Short Communication

Energy and ash contents of sandy beach macrofauna from the West Coast of South Africa

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Received 14 October 1992; accepted 21 May 1993

The energy values and ash contents of 15 species of macrofauna found on three exposed sandy beaches on the west coast of South Africa were examined over an 18-month period. The values obtained ranged from a mean of 26,65 $kJ.g^{-1}$ ash-free dry weight (AFDW) in the haustoriid amphipod *Urothoe grimaldii* to 19,83 $kJ.g^{-1}$ for the bivalve *Donax serra* and the values obtained are applied to biomass data for the three beaches. A pattern of decreasing energy content with increasing mean body weight was observed. No patterns of seasonal or regional variation were detected in either energy values or ash contents. Ash contents depended on taxonomic group (owing to morphological effects) and the mean size of the species; in the case of the Crustacea increasing with size within a given taxonomic grouping. The mean energy value for the 15 species was 23,81 $kJ.g^{-1}$, higher than the 23,09 $kJ.g^{-1}$ conversion factor obtained by Brey, Rumohr & Ankar (1988) for aquatic macrobenthic invertebrates in general, and in accordance with the suggestion by Slobodkin & Richman (1961) that energy contents are affected by the extent of storage for adverse conditions.

Die energiewaardes en asinhoud van 15 spesies van makrofauna gevind op drie blootgestelde sanderige strande aan die weskus van Suid Afrika is oor 'n tydperk van 18 maande bestudeer. Die bevindinge wissel van 'n gemiddelde waarde van 26,65 $kJ.g^{-1}$ asvrye droë gewig (ADG) in die haustoriede amfipood *Urothoe grimaldii* tot 19,83 $kJ.g^{-1}$ ADG vir die tweekleppige *Donax serra*, en die bevindinge word toegepas op die biomassa-data van die bogenoemde drie strande. 'n Tendens van afnemende energie-inhoud met toenemende gemiddelde liggaamsgewig was waarneembaar. Geen seisoensgebonde- of streeksvariasies was waarneembaar in die energiewaardes of in die asinhoud nie. Asinhoud is afhanklik van die taksonomiese groep (as gevolg van morfologiese effekte) en die gemiddelde grootte van die spesies, en in die geval van die Crustacea is daar 'n toename in grootte binne 'n gegewe taksonomiese groepering. Die gemiddelde energiewaarde vir die 15 spesies was 23,81 $kJ.g^{-1}$ ADG, hoër as die 23,09 $kJ.g^{-1}$ wisselfaktor wat deur Brey, Rumohr & Ankar (1988) voorgestel word vir akwatiese makrobentiese Invertebrata oor die algemeen en dit is in ooreenstemming met die voorstel van Slobodkin & Richman (1961) dat energie-inhoud hoër is hoe ongunstiger die heersende toestande is.

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The old view that sandy beaches are of little ecological interest has changed. Formerly, they were generally ignored or regarded as ecological deserts, chiefly because their inhabitants adopt a burrowing mode of life and are therefore mostly hidden. Because of the unstable substratum, no primary producers of significance occur intertidally, although McLachlan (1983) has shown that on certain beaches, surf-zone phytoplankton play an important role in a larger beach – surf zone ecosystem. As a result, the intertidal fauna of sandy beaches generally has no grazers. The macrofauna of sandy beaches therefore consists mainly of filter-feeders and opportunistic feeders that adopt either carnivorous or scavenging habits, depending on what opportunities present themselves.

The new view of sandy beaches includes not only the occasional role of surf-zone phytoplankton mentioned above, but also an understanding of their physical functioning as a response to wave energy (Short & Wright 1983) and the fact that they often form the predominant shore type (Bally, McQuaid & Brown 1984). They are seen to be fascinating, complex and dynamic ecological entities, of which the benthic macrofauna remain the best studied and understood biological component.

The energy content of animals reflects, to a certain extent, their environment. Those animals that can be assured of a steady supply of food do not need to lay down energy reserves, whereas animals dependent on very erratic food supplies do need these. In the course of a study on the ecology of three sandy beaches on the west coast of South Africa, macrofaunal animals were routinely analysed for energy and ash content. The South African west coast is an upwelling coastline off which lies one of the world's major fisheries. The beaches along this coast have been shown to support a higher macrofaunal biomass than most other beaches not receiving such an energy subsidy (Bally 1987). In this paper the results obtained from the energy and ash content analyses are discussed in relation to results obtained in other studies.

A recent review by Brey, Rumohr & Ankar (1988) of published data on energy contents of macrobenthic invertebrates gives general conversion factors from weight to energy. It is interesting to note, however, that apparently all the data is derived from northern hemisphere organisms. Aside from the study by Field, Griffiths, Jarman, Zoutendyk, Velimirov & Bowes (1980), on organisms associated with kelp beds, the results presented in this paper may well be among the first derived from organisms from a cool temperate region of the southern hemisphere, as well as being the first community analysis of organisms from a sandy beach environment.

Macrofaunal animals were collected from three exposed sandy beaches on the west coast of South Africa at 3-monthly intervals over a period of 18 months. The beaches were at Melkbosstrand, Yzerfontein and Rocherpan, lying some 30, 75 and 150 km to the north of the city of Cape Town respectively. Some characteristics of the beaches and their sediments are given in Table 1.

Animals were removed from the sediments at low tide, by washing the sediment through 1 mm-mesh sieves and collecting the retained organisms. After collection, the samples were stored in 10% formalin, as outlined in Field *et al.* (1980). In the laboratory, samples were sorted and identified under fresh water, dried to constant weight, weighed, then

Table 1 Characteristics of three sandy beaches on the west coast of South Africa. Exposure is according to McLachlan (1980). Data from Bally (1987)

	Melkbosstrand	Yzerfontein	Rocherpan
Position	33°40'54"S 18°25'32"E	33°10'38"S 18°09'41"E	32°35'27"S 18°18'11"E
Mean grain size (phi)	2,25	2,31	1,60
Mean beach width (m)	90	60	49
Number of macrofaunal species	17	16	13
Macrofaunal biomass (g AFDW.m^{-1})	324	683	92
Range of $CaCO_3$ content of sand (%)	21–38	30–59	1–17
Exposure	16	15	14

placed in 1 mol.dm^{-3} hydrochloric acid to remove calcium carbonate — a major source of endothermy in bomb calorimetry (Paine 1966). The sorting of animals under fresh water also serves to wash out any inorganic salts which may affect subsequent analyses (Platt, Brown & Irwin 1969), while decalcification by hydrochloric acid does not significantly alter energy values (Thayer, Schaaf, Angelovic & La Croix 1973). Once all effervescence had ceased for approximately 10 min, the samples were washed in fresh water and dried to constant weight at 60°C before reweighing.

The dried samples were ground up in a Wig-L-Bug dental mill until finely powdered. The powders were then made up into pellets weighing approximately 10 mg for combustion in a Phillipson microbomb calorimeter. For each sample, energy values were determined in triplicate. Values for ash were determined by weighing the residue left after combustion of samples in a muffle furnace at 500°C for periods of 4–6 h.

Not all the species found on the beaches could be sampled, usually owing to the small sample sizes involved. The species analysed in this study are listed in Table 2.

Energy values

Energy values were found to vary throughout the course of the year. This variation did not, however, appear to follow any seasonal pattern, since the types of variations of the first six months were not repeated in the final six months of the 18-month study period. In addition, patterns of variation exhibited by species on any one beach were not observed in that species on the other beaches. As no seasonal or regional patterns were detected, it was decided to pool results for all beaches and all seasons.

Table 2 lists the energy contents of the species investigated in this study. The high value recorded for *Urothoe grimaldii* (26,65 kJ.g^{-1} AFDW) compares with the value of 26,39 kJ.g^{-1} AFDW measured by Green (1971) for the amphipod *Pontoporeia affinis*. On the other hand, the mean of 25,88 kj g^{-1} AFDW obtained for *Talorchestia capensis* compares with the 21,74 kJ.g^{-1} AFDW found by Muir (1977) for juveniles of the same species, and 20,69 kJ.g^{-1} AFDW in *T. margaritae* (Venables 1981).

The mean energy content of the nemertean *Cerabratulus fuscus* (24,08 kJ.g^{-1} AFDW) was also higher than the value of 5,33 kcal (22,28 kJ.g^{-1} AFDW) obtained for unidentified nemerteans by Wacasey & Atkinson (1987). The energy content for *Donax serra* (19,83 kJ.g^{-1} AFDW without shell) compares with 17,34 kj.g^{-1} AFDW obtained by Stenton-Dozey & Brown (1988) for gill tissue in the same species and with 2,26 kcal.g^{-1} (9,45 kJ.g^{-1} with shell) obtained for *D. variabilis* by Armitage & Alevizon (1980), and is substantially lower than the median of 22,79 kJ.g^{-1} AFDW calculated for bivalves by Brey, Rumohr & Ankar (1988).

Prus (1970) and Griffiths (1977) suggested that energy

Table 2 Species sampled for energy and ash contents in this study, and their energy contents

Phylum/ subphylum	Class/Order	Species	Value range	Mean values ± *SD*	*N*
Crustacea	Isopoda	*Tylos granulatus* Krauss	18,1–25,9	21,56±2,18	36
		Pontogeloides latipes Barnard	22,2–26,5	23,85±1,02	48
		Eurydice longicornis (Studer)	21,9–26,8	24,32±1,40	54
		Excirolana natalensis (Vanhohoffen)	19,3–27,8	21,95±1,70	51
		Niambia sp.	22,4–26,5	25,73±2,03	27
	Amphipoda	*Talorchestia capensis* (Dana)	24,1–27,6	25,88±0,99	51
		Pseudharpinia excavata (Chevreux)	22,2–28,0	25,16±1,74	48
		Urothoe grimaldii Chevreux	25,2–20,0	26,65±1,05	30
	Mysidacea	*Gastrosaccus psammodytes* O. Tattersall	22,2–27,2	23,72±1,49	51
Mollusca	Bivalvia	*Donax serra* Roding	16,8–22,3	19,83±2,00	54
Annelida	Polychaeta	*Scolelepis squamata* (Muller)	21,7–25,1	23,71±0,83	36
		Sigalion capense Day	21,7–27,8	23,38±2,15	18
		Nepthys capensis Day	22,4–26,5	24,24±1,22	21
	Oligochaeta	Unidentified lumbricid	22,2–24,2	23,10±0,80	12
Nemertea	Heteronemertea	*Cerebratulus fuscus* McIntosh	22,2–25,9	24,08±1,00	30

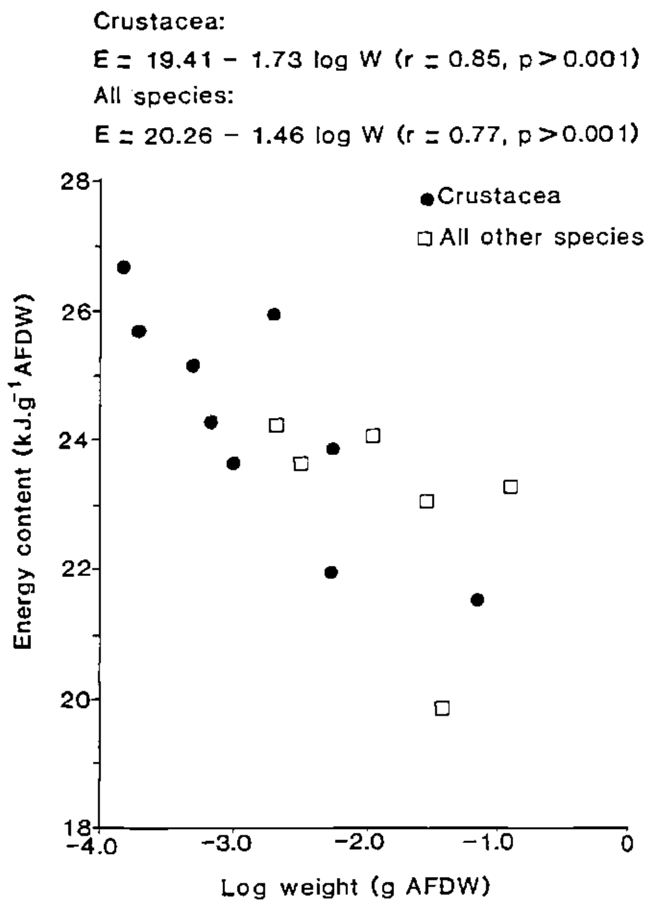

Figure 1 The relationship between species energy content and log mean ash-free dry weight. Equations describe relationships between these factors for Crustacea and for all species studied. E = energy content (kJ.g^{-1} AFDW), W = mean weight of species (g AFDW).

contents may depend on the size or weight of the animals involved. This is reflected in Figure 1, in which mean energy content of the 15 species is plotted against the log of the mean weight of individuals of those species. Equations describing the relationships are given both for all the species and for the crutstacean species alone. From this, it appears that the energy content per unit weight in sandy beach organisms is a function of their weight, at least within the environmental conditions and size ranges measured.

It should be noted, however, that some of the highest energy contents were obtained from very small samples. In some cases, all the animals of a species collected from sieving 1,2 m^3 of sand (the standard amount sifted each time the beaches were sampled) were used to make up two 10-mg pellets. This reflects not only the small size of the organisms, but also very low population densities. The high energy values obtained may thus be a function of the small samples that it was sometimes necessary to use, possibly owing to increased variance.

According to Cummins & Wuycheck (1971), the range of energy values in animals is 3,3 to 9,4 kcal.g^{-1} AFDW (13,81 to 39,35 kJ.g^{-1} AFDW). The results obtained for the macrofauna from South African west coast sandy beaches fall well within this range. Cummins & Wuycheck found the average value to be 5,6 kcal (23,41 kJ.g^{-1} AFDW), slightly lower than the average of 23,81 kJ.g^{-1} AFDW found in this study. The results from this study, however, are significantly higher than the 23,09 kJ.g^{-1} AFDW conversion factor recommended by Brey, Rumohr & Ankar (1988) for aquatic macrobenthic invertebrates. This is in accordance with the suggestion of Slobodkin & Richman (1961) that energy contents are affected by the extent of energy storage for adverse conditions, since high energy (i.e. exposed) beaches are highly unpredictable environments for macrofauna (Bally 1981).

Table 3 Contribution by species to total energy content of macrofauna on three study beaches. Figures in brackets are percentages of total macrofaunal biomass from Bally (1981). Energy value for *Bullia digitalis** (Dillwyn) (21,13 kJ.g^{-1} AFDW) from Stenton-Dozey & Brown (1988)

	Energy content (kJ.m^{-1} strip of beach)					
Species	Melkbosstrand		Yzerfontein		Rocherpan	
T. granulatus	352,14	(5,04)	7,27	(0,05)	26,38	(1,30)
P. latipes	172,76	(2,23)	257,18	(1,58)	58,61	(2,60)
E. longicornis	252,80	(3,21)	544,35	(3,28)	22,47	(1,00)
E natalensis	8,15	(0,12)	16,67	(0,11)	132,72	(6,83)
Niambia sp.	0,01	(< 0,01)	0,69	(0,03)	–	–
T. capensis	1,63	(0,02)	3,15	(0,02)	12,69	(0,53)
P. excavata	8,55	(0,11)	16,51	(0,10)	0,95	(0,71)
U. grimaldii	1,32	(0,02)	0,19	(<0.01)	0,00	(<0,01)
G. psammodytes	68,07	(0,88)	84,75	(0,52)	53,85	(2,45)
D. serra	3381,70	(52,59)	735,44	(54,35)	1513,59	(82,53)
*B. digitalis**	387,36	(5,65)	346,79	(2,40)	15,79	(0,81)
S. squamata	1831,12	(23,28)	5796,62	(35,82)	–	–
S. capense	234,68	(3,10)	266,47	(1,67)	–	–
N. capensis	6,87	(0,09)	1,67	(0,01)		
Oligochaete	88,45	(1,18)	–	–	–	–
C. fuscus	5,06	(0,07)	4,59	(0,02)	2,47	(0,07)
Total	6782,70		14702,74		1846,21	

Table 3 lists the contributions by the species studied to the total energy value of the macrofauna on the three study beaches. This table shows the considerably greater accuracy that can be obtained by using energy values for individual species rather than by the application of an overall conversion factor. The totals are between 9 and 14% lower than estimates obtained from the use of the conversion factor of 23,81 $kj.g^{-1}$ AFDW, owing to the fact that a large proportion of the biomass is made up by the bivalve *Donax serra* which has a comparatively low energy content.

Ash contents

The results of the ash analyses are given in Table 4. There appears to be little information in the literature on ash contents in general, and even less on that of sandy beach organisms. Wacasey & Atkinson 1987) found ash values of 27,1 and 15,6% for *Nephtys ciliata* and *N. paradoxa* respectively, compared with 32,86% in *N. capensis* (this study). The mean ash content of the 16 polychaete species covered by Wacasey & Atkinson's study was 23,8%. In the mysid *Gastrosaccus psammodytes*, the ash content ranged from 14,5 to 53,2% of dry weight, as opposed to an ash value of 12% reported for a tropical species of *Gastrosaccus* (Austin 1970).

The high ash content of the lumbricid oligochaete is due to its feeding mode of ingesting sand. Animals that were used in this study did not have their digestive tracts cleared of sand prior to analysis.

A major component of ash in crustaceans is calcium carbonate since they posses a relatively thick chitinous exoskeleton that is usually calcified (Barnes 1980). All else being equal, the size of the animal will influence the relative proportion of calcium carbonate according to the surface area to volume ratio. Thus, the larger the animal, the smaller should be the percentage of calcium carbonate of the total body weight.

Countering the above tendency, however, is one of the limiting factors in exoskeletons, namely, their increasing weakness with size (Currey 1970). Thus in large crustaceans it is necessary to fortify the exoskeleton with increasing amounts of calcium carbonate. This factor appears to dominate the one discussed earlier, as can be seen from the isopods of this study. A similar effect is observed in the amphipods. Figure 2 plots the relationship between the log of body weight and percentage ash content, and an equation describing this relationship is given for the crustacean species.

Table 4 Percentage ash contents of sandy beach species

Species	Range of values (%)	Mean values (%)±*SD*	Mean weight (g AFDW)
Tylos granulatus	45–72	61,92 ± 8,11	0,0668
Pontogeloides latipes	22–54	41,00 ± 9,15	0,0059
Eurydice longicornis	22–60	34,30 ± 10,56	0.0007
Excirolana natalensis	22–52	36,38 ± 9,63	0,0054
Niambia sp.	25–39	31,44 ± 4,69	0,0002
Talochestia capensis	30–68	46,18 ± 10,25	0,0020
Pseudharpinia excavata	24–53	37,38 ± 9,40	0,0005
Urothoe grimaldii	21–44	29,60 ± 6,96	0,0001
Gastrosaccus psammodytes	15–53	32,71 ± 10,92	0,0010
Donax serra	2–21	8,89 ± 4,39	0,0399
Scolelepis squamata	15–37	26,17 ± 7,67	0,0030
Sigalion capense	18–38	28,00 ± 8,46	0,1266
Nepthys capensis	12–45	32,36 ± 10,61	0,0021
Oligochaete	66–69	67,75 ± 1,26	0,0313
Cerebratulus fuscus	15–55	34,20, ± 14,29	0,0109

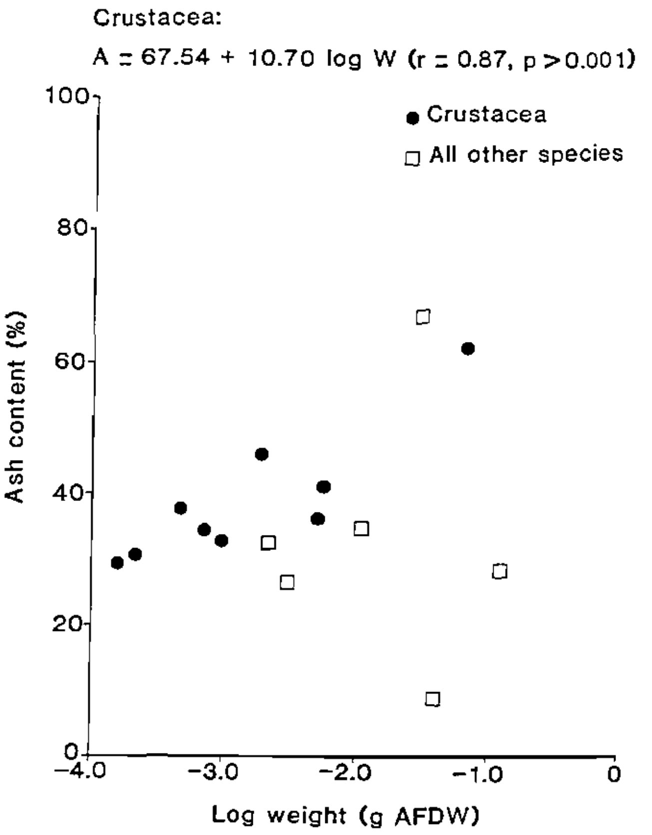

Figure 2 The relationship between percentage ash and log mean ash-free dry weight. Equation describes relationship between these factors for Crustacea studied. A = ash content (%), W = mean weight of species (g AFDW).

Conclusions

Energy contents of individual sandy beach species fall within previously reported ranges for their taxonomic groups. As an ecologically discrete grouping, however, their energy contents are higher than the norm. In addition, there appears to be a negative relationship between body weight and energy content. Ash contents were found to vary greatly and with no apparent consistency, except in the Crustacea where percentage ash contents are a function of body weight.

Acknowledgements

This work was carried out as part of a PhD in Zoology at the University of Cape Town, while the author was the recipient of a bursary from the CSIR. I am grateful to Professors A.C. Brown and C.L. Griffiths for their guidance during the study. Dr L.J. Michell kindly provided the Afrikaans abstract.

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