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Biochemical and energetic composition of bathyal echinoids and an asteroid, holothuroid and crinoid from the Bahamas

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Abstract. The biochemical and energetic composition of body components of ten species of bathyal echinoids, and an asteroid, a holothuroid and a stalked crinoid were determined from individuals sampled from a variety of deep-water sites near the Bahamas (north Caribbean Sea) in October 1988. When compared with other studies of echinoderms, no geographic- or depth-related differences in biochemical or energetic composition were found. Body-wall tissues were composed primarily of skeletal material (mineral ash), but were comparatively high in organic material in the echinothuriid echinoids, and the asteroid and holothuroid. Gut tissues and pyloric cecae had high levels of lipid and protein, indicating their potential role in nutrient storage. Body-wall tissues were generally low in energy, but were highest in the echinoids *Araeosoma belli* (7.7 kJ g^{-1} dry wt) and *Sperosoma antillense* (8.0 kJ g^{-1} dry wt), the asteroid *Ophidiaster alexandri* (8.9 kJ g^{-1} dry wt), and the holothuroid *Eostichopus regalis* (13.1 kJ g^{-1} dry wt). Energy levels of gut and pyloric cecal tissues were two to three times higher than those of body-wall tissues. Total somatic tissue energy values varied greatly among species, ranging from 1.5 kJ in the echinoid *Aspidodiadema jacobyi* to 142.1 kJ in *E. regalis*. As the bathyal echinoderms examined in this study occur in great abundance, they represent a significant reservoir of organic and inorganic materials and energy in deep-water benthic systems.

Introduction

The biochemical and energetic composition of echinoderm body-components has been reported for a number of shallow-water tropical, temperate, and polar environments (Giese 1966, 1976, Lawrence 1973, Lawrence and Guille 1982, Magniez 1983, McClintock and Pearse 1987a, b, Wacasey and Atkinson 1987, McClintock 1989a, b). However, few studies have examined the biochemical and energetic composition of bathyal and abyssal echinoderms. Sibuet and Lawrence (1981) and

Walker et al. (1987a, b) reported on the biochemical and energy content of common bathyal and abyssal elaspodid and aspidochirote holothurians from the Atlantic Ocean. These authors noted that dense populations of echinoderms often dominate megafaunal biomass in deep Atlantic Ocean waters. At bathyal depths (300 to 900 m) in the vicinity of the Bahamas in the northern Caribbean Sea, benthic megafaunal biomass is also dominated by echinoderms (J. Miller personal communication). Regular and irregular echinoids are particularly abundant, and holothuroids and stalked crinoids occur in large populations (C. Young and L. Cameron unpublished data).

The purpose of the present study was to provide information on the biochemical and energetic composition of somatic tissues of bathyal echinoderms. This information is of comparative interest with regard to shallow-water species and species from temperate and polar latitudes, and may provide insight into the functional role of echinoderm body-tissues. Moreover, when coupled with measurements of echinoderm densities, these data can be used to estimate the energetic densities of bathyal echinoderm populations.

Materials and methods

Adults of ten species of echinoids, the asteroid *Ophidiaster alexandri*, the holothuroid *Eostichopus regalis*, and the crinoid *Neocrinus decorus* were collected using a manned submersible (Table 1). The location and depth of collection was recorded for each species. Individuals were dissected aboard ship, and the somatic tissues were frozen until lyophilization. Echinoids were dissected into body wall, lantern, and gut tissues. In species with long spines, the spines were separated from the body wall and treated as a separate body component. The asteroid was dissected into body wall and pyloric cecae, the holothuroid into body wall and gut, and the crinoid into arms, stalks, and cirri. Intact body components were weighed, subsampled, lyophilized, reweighed, and ground into a fine powder in a Wiley Mill.

TCA-soluble carbohydrate and NaOH-soluble protein were measured spectrophotometrically using the techniques of Lowry et al. (1951) and Dubois et al. (1956), respectively. Chloroform-methanol-soluble lipid was determined gravimetrically using the technique of Freeman et al. (1957). Ash was measured by placing lyo-
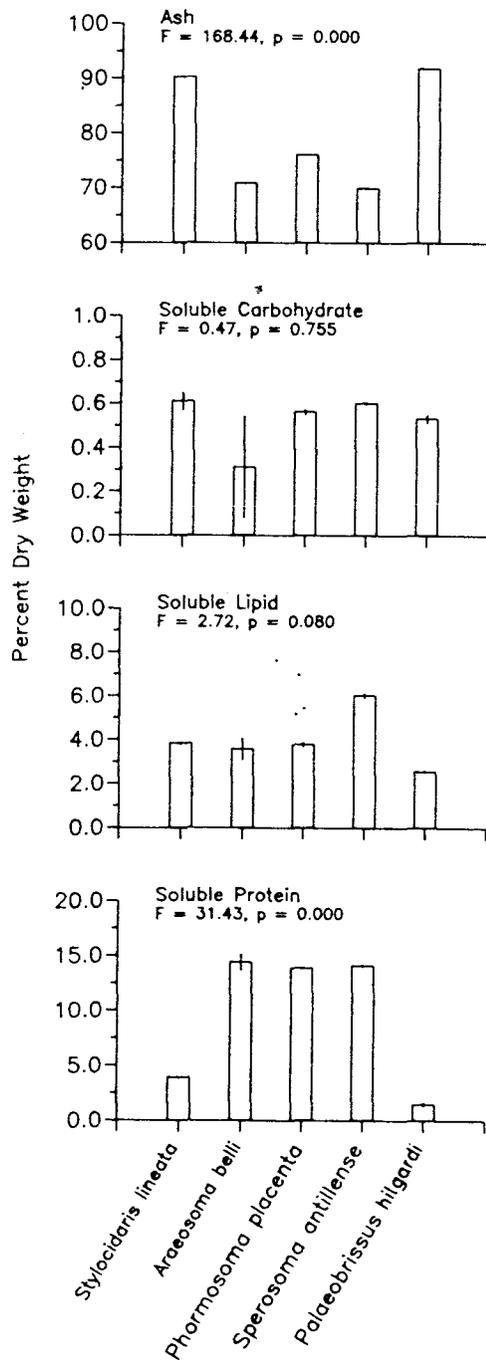
Table 1. Collection locations and depths for bathyal echinoderms collected in October 1988 for biochemical and energetic analyses

Species	Longitude; Latitude	Location	Depth (m)
Class Echinoidea			
Subclass Perischoechinoidea			
Order Cidaroida			
Family Cidaridae			
Calocidaris micans	23°55.9'N; 74°33.52'W	French Bay, San Salvador	484–493
Stylocydaris lineata	24°2.25'N; 75°28.15'W	Tartar Bank, Cat Island	617
Subclass Euechinoidea			
Superorder Diadematacea			
Order Echinothurioida			
Family Echinothuriidae			
Araeosoma belli	24°2.01'N; 74°32.40'W	Cockburn Town, San Salvador	676–722
Phormosoma placenta	24°3.55'N; 74°32.29'W	Cockburn Town, San Salvador	676–722
Sperosoma antillense	24°6.35'N; 74°32.7'W	Rocky Point San Salvador	291
Order Diadematoida			
Family Aspidodiadematidae			
Aspidodiadema jacobyi	24°2.01'N; 74°32.40'W	Cockburn Town, San Salvador	728
Superorder Atelostomata			
Order Spatangoida			
Family Asterostomatidae			
Archaeopneustes histrix	24°2.01'N; 74°32.40'W	Cockburn Town, San Salvador	607
Linopneustes longispinus	24°02.5'N; 74°32.40'W	Cockburn Town, San Salvador	662
Palaeopneustes cristatus	24°02.5'N; 74°32.40'W	Cockburn Town, San Salvador	584
Palaeobrissus hilgardi	24°02.5'N; 74°32.4'W	Cockburn Town, San Salvador	637–659
Class Stelleroidea			
Subclass Asteroidea			
Order Valvatida			
Family Ophidiasteridae			
Ophidiaster alexandri	24°2.25'N; 75°28.15'W	Tartar Bank, Cat Island	636–669
Class Holothuroidea			
Order Aspidochirota			
Family Stichopodidae			
Eostichopus regalis	25°27.52'N; 76°54.32'W	Egg Reef	421
Class Crinoidea			
Order Isocrinida			
Family Isocrinidae			
Neocrinus decorus	23°57.42'N; 74°34.45'W	Sandy Point, San Salvador	479

philized tissues into a muffle furnace at 500°C for 4 h (Paine 1971). The remaining organic refractory material was considered to be NaOH-insoluble protein (Lawrence and Kafri 1979). The energetic composition of the tissue was calculated by multiplying the values of each of the organic classes by energy equivalents (Brody 1945).

The total amount of energy allocated to each somatic tissue was calculated by multiplying the kJ g^{-1} dry wt tissue of each component by the total dry wt of the intact body component. These values were summed, yielding the total somatic energy content of an individual.

An ANOVA was used to make comparisons of body-wall biochemical compositions within those groups of echinoids whose body-wall tissues were combined with short spines, and those whose body-wall tissues were analyzed separately. Percentage data were transformed before statistical analysis using an arc-sine transformation. When significant differences were detected with the ANOVA, 95% confidence limits allowed an evaluation of where significant differences occurred.

Results

The biochemical composition of the body-wall tissues are presented in Table 2. The body-wall tissues of echinoids from which the body wall and spine measurements were combined were composed primarily of mineral ash, with values ranging from 69.8% dry wt in the echinothuriid

Fig. 1. Biochemical composition (ash, soluble carbohydrate, soluble lipid, soluble protein) of body wall and associated short spines of five species of bathyal echinoids collected in October 1988 from Bahamas. Histograms show means ($\pm$ 1 SE: bars) of three individuals except for *P. hilgardi* ($n = 5$). Also shown are F values and associated probability estimations for each ANOVA
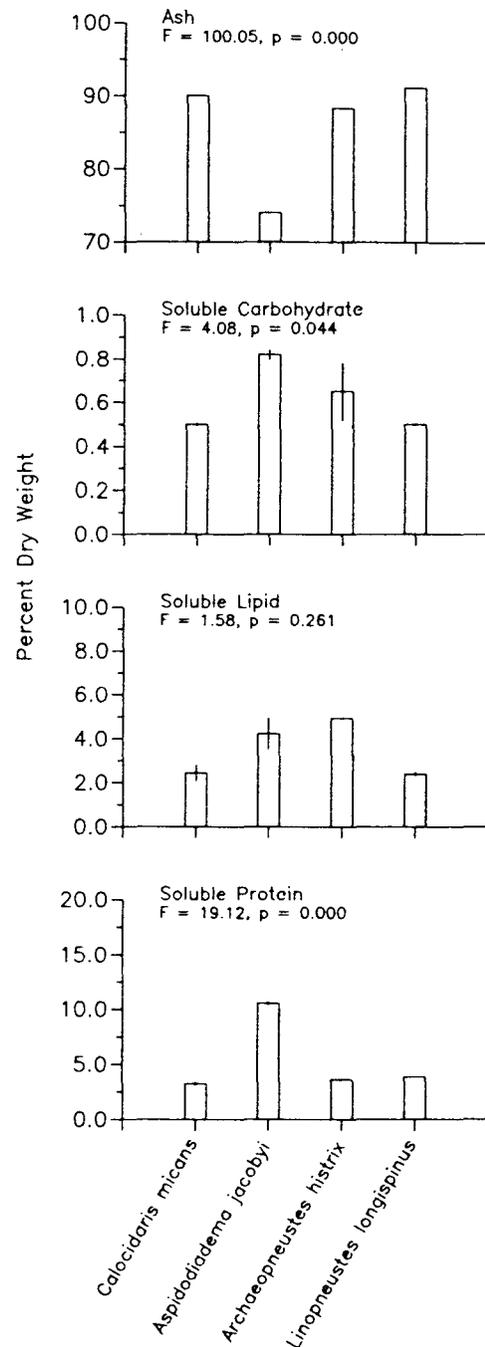
Fig. 2. Biochemical composition (ash, soluble carbohydrate, soluble lipid, soluble protein) of body wall (no spines included) of four species of bathyal echinoids collected in October 1988 from Bahamas. Histograms show means ($\pm$ 1 SE: bars) of three individuals except for *A. histrix* ($n = 4$). Also shown are F values and associated probability estimations for each ANOVA

Table 2. Biochemical composition (% dry wt) of bathyal echinoderms collected from Bahamas in October 1988. Values are means for sample sizes of 2; means ± 1 SD are given for sample sizes > 2. *, **: 2 and 3 pooled samples, respectively

Species	n	Ash	Carbohydrate, soluble	Lipid, soluble	Protein	
					soluble	insoluble
Class Echinoidea						
Calocidaris micans						
body wall	3	90.0 ± 1.4	0.5 ± 0.1	2.7 ± 1.7	3.3 ± 1.4	3.5 ± 1.4
spines	1	93.7	0	0.4	2.0	3.9
lantern	1**	59.0	0.6	1.2	4.0	35.2
gut	1**	15.5	1.8	17.9	28.8	36.0
Stylocidaris lineata						
body wall	3	90.2 ± 0.6	0.6 ± 0.3	3.8 ± 0.8	3.9 ± 0.8	1.4 ± 0.8
spines	1	96.6	0.4	1.2	0	1.8
lantern	3	89.4 ± 1.3	0.5 ± 0.1	1.8 ± 2.0	5.1 ± 3.1	3.2 ± 0.1
gut**	1	25.3	1.2	16.5	36.2	20.7
Araeosoma belli						
body wall + spines	3	70.7 ± 2.3	0.5 ± 0.4	3.9 ± 2.5	14.7 ± 5.9	11.4 ± 2.4
lantern	3	82.3 ± 2.4	0.5 ± 0.5	2.7 ± 1.0	5.2 ± 3.4	9.3 ± 3.2
gut	1**	20.5	1.8	21.5	32.1	24.1
Phormosoma placenta						
body wall + spines	3	76.01 ± 1.7	0.6 ± 0.2	3.8 ± 1.1	13.9 ± 3.7	5.7 ± 2.4
lantern	3	83.5 ± 2.3	0.5 ± 0.1	1.8 ± 0.1	6.6 ± 2.4	7.4 ± 3.9
gut	1	43.9	1.4	14.1	27.2	13.4
Sperosoma antillense						
body wall + spines	3	69.8 ± 2.6	0.6 ± 0.1	6.1 ± 1.6	14.1 ± 2.1	9.4 ± 2.4
lantern	3	84.5 ± 1.6	0.5 ± 0.1	3.0 ± 1.5	8.6 ± 1.1	3.3 ± 2.0
gut	1	23.2	1.6	22.6	30.4	22.2
Aspidodiadema jacobyi						
body wall	3	74.0 ± 1.7	0.8 ± 0.3	4.6 ± 3.1	10.6 ± 2.2	9.9 ± 1.2
spines	1	86.3	1.1	1.8	5.6	5.2
lantern	1*	88.9	0.6	5.1	3.5	1.9
Archaeopneustes histrix						
body wall	4	88.4 ± 1.2	0.7 ± 0.1	4.9 ± 0.5	3.6 ± 0.8	2.4 ± 1.2
spines	1	91.8	0.7	0.2	0.5	7.2
gut	1*	35.3	0.9	10.7	29.5	23.6
Linopneustes longispinus						
body wall	3	91.0 ± 0.1	0.5 ± 0.1	2.4 ± 0.9	3.7 ± 0.6	2.2 ± 1.2
spines	1	92.3	0.4	0.8	1.7	4.8
gut	1**	44.9	1.7	15.1	15.5	22.8
Palaeopneustes cristatus						
body wall + spines	2	90.9	0.9	1.9	1.4	5.1
gut	1*	47.4	1.2	10.4	37.0	4.0
testes	1	19.2	0.7	32.9	20.4	26.8
Palaeobrissus hilgardi						
body wall + spines	5	91.8 ± 1.0	0.5 ± 0.2	2.6 ± 0.6	1.6 ± 0.9	3.5 ± 1.8
gut	1**	52.0	1.4	4.0	33.4	9.2
Class Stelleroidea						
Ophidiaster alexandri						
body wall	1	64.6	0.7	4.0	19.2	11.5
pyloric ceca	1	11.2	1.7	23.2	32.3	31.6
Class Holothuroidea						
Eostichopus regalis						
body wall	2	51.6	1.4	10.7	18.4	18.0
gut	1*	60.3	0.4	9.1	11.7	18.5
Class Crinoidea						
Neocrinus decorus						
arms	2	82.1	0.9	2.7	8.8	5.7
stalk	2	91.8	0.7	1.6	0.7	5.3
cirri	2	93.6	0.3	1.0	1.5	3.7

Table 3. Energetic composition (kJ g^{-1}dry wt) of bathyal echinoderms collected from Bahamas in October 1988. Values are means for sample sizes of 2; means ±1 SD are given for samples > 2. *, **: 2 and 3 pooled samples, respectively

Species	n	Carbohydrate, soluble	Lipid, soluble	Protein soluble	Protein insoluble	Total
Class Echinoidea						
Calocidaris micans						
body wall	3	0.1 ± 0.02	0.6 ± 0.1	0.5 ± 0.4	0.6 ± 0.4	1.8
spines	1	0	0.1	0.5	0.9	1.5
lantern	1**	0.1	0.5	0.9	8.3	9.8
gut	1**	0.3	7.1	6.8	8.5	22.7
Stylocidaris lineata						
body wall	3	0.1 ± 0.05	1.5 ± 0.3	0.9 ± 0.2	0.3 ± 0.2	2.8
spines	1	0.1	0.4	0	0.4	0.9
lantern	3	0.1 ± 0.01	0.7 ± 0.2	1.2 ± 0.7	0.7 ± 0.1	3.6
gut	1**	0.2	6.6	8.6	4.9	20.3
Araeosoma belli						
body wall + spines	3	0.1 ± 0.1	1.5 ± 1.1	3.5 ± 1.4	2.6 ± 2.2	7.7
lantern	3	0.1 ± 0.1	1.1 ± 0.4	2.7 ± 1.0	2.2 ± 1.0	6.1
gut	1**	0.3	8.5	7.6	5.7	22.1
Phormosoma placenta						
body wall + spines	3	0.1 ± 0.02	1.6 ± 0.5	3.4 ± 0.2	1.4 ± 0.6	6.5
lantern	3	0.1 ± 0.05	0.7 ± 0.1	1.7 ± 0.5	1.7 ± 0.9	3.5
gut	1	0.3	5.5	6.4	3.3	15.5
Sperosoma antillense						
body wall + spines	3	0.1 ± 0.01	2.4 ± 0.6	3.3 ± 0.5	2.2 ± 0.6	8.0
lantern	3	0.1 ± 0.02	1.2 ± 0.6	2.0 ± 0.3	0.8 ± 0.5	4.1
gut	1	0.3	8.9	7.2	5.3	21.7
Aspidodiadema jacobyi						
body wall	3	0.1 ± 0.05	1.9 ± 1.2	2.5 ± 0.6	2.3 ± 0.2	6.8
spines	1	0.1	0.7	1.4	1.2	3.4
lantern	1*	0.1	2.0	0.8	0.5	3.4
Archaeopneustes histrix						
body wall	4	0.1 ± 0.01	2.0 ± 0.2	0.9 ± 0.2	0.4 ± 0.3	3.4
spines	1	0.1	0.2	0.6	1.7	2.0
gut	1*	0.2	4.2	6.9	5.6	16.9
Linopneustes longispinus						
body wall	3	0.1 ± 0.02	2.4 ± 0.6	0.9 ± 0.1	0.5 ± 0.3	3.9
spines	1	0.1	0.3	0.4	1.1	1.9
gut	1**	0.3	6.0	5.4	3.7	15.4
Palaeopneustes cristatus						
body wall + spines	2	0.2	0.7	0.3	1.7	2.9
gut	1*	0.2	4.1	8.7	1.0	14.0
Palaeobrissus hilgardi						
body wall + spines	5	0.1 ± 0.02	1.4 ± 1.3	0.3 ± 0.2	0.7 ± 0.2	2.5
gut	1**	0.3	1.5	7.8	2.2	14.3
Class Stelleroidea						
Ophidiaster alexandri						
body wall	1	0.1	1.6	4.5	2.7	8.9
pyloric ceca	1	0.3	9.2	7.6	7.5	24.6
Class Holothuroidea						
Eostichopus regalis						
body wall	2	0.2	4.3	4.4	4.2	13.1
gut	1*	0.1	3.6	2.7	4.3	10.7
Class Crinoidea						
Neocrinus decorus						
arms	2	0.1	1.0	2.1	1.4	4.6
stalk	2	0.1	0.6	0.2	1.2	2.1
cirri	2	0.1	0.4	0.3	0.9	1.7

Table 4. Test diameter, dry wt, and kJ of individual somatic body components and total somatic energy content of representative individuals of bathyal echinoids collected from Bahamas. Gut tissues were not collected for *Aspidodiadema jacobyi*. Values in parentheses are percentages of total. Asterisk indicates species in which spines were included with test; in other cases, dash indicates not applicable or no data available

Parameter	*Calocidaris micans*	*Stylocidaris lineata*	*Araeosoma belli*	*Phormosoma placenta*	*Sperosoma antillense*	*Aspidodiadema jacobyi*	*Archaeopneustes histrix*	*Linopneustes longispinus*	*Palaeopneustes cristatus*	*Paleobrissus hilgardi*
Test diam (cm)	5.4	3.1	10.0	5.3	7.4	1.4	9.1	11.1	10.4	5.0
Gravimetric composition (g dry wt)										
body wall	14.07	4.15	7.08*	1.13*	2.62*	0.13	10.69	20.54	2.13	2.16*
spines	16.02	4.00	–	–	–	0.14	3.45	2.34	–	–
lantern	2.77	0.65	1.24	0.26	0.57	0.03	–	–	–	–
gut	0.72	0.08	0.99	0.20	0.44	–	0.31	0.40	0.65	0.04
Energetic composition (kJ)										
body wall	25.3 (27)	11.6 (61)	54.5 (65)	7.3 (65)	21.0 (64)	0.7 (47)	36.3 (75)	80.1 (88)	82.6 (84)	5.4 (90)
spines	24.0 (26)	3.6 (19)	–	–	–	0.4 (26)	6.9 (14)	4.4 (5)	–	–
lantern	27.1 (29)	2.3 (12)	7.6 (9)	0.9 (8)	2.3 (7)	0.4 (27)	–	–	–	–
gut	16.3 (18)	1.6 (8)	21.9 (26)	3.1 (27)	9.5 (29)	–	5.2 (11)	6.2 (7)	15.9 (16)	0.6 (10)
Total	92.7	19.1	84.0	11.3	32.8	1.5	48.4	90.7	98.5	6.0

Table 5. Length, height, dry wt, and kJ of individual somatic body components, and total somatic energy content of representative individuals of bathyal asteroid, holothuroid and crinoid collected from Bahamas. Values in parentheses are percentages of total; —: not applicable

Parameter	*Ophidiaster alexandri* (asteroid)	*Eostichopus regalis* (holothuroid)	*Neocrinus decorus* (crinoid)
Arm length (cm)	6.2	–	–
Body length (cm)	–	19.5	–
Body height (cm)	–	–	72.5
Gravimetric composition (g dry wt)			
body wall	4.18	10.07	–
arms	–	–	7.24
pyloric ceca	0.77	–	–
gut	–	0.95	–
stalk	–	–	9.07
cirri	–	–	1.76
Energetic composition (kJ)			
body wall	37.2 (66)	131.9 (93)	–
arms	–	–	33.3 (60)
pyloric ceca	18.9 (34)	–	19.0 (34)
gut	–	10.2 (7)	3.0 (6)
stalk	–	–	–
cirri	–	–	–
Total	56.1	142.1	55.3

echinoid *Sperosoma antillense* to 91.8% dry wt in the spatangoid echinoid *Palaeopneustes hilgardi*. Levels of ash were significantly ($P < 0.05$) higher in the body wall and spines of *S. antillense* than in the other two echinothuriids (*Araeosoma belli, Phormosoma placenta*), while all echinothuriids had significantly ($P < 0.05$) lower ash levels than spatangoids (Fig. 1). The body-wall and spines of the spatangoid echinoids (*Stylocidaris lineata* and *Palaeopneustes hilgardi* had significantly ($P < 0.05$) lower levels of NaOH-soluble protein than that of the echinothuriids (Fig. 1). No significant differences in levels of lipid or TCA-soluble carbohydrate were detected in the five echinoids for which body-wall and spines were combined. Body-wall tissues of echinoids for which only the body wall was examined also showed differences in proximate composition. The small diadematoid echinoid *Aspidodiadema jacobyi* had significantly ($P < 0.05$) less ash, and higher TCA-soluble carbohydrate and NaOH-soluble protein than the other three species examined (*Calocidaris micans, Archaeopneustes histrix, Linopneustes longispinus*) (Fig. 2).

Mineral ash dominated the composition of the body-wall tissues of the asteroid *Ophidiaster alexandri* (64.6% dry wt) and the holothuroid *Eostichopus regalis* (51.6% dry wt), although levels were lower than in body-wall tissues of echinoids (Table 2). The crinoid *Neocrinus decorus* had very high levels of mineral ash in all body components (arms, stalk, cirri: 82.1 to 93.6% dry wt). Among the organic constituents of echinoid, asteroid, and holothuroid body-wall tissues, levels of NaOH-soluble protein (1.4 to 19.2% dry wt) and insoluble protein

(refractory organic material: 1.4 to 18.0% dry wt) were generally highest. This was also true for the arms, stalk, and cirri of N. decorus. With the exception of the regular echinoid Sperosoma antillense and the holothuroid E. regalis, levels of lipid in body-wall tissues were generally very low (1.9 to 4.6% dry wt). This was also the case for the arms, stalk, and cirri of N. decorus. TCA-soluble carbohydrate levels were very low in echinoid, holothuroid, and asteroid body-wall and all crinoid tissues (0.5 to 1.4% dry wt).

The organic composition of the gut tissues of the echinoids and holothuroid was dominated by NaOH-soluble and insoluble protein (cumulative vales ranged from 30.2 to 64.8% dry wt), with widely variable levels of lipid (4.0 to 22.6% dry wt), and low levels of TCA-soluble carbohydrate (0.9 to 1.8% dry wt) (Table 2).

The energy levels associated with each of the organic constituents and energy levels (kJ g^{-1} dry wt) of body tissues are presented in Table 3. Patterns of energetic composition were similar to biochemical composition. In the echinoids, body-wall tissues were generally low in energy (1.8 to 8.0 kJ g^{-1} dry wt). Crinoid body components and echinoid spines and lanterns also had low levels of energy. Higher levels of energy occurred in gut tissues, ranging from 10.7 kJ g^{-1} dry wt in the holothuroid Eostichopus regalis to 22.7 kJ g^{-1} dry wt in the echinoid Calocidaris micans.

Total somatic energy contents of bathyal echinoderms (Tables 4 and 5) varied from a low of 1.5 kJ in the echinoid Aspidodiadema jacobyi (test diameter = 1.4 cm) to a high of 142.1 kJ in the holothuroid Eostichopus regalis (body length = 19.5 cm).

Discussion

The biochemical composition of the body components of these bathyal echinoderms are similar to those from shallow-water temperate (Giese 1966, 1976, Lawrence and Guille 1982, McClintock 1989 b), tropical (Lawrence 1973, Lawrence and Guille 1982) and polar (Lawrence and Guille 1982, McClintock and Pearse 1987 a, b, McClintock et al. 1988) environments. Comparisons with other bathyal and abyssal echinoderms are restricted to holothurians (Sibuet and Lawrence 1981, Walker et al. 1987 a, b), of which only one species was investigated in the present study. The biochemical composition of the body wall and gut tissues of the bathyal holothuroid Eostichopus regalis was similar to the 17 species of bathyal and abyssal holothuroids examined in earlier studies. Although the small number of asteroids, holothuroids, and crinoids examined precludes a broad comparison among these groups, clearly the differences in biochemical composition of bathyal echinoids cannot be related to geographic or depth-specific factors. Lawrence and Guille (1982) indicated that the similarity in composition reflects fundamental characteristics of echinoderm body-components which determine their composition.

The body-wall tissues of bathyal echinoids are composed primarily of skeletal material. The greater levels of skeletal material in the body-wall tissues of spatangoids than cidaroids, echinothuriids and diadematids may be related to a decreased need for structural proteinaceous material (connective tissue) to support the ossicles and plates of the test of the spatangoids. Levels of protein (NaOH-soluble and insoluble) were lower in the body-wall tissues of the spatangoids than the other echinoids examined. Echinoid spines were also high in mineral ash; small amounts of lipid and protein occur in species with an epithelial layer surrounding the spines. The lanterns of all but the spatangoids were generally high in mineral ash, as found by Lawrence and Guille (1982) for shallow-water echinoids. However, the lantern of Calocidaris micans had comparatively high levels of insoluble protein. Presumably this protein is structural in nature and a constituent of connective tissue. Large amounts of connective tissue associated with the lantern may reflect feeding habit, and the need to strengthen a lantern used to rasp at hard materials.

The body-wall tissues of the asteroid Ophidiaster alexandri and the holothuroid Eostichopus regalis had higher organic contents and lower mineral ash content than echinoids (however the body wall of the echinothuriids has a high organic content). This is related to a decrease in the degree of skeletalization and high levels of protein. Krishnan (1968) found that protein is the primary organic constituent of body wall tissues of Holothuria scabra, and serves as a principal component of the abundant connective tissues. These body-wall tissues may provide a substantial reservoir of nutrients and energy (Giese 1976, Prim et al. 1976, McClintock 1989 b, Saito and Watts 1989). The ability to store nutrient reserves may be of particular importance in species occupying bathyal and abyssal depths, where nutrient availability may be highly episodic (Sanders et al. 1965, Menzies et al. 1973, Rowe and Staresinic 1979). The arms and cirri of the bathyal stalked crinoid Neocrinus decorus are higher in skeletal material than the antarctic comatulid Promachocrinus kerguelensis (McClintock and Pearse 1987 a). As a supporting structure, it is composed primarily of skeletal material.

The echinoid and holothuroid gut tissues contain 2 to 3 times higher levels of organic constituents than body-wall tissues. Gut lipid levels as high as 10 to 23% dry wt were common in bathyal echinoderms. High species-specific variations in levels of organic constituents reflect the dynamic nature of this tissue and its possible role in nutrient storage. Klinger et al. (1988) found that the gut tissues of the echinoid Lytechinus variegatus may serve for short-term nutrient storage. The pyloric caeca of the asteroid Ophidiaster alexandri were also high in organic constituents and could have a nutrient-storage function.

The energetic level of the body-wall tissues of echinoids and the arms, stalk, and cirri of the crinoid were low (1.8 to 4.6 kJ g^{-1} dry wt). However, the echinoids Araeosoma belli, Phormosoma placenta, Sperosoma antillense and Aspidodiadema jacobyi had body-wall tissues with twice these levels of energy (6.5 to 8.0 kJ g^{-1} dry wt). Higher levels of energy are attributable to energy bound in soluble and insoluble protein, and may reflect greater amounts of connective tissue and lesser amounts of skele-

tal elements in the body wall of these echinoids. *Araeosoma belli* possesses a flexible test. Apparently its vulnerability to predation is offset by the presence of poisonous spines. The energy content of the body-wall tissues of the asteroid *Ophidiaster alexandri* was similar to these echinoids, while the body-wall tissues of the holothuroid *Eostichopus regalis* contained higher levels of energy (13.1 kJ g^{-1} dry wt). This is the result of high levels of energy derived from protein. Walker et al. (1987a, b) also found high levels of energy associated with protein in the body wall of bathyal and abyssal holothuroids.

The bathyal echinoderms examined in this study are very patchy in their distribution but often occur in high densities and are the most abundant benthic megafauna (C. Young and L. Cameron personal observation). Therefore, their contribution to benthic biomass is considerable. Similarly, Khripounoff and Sibuet (1980), Sibuet and Lawrence (1981) and Walker et al. (1987a, b) indicate that echinoderms, such as deposit-feeding holothurians, represent a high percentage (40 to 45%) of the total bathyal and abyssal biomass in the Atlantic Ocean. The somatic energy content of adult bathyal echinoids can be high and varies almost one-hundred fold (1.5 to 98.5 kJ). Representatives of different classes of echinoderms may have vastly different energy contents. For example, the bathyal asteroid *Ophidiaster alexandri* and the crinoid *Neocrinus decorus* contain 55 to 56 kJ, while the holothuroid *Eostichopus regalis* contains 142 kJ. These values represent the amount of energy in the somatic tissue only. The presence of mature gonads in these echinoderm species would increase their individual energy contents. Lawrence (1985) pointed out that the development of gonads to reproductive maturity affects the amount of energy present in an individual. Walker et al. (1987a) found that mature ovaries represented 3 to 25% of the total energy content in five species of deep-sea elaspodid holothuroids. Clearly, the bathyal echinoderms examined in this study represent a significant store of materials and energy within deep-sea benthic systems.

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