ/g SD	Dry weight ash free KJ/g	Wet weight KJ/g	% shell weight
Arthropoda								
Crustacea								
Stomatopoda								
Squilla empusa	15	28	61	15.3	1.1	21.0	5.8	
Amphipoda								
Hyperia galba	8	26	80	18.6	1.2	24.7	3.6	
Ampelisca agassizi	7	47	22	10.5	0.6	18.5	8.8	
Unciola irrorata	4	41	20	13.9	0.7	33.0	11.1	
Gammarus annulatus	8	67	88	13.7	0.6	18.4	1.7	
Leptocheirus pinguis	4	51	64	5.9	0.3	12.0	2.0	
Mysidacea								
Neomysis americana	4	...	...	16.1	2.0	...	...	
Euphausidacea								
Meganyctiphanes norvegica	15	22	82	19.4	0.7	24.9	3.4	
Decapoda								
Penaeus aztecus	5	16	51	18.2	0.5	21.6	8.9	
Sicyona typica	5	26	66	14.4	0.2	19.4	4.9	
Pasiphaea tarda	5	18	...	18.7	0.7	22.7	...	
Paleomonetes vulgaris	8	17	75	14.7	0.6	21.9	4.6	
Dichelopandalus leptocerus	28	22	70	18.7	0.6	24.5	5.5	
Crangon septemspinosa	26	28	79	16.2	0.6	18.4	3.7	
Homarus americanus	5	36	68	13.8	1.4	21.6	4.8	
Pagurus acadianus	5	28	63	18.5	1.6	22.7	6.9	
Pagurus bernhardus	4	34	57	14.1	1.1	21.3	6.0	
Pagurus pollicarpus	5	41	63	18.4	0.2	30.3	6.6	
Hyas araneus	10	55	67	8.5	0.4	18.0	2.8	
Libinia emarginata	11	45	63	12.6	0.5	19.9	5.4	
Pelia mutica	3	51	66	10.3	0.1	21.1	3.3	
Cancer irroratus	15	41	70	12.8	0.9	20.7	3.7	
Eurypanopeus depressus	5	50	...	4.5	1.9	9.0	...	
Echinodermata								
Holothuroidea								
Cucumaria frondosa	3	15	76	14.1	0.6	16.6	3.4	
Thyone scabra	3	71	61	6.0	0.2	20.6	2.3	
Caudina arenata	5	37	42	14.9	0.1	23.6	8.6	
Echinoidea								
Arbacia punctulata	7	90	78	2.8	0.3	28.0	0.6	
Strongylocentrotus droebachiensis	10	82	60	5.1	0.6	28.0	2.0	
Echinarachnius parma	26	85	45	3.6	0.6	24.0	2.0	
Moira atropos	4	85	80	3.5	0.2	23.3	0.7	
Stelleroidea								
Ctenodiscus crispatus	5	61	68	9.2	0.2	23.6	2.8	
Henricia sp.	2	43	65	9.8	1.2	17.2	3.4	
Asteria forbesi	3	65	70	7.2	0.3	20.5	2.2	
Leptasterias tenera	4	49	71	10.7	0.4	21.0	3.1	
Ophioderma brevispina	3	79	42	3.7	0.2	17.6	2.1	
Ophiopholis aculeata	7	68	62	4.7	0.4	14.7	1.8	
Chordata								
Tunicata								
Amaroucium pellucidum	4	58	86	9.7	0.8	23.1	1.4	
Ascidia callosa	5	70	...	15.2	1.0	24.8	...	
Boltenia ovifera	6	28	88	14.7	0.6	20.4	3.2	
Molgula manhattensis	3	63	...	3.4	0.9	9.2	...	
Salpidae	2	51	95	8.9	0.8	18.2	0.4	
Pisces								
Chondrichthyes								
Isurus oxyrhinchus	5[b]	5	...	20.6	0.9	21.7	...	
Lamna nasus	5[b]	6	...	20.0	0.5	21.2	...	
Carcharhinus plumbeus	10[b]	7	...	19.9	0.8	21.4	...	
Prionace glauca	11[c]	7	...	18.4	0.5	20.0	...	
Squalus acanthias	31[b]	6	67	25.8	0.8	30.6	8.6	
Raja erinacea	10	16	82	17.6	0.7	21.0	3.2	

Appendix (continued)

Taxa	No. of combus-tions	Dry weight % ash	% H_2O	Dry weight KJ/g Mean	SD	Dry weight ash free KJ/g	Wet weight KJ/g	% shell weight
Osteichthyes								
Conger oceanicus	6	8	67	29.8	1.7	32.4	9.8	
Ophichthus cruentifier	4	14	71	19.8	0.8	22.9	5.8	
Alosa sapidissima	5	11	75	19.6	0.5	22.1	4.9	
Alosa aestivalis	15	12	69	22.2	0.7	25.0	7.7	
Alosa mediocris	5	11	74	21.1	0.4	23.8	5.5	
Alosa pseudoharengus	24	12	71	21.7	0.5	24.5	6.4	
Clupea harengus	20	8	57	25.1	2.3	27.2	10.6	
Brevoortia tyrannus	10	13	65	21.4	0.4	24.6	7.5	
Etrumeus teres	17	14	73	20.4	0.5	23.6	5.5	
Opisthonema oglinum	5	11	74	24.8	0.9	27.7	6.4	
Sardinella aurita	5	14	70	19.9	0.1	23.1	6.0	
Anchoa hepsetus	24	16	71	19.9	0.4	23.6	5.8	
Anchoa mitchilli	5	14	72	21.2	0.5	24.6	5.9	
Synodus foetens	5	17	75	18.3	0.5	22.1	4.6	
Lophius americanus	6	13	91	18.5	0.8	21.3	1.7	
Gadus morhua	9	16	78	18.2	0.3	21.6	4.2	
Pollachius virens	5	13	74	19.2	1.8	21.9	5.0	
Urophycis chuss	10	14	80	19.4	0.5	22.6	3.8	
Urophycis regia	3	10	78	21.3	0.7	23.6	4.7	
Urophycis tenuis	3	14	67	19.2	0.3	22.3	6.3	
Melanogrammus aeglefinus	4	17	78	20.3	0.7	24.3	4.5	
Enchelyopus cimbrius	5	16	80	18.0	0.6	21.6	3.6	
Merluccius bilinearis	10	13	79	21.3	0.3	24.6	4.6	
Macrozoarces americanus	9	13	76	19.2	0.2	22.0	4.7	
Scomberesox saurus	5	9	62	22.3	0.7	24.6	8.5	
Menidia menidia	10	13	66	21.2	0.7	24.4	7.3	
Sebastes marinus	15	20	75	18.5	1.1	23.1	4.4	
Prionotus carolinus	5	22	75	17.7	1.1	22.7	4.4	
Hemitripterus americanus	6	16	86	18.1	0.5	21.5	2.5	
Myoxocephalus octodecemspinosus	5	17	74	20.8	0.6	25.1	5.4	
Triglops murrayi	5	16	80	18.1	0.6	21.5	3.6	
Triglops nybelini	5	14	73	19.4	1.2	22.5	5.2	
Citharichthys arctifrons	5	14	78	19.4	0.2	22.5	4.3	
Paralichthys oblongus	10	13	75	22.0	0.3	25.4	5.5	
Scophthalmus aquosus	3	13	86	22.2	0.2	25.4	3.1	
Hippoglossoides platessoides	3	15	77	17.7	0.2	21.0	4.1	
Limanda ferruginea	12	16	75	17.6	0.6	20.9	4.4	
Liopsetta putnami	5	17	78	17.1	0.1	20.7	3.8	
Pseudopleuronectes americanus	5	15	78	16.4	0.6	19.4	3.6	
Symphurus plagiusa	4	16	67	19.0	0.7	22.7	6.3	
Sphoeroides maculatus	4	15	74	19.4	1.2	22.8	5.1	
Pomatomus saltatrix	5	20	77	20.8	0.8	25.0	4.8	
Caranx chrysos	5	16	68	17.7	0.3	21.1	5.7	
Chloroscombrus chrysurus	5	14	63	23.9	0.5	27.9	8.8	
Selar crumenopthalmus	5	14	70	16.4	6.9	19.0	4.9	
Seriola dumerili	3	15	75	18.4	0.4	21.5	4.6	
Decapterus punctatus	5	13	68	18.8	0.4	21.6	6.0	
Stenotomus chrysops	14	16	73	21.5	0.2	25.6	6.1	
Cynoscion regalis	4	13	76	20.1	0.7	23.0	4.8	
Leiostomus xanthurus	11	17	65	20.1	0.5	24.0	7.0	
Tautogolabrus adspersus	5	11	70	22.2	0.5	24.9	6.6	
Lumpenus maculatus	8	12	71	20.2	0.6	22.2	5.6	
Ammodytes americanus	20	12	69	21.7	0.6	24.8	6.8	
Scomber japonicus	15	12	71	21.6	0.2	24.4	6.2	
Scomber scombrus	28	8	75	24.1	1.9	26.2	6.0	
Thunnus albacares	6[d]	...	...	23.4	0.6	...	...	
Acanthocybium solanderi	6[b]	6	...	23.4	1.5	24.9	...	
Xiphias gladius	5[e]	4	...	27.5	0.6	28.8	...	
Peprilus triacanthus	25	11	74	24.2	0.3	27.2	6.2	
Peprilus alepidotus	5	11	73	22.9	0.4	25.8	6.2	
Cetacea								
Lagenorhynchus acutus	8[e]	1	...	33.3	0.7	33.6	...	

[a] Without shell. [b] Dorsal section without skin. [c] Middle section including viscera. [d] Mixed muscle fillet without skin. [e] Dorsal section with skin.

Appendix

Energy equivalents of 151 marine organisms from the continental shelf of the Northwest Atlantic from Nova Scotia to North Carolina. Values are for whole bodies except where specified by footnotes. Shell weight as percentage of total body weight is given for each species analyzed with shells removed.

Taxa	No. of combus-tions	Dry weight % ash	$\%H_2O$	Dry weight KJ/g Mean	Dry weight KJ/g SD	Dry weight ash free KJ/g	Wet weight KJ/g	% shell weight
Porifera								
Suberites ficus	3	52	87	11.6	0.4	23.9	1.5	
Cnidaria								
Hydrozoa								
Syncoryne sp.	3	61	75	7.4	0.4	19.0	1.9	
Scyphozoa								
Cyanea cappilata	5	45	99	11.8	0.7	21.5	0.1	
Aurelia aurita	6	48	95	8.8	0.7	16.3	0.4	
Anthozoa								
Renilla reniformis	3	40	58	6.4	0.1	10.7	2.7	
Metridium senile	3	11	84	18.0	0.1	20.3	2.9	
Ceriantheopsis americanus	12	14	75	18.4	0.6	21.3	4.7	
Rhynchocoela								
Cerebratulus sp.	7	10	78	23.2	0.4	23.3	4.6	
Bryozoa								
Bugula flabellata	5	69	72	8.2	0.7	26.5	2.3	
Brachiopoda								
Terebratulina septentrionalis	4	91	67	7.6	0.7	...	2.5	(24)
Mollusca								
Gastropoda								
Polinices heros	8[a]	10	67	19.9	0.7	22.0	5.9	(46)
Buccinum undatum	8[a]	10	57	18.7	0.9	19.9	7.7	(60)
Colus stimpsoni	4[a]	13	72	18.5	0.5	20.6	5.2	(61)
Colus pygmaeus	4	88	73	3.5	0.2	22.7	0.9	
Neptunea lyrata	7[a]	13		18.2	0.3	21.0	...	
Busycon carica	3[a]	10	73	18.3	0.01	20.2	4.9	(64)
Busycon canaliculatum	5[a]	9	73	19.9	0.3	21.9	5.4	(50)
Lamelledorididae	3	21	78	19.4	0.04	24.6	4.3	
Bivalvia								
Nucula proxima	3[a]	15	84	20.4	0.2	24.0	3.3	(43)
Nucula proxima	4	84	40	3.7	0.3	23.1	2.2	
Modiolus modiolus	8[a]	12	78	19.8	0.7	22.6	4.3	(52)
Chlamys islandicus	3[a]	16	73	19.5	0.4	23.2	5.3	(50)
Placopecten magellanicus	15[a]	15	78	18.5	0.4	21.8	3.0	(44)
Astarte undata	14[a]	12	67	18.0	0.8	21.3	6.2	(80)
Cyclocardia borealis	8[a]	27	90	14.0	0.8	19.2	1.3	(74)
Arctica islandica	294[a]	20	88	15.4	0.2	19.7	1.6	(48)
Spisula solidissima	21[a]	18	81	16.5	0.3	20.2	2.9	(42)
Ensis directus	3[a]	...	83	16.8	0.1	...	2.9	(30)
Periploma leanum	2	...	74	4.8	0.2	...	0.3	
Cephalopoda								
Illex illecebrosus	10	7	69	22.0	0.7	23.6	7.1	
Loligo pealei	14	8	72	20.4	0.5	21.4	5.6	
Lolliguncula brevis	3	14	82	21.3	0.1	24.5	3.8	
Octopus vulgaris	11	19	...	17.9	1.6	20.0	...	
Annelida								
Polychaeta								
Aphrodita hastata	18	34	81	13.4	0.6	20.1	2.4	
Glycera americana	3	12	79	18.8	0.2	21.8	4.0	
Ophioglycera gigantea	3	12	83	19.6	0.5	23.3	3.3	
Nephtys incisa	13	16	74	17.9	1.0	22.3	4.4	
Aglaophamus igalis	5	21	76	15.9	6.3	20.2	3.8	
Ophelia bicornis	5	64	...	7.5	0.6	21.1	...	
Ophelia denticulata	5	56	64	13.5	0.8	30.3	4.9	
Lumbrineris fragilis	2	—	65	21.3	0.1	...	4.7	
Terebellides stroemis	3	12	58	16.4	0.1	18.6	6.9	
Pherusa affinis	21	43	39	14.4	0.9	23.7	7.6	
Chone infundibuliformis	5	11	76	16.0	0.4	18.0	3.8	