

ENERGY CONTENT OF MACROBENTHIC INFAUNA FROM THE CONTINENTAL SHELF ENVIRONMENT IN THE SOUTHWESTERN GULF OF MEXICO

*Contenido Energético de la Infauna Macrobéntica para la Plataforma Continental
en el Suroeste del Golfo de México*

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ABSTRACT

Energy content of infaunal macrobenthos from the continental shelf environment in the SW Gulf of Mexico provide for the first time caloric values for a tropical marine system. The highest values correspond to benthic fish larvae and juveniles; polychaete, crustacea and mollusks show the next highest values; echinoderms have the lowest energy content. The results discussed within the latitudinal gradient suggest that tropical benthic organisms have significantly lower values in contrast to higher values reported in the literature, which can be attributed to the more stable environment and to the smaller sizes of the marine benthic macrofauna in the tropics. Trends of the caloric contents observed with increasing depth and the distribution of content of organic nitrogen in surficial sediment show that organisms with highest energy content occur associated to richer grounds.

Key words: Macrofauna, benthos, energy content, Gulf of Mexico, continental shelf.

RESUMEN

Este trabajo presenta el contenido de energía para la infauna macrobéntica del ambiente de plataforma continental en el suroeste del Golfo de México y provee por vez primera valores de contenido calórico para el ambiente marino tropical. Los valores más elevados reconocidos corresponden a larvas y juveniles de peces bénticos; los poliquetos, los crustáceos y los moluscos tienen valores elevados inmediatos; los equinodermos mostraron los valores de contenido de energía más bajos. Los resultados analizados en el marco latitudinal sugieren que los organismos bentónicos tropicales tienen valores significativamente más bajos en contraste a los valores registrados en la literatura para altas latitudes, lo cual se puede atribuir al ambiente más estable en el trópico y a las tallas más pequeñas de la infauna macrobéntica marina en el mismo. La tendencia de variación del contenido calórico observado con el incremento de profundidad y con la distribución del contenido de nitrógeno orgánico en sedimento superficial indica que los organismos con contenido de energía mayor ocurren asociados a los fondos más enriquecidos.

Palabras clave: Macrofauna, bentos, contenido de energía, Golfo de México, plataforma continental.

Introduction

The acquisition of energy is the main objective of the search for food, the prey choice being determined by the prey species (Palmer, 1984) and size (Broom,

1982). Ecological energy flow is in the form of potential energy (ΔH) and is expressed as a gradient of standing crop and trophic levels (Slobodkin, 1960). It can be measured by direct combustion of dried tissue. A certain amount of energy, mainly the unfolding of proteins, carbohydrates and lipids, is lost prior to combustion in the drying process but this has been rarely evaluated in the ecological sense (Wiegert, 1968). The energy content of an organism, being

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referred to in this paper, is the amount of calories released by burning the organism under normal atmosphere and is measured as heat.

Energy transformation between organisms and circuits of energy in nature is of fundamental interest to modellers. Potential energy content is considered as the energy input and flow of materials. The gross inflow can be expressed in units of energy per time per area, being the food made available to the animal or to the population from some outside source (Slobodkin, 1960). Energy content, the prey abundance and its vulnerability are factors that integrate the food value in the selectivity of potential prey. Energy content can vary intraspecifically with life history, size, season and feeding regime (Cummins & Wuycheck, 1971; Wissing *et al.*, 1973; Griffiths, 1977).

The existing studies that refer and provide energy values for aquatic organisms date back to the early sixties (Grodzinski *et al.*, 1975; Crisp, 1984). These studies focused solely on high and intermediate latitude species, both benthic (Brawn *et al.*, 1968; Duarte *et al.*, 1980; Atkinson & Wakasey, 1976, 1983; Wakasey & Atkinson, 1987) and planktonic (Norrbinn & Båmstedt, 1984; Ross & Quetin, 1989). Caloric values were recorded in offshore zooplankton and demersal fauna of the northern Gulf of Mexico (Wissing *et al.*, 1973). Most of these studies have provided the basis for constants used in ecological energetics that have been applied in tropical aquatic environments.

The current study was undertaken to obtain caloric contents for infaunal macrobenthos from the continental shelf environment in the SW Gulf of Mexico and provide for the first time caloric values for a tropical marine system. The values will be discussed within the distributional patterns observed in a depth gradient and the organic matter content in surficial sediment expressed as percentage of organic nitrogen.

Materials and methods

Sediment was collected with a Smith-McIntyre grab in 12 stations located along transects on the continental shelf off Alvarado lagoon (18° 47' to 20° 18' N and 95° 35' to 95° 45' W) in the SW Gulf of Mexico during the OGMEX.13 cruise in 1996 (Table 1). Benthic fauna was obtained from soft bottoms at depths of 15 to 85m. The sediment was sieved through 0.25, 0.50 and 1mm mesh openings, organisms retained were

sorted and rinsed in sea-water and distilled water. They were identified to the highest taxonomic level and dried onboard at 60°C for 48 hours. Shells were removed in mollusks, before and after drying. In echinoderms dry weight includes skeletal material, in crustacea exoskeletons are included. Dried animals were stored in a desiccator to keep weight constant.

The individual dry weight of each specimen was evaluated on an electronic thermobalance with a stated precision of $\pm 0.1\mu\text{g}$. Calorimetric determinations were made with a Differential Scanning Calorimeter (DSC), Thermal Instruments model 2000 coupled to a PC system, following the manufacturers protocol. Each sample was placed individually in open aluminum panels and set one at a time on the pre-calibrated DSC cell, temperature rise was 20°C. min⁻¹. Corrections for errors caused by high carbonate content (Paine, 1966), water in hydrated exoskeletons (Griffiths, 1977) and the formation of acid (Cummins & Wuycheck, 1971) were determined and applied to all calculations. Caloric values have been expressed as joules per g dry weight (J. g⁻¹ DW).

The variation of energy values in the taxonomic groups was described and compared to other studies. Trends according to the depth gradient and the content of organic nitrogen in sediment were analyzed and allowed to explain patterns of change in the shelf environment.

Table 1. Samples location, depth, content of organic nitrogen in sediment and bottom temperature. Abbreviations: N= North, W= West, m=metres, n=number of specimens analyzed.

Station #	Latitude N	Longitude W	Depth (m)	Norg %	Temp. °C	n
26	18° 50.97	95° 45.96	24	0.050	26	3
28	18° 48.56	95° 44.03	15	0.083	28	3
31	18° 51.16	95° 42.02	34	0.001	22	2
32	18° 49.19	95° 42.04	25	0.001	26	2
37	18° 51.99	95° 40.12	48	0.068	20	1
38	18° 51.21	95° 37.43	49	0.087	20	2
40	18° 47.25	95° 37.98	40	0.055	22	1
44	18° 50.46	95° 35.85	51	0.080	20	2
50	20° 10.98	96° 41.04	29	0.054	25	2
51	20° 13.27	96° 43.25	26	0.051	26	1
52	20° 14.07	96° 41.01	46	0.070	21	1
54	20° 18.12	96° 37.04	85	0.075	18	3

Results

The energy values determined for 23 specimens of macrobenthic infauna are presented in Table 2. The highest energy values are found in benthic fish (larvae and juveniles) ($635 \pm 335 \text{ J.g}^{-1}$). The polychaetes and crustacea show the next highest energy values with 528 ± 577.5 and $501 \pm 650.6 \text{ J.g}^{-1}$, respectively. Mollusks ($266 \pm 205.3 \text{ J.g}^{-1}$) and echinoderms ($20 \pm 0.001 \text{ J.g}^{-1}$) show the lowest energy content. Figure 1 summarizes the mean energy values for the five taxonomic groups. A wide range of values, within and between taxonomic groups, is observed.

The energy contents and high abundances of polychaetes and crustacea provide both taxa with high scores in food value available to predators. In contrast, the food value of other taxa is defined lower due to their low abundance, their low energy content or both factors combined. Fish larvae and juveniles are not as abundant as polychaetes or crustacea but are 30% richer in its energy content. Mollusks would require to be at least several times more abundant to provide their predators with an equivalent energy supply. The

low energy content of echinoderms suggest an insignificant food value.

The energy values diminish for both polychaetes and mollusks in the depth gradient. The values of polychaete and crustacea correlate high with depth being $r^2=0.50$ and $r^2=0.74$, respectively. The trend was different in fish and crustacea, their energy content increased with depth (Fig. 2).

Energy content increases with larger content of organic nitrogen in sediment (Fig. 3). The values of polychaete and crustacea correlate low with organic nitrogen, $r^2=0.40$ and $r^2=0.42$, respectively. Additional values are needed to recognize the correlation of the other three groups along the organic nitrogen gradient.

Discussion

The examination of the caloric values reveals that most of the taxa do not differ significantly from each other, however a large intraspecific variability is recorded. Several reports have demonstrated that caloric values within taxonomic groups are distributed around a

Table 2. Species composition and taxonomic groups per cruise station, size of specimen, weight and energy content. Abbreviations: DW= dry weight analyzed, SS= amount of sample analyzed, EC= energy content.

Station #	Species	Taxonomic group	Size mm	DW g	SS g	E.C. J.g^{-1}
26	<i>Megalomma bioculatum</i>	Polychaeta	19	0.0098	0.0092	454.40
	<i>Lepidastenia varius</i>	Polychaeta	14	0.0061	0.0059	700.67
	<i>Paguristes sericeus</i>	Crustacea	26	0.0019	0.0018	185.70
28	<i>Callianassa atlantica</i>	Crustacea	20	0.0015	0.0014	270.00
	<i>Tetraxanthus rathbunae</i>	Crustacea	15	0.0051	0.0047	68.98
	<i>Neanthes micromma</i>	Polychaeta	21	0.0011	0.0010	1937.00
31	<i>Leiochrides africanus</i>	Polychaeta	16	0.0043	0.0036	360.20
	<i>Leptochela serratorbita</i>	Crustacea	12	0.0003	0.0028	198.70
32	<i>Ophionereis sp.</i>	Echinodermata	12	0.0068	0.0055	16.00
	<i>Periclimenes americanus</i>	Crustacea	15	0.0012	0.0010	214.00
37	<i>Coryphopterus sp.</i>	Pisces	11	0.0071	0.0050	303.80
38	<i>Processa sp.</i>	Crustacea	22	0.0018	0.0015	378.60
	<i>Callianassa major</i>	Crustacea	25	0.0033	0.0023	2219.50
40	<i>Cossura delta</i>	Polychaeta	22	0.0048	0.0038	254.50
44	<i>Sonata carinata</i>	Polychaeta	24	0.0046	0.0034	504.70
	<i>Axiopsis oxypleura</i>	Crustacea	18	0.0025	0.0021	886.40
50	<i>Marginella sp.</i>	Gastropoda	10	0.0039	0.0038	71.54
	<i>Rhithropanopeus harrisi</i>	Crustacea	21	0.0061	0.0046	77.92
51	<i>Fasciolaria sp.</i>	Gastropoda	14	0.0056	0.0043	545.90
52	<i>Tellina sp.</i>	Bivalvia	8	0.0018	0.0018	177.50
54	<i>Scoletoma verrilli</i>	Polychaeta	12	0.0289	0.0274	3.58
	<i>Paraprionospio pinnata</i>	Polychaeta	9	0.0201	0.0185	22.75
	<i>Chaenopsis sp.</i>	Pisces	26	0.0089	0.0063	970.90

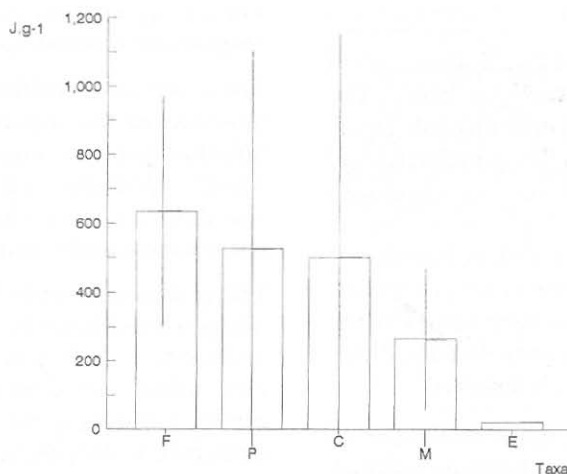


Figure 1. Energy content mean values and standard deviations (lines) of infaunal macrobenthic taxa in the continental shelf environment of the SW Gulf of Mexico. Abbreviations: C= Crustacea, E= Echinoderm, F= Fish (larvae and juvenile), M= Mollusks, P= Polychaetes.

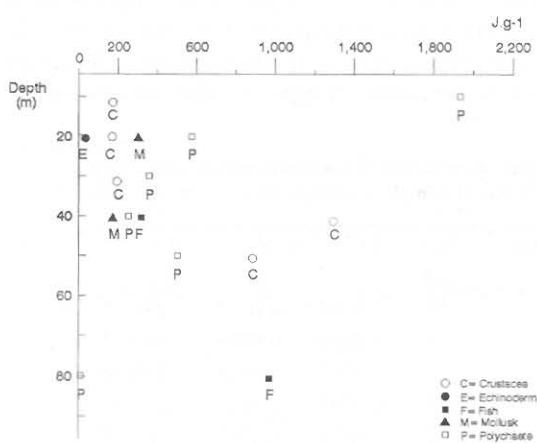


Figure 2. Mean energy content per taxonomic group along the depth gradient.

mean that is similar for most groups (Wacasey & Atkinson, 1987) which indicates a consistent biochemical composition which is reflected in the caloric value (Slobodkin & Richman, 1961; Griffiths, 1977). The echinoderms are lower than the community mean (471 J.g⁻¹) which is associated with organic material of diminished caloric value; other authors have stressed that deviations observed by groups with low energy content (sponges, ophisthobranch, etc.) are attributed to higher ash content (Tyler, 1973; Wacasey & Atkinson, 1987).

The energy values obtained in this study are closer to the lower end of values recorded by authors in high

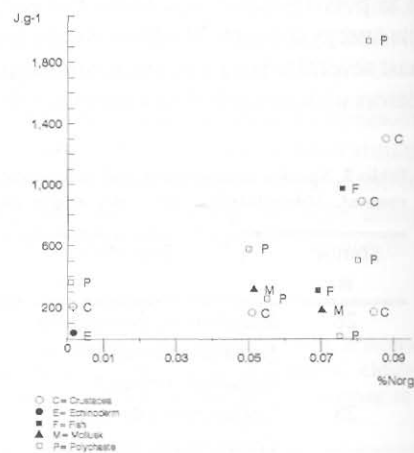


Figure 3. Variability of the mean energy content in macrobenthic infauna vs the content of organic nitrogen in sediment.

and intermediate latitudes (Paine, 1964; Cummins & Wuychek, 1971; Wissing *et al.*, 1973; Griffiths, 1977; Duarte *et al.*, 1980). This latitudinal difference in the caloric content is explained with the environmental predictability hypothesis (Slobodkin & Richman, 1961). Species living in environments where the food supply is unpredictable or varies in abundance and quality should store energy (Childress & Nygaard, 1974). Environments in lower latitude provide more stable situations and species do not need to store fat as in higher latitudes. Fat, having higher energy content, is usually stored resulting in higher caloric value (Griffiths, 1977). Some authors have suggested that

some groups in the benthos use carbohydrate as their main storage compound (Giese, 1966; Calow & Jennings, 1974). Lipid content in euphausiids and C:N in zooplankton have shown to increase with latitude (Mauchline & Fisher, 1969; Omori, 1969).

This same hypothesis can be applied to the depth gradient and the spatial variability of content of organic nitrogen in surficial sediments. Both factors are related with potential food supply utilized by infauna. The depth correlates with the supply of phytodetritus in the form of particulate organic matter to the benthos; the organic nitrogen relates with the amount and quality of detritus in the surficial sediment. The increasing energy value with higher percentages of organic nitrogen is consistent with results obtained in higher latitudes. Calorific values increase with the proportion of organic matter as food factor (Norrbin & Båmstedt, 1984). Results suggest that feeding in richer grounds will provide higher energy content at a constant rate. As example the largest fishery in the SW Gulf of Mexico is located in bottoms with highest infaunal biomass (Soto & Escobar, 1995) where the highest benthic metabolic rates are recorded (Falcón, 1998). Nutritional conditions and trophic level will yield caloric content variability within taxa (Salonen *et al.*, 1976). Metabolic rates outside enriched areas are adjusted to lower energy income levels (Paloheimo & Dickie, 1966).

Size changes with latitude and in most organisms has a significant influence on the calorific value (Cummins & Wuycheck, 1971). The lower energy values recorded in the SW Gulf of Mexico may be related to the smaller sizes encountered. Records from the northern Gulf of Mexico show that the lowest values commonly occur in benthic species, mostly exemplified in bottom dwelling invertebrates (Wissing *et al.*, 1973). Our results are consistent with this trend, in spite of the size range difference. A larger number of samples that considers diverse trophic levels and seasons will allow to establish more robust patterns of the differences described above. The number of samples and the size of the organisms analyzed in this study requires a new design that includes the appropriate extraction technique to distinguish between structural and stored lipid biochemically as well as the proportions of carbohydrates and proteins.

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