Vol. 10: 297–305, 1983 | MARINE ECOLOGY – PROGRESS SERIES
Mar. Ecol. Prog. Ser. | Published January 20

Nutrition of Deposit-Feeding Holothuroids and Echinoids (Echinodermata) from a Shallow Reef Lagoon, Discovery Bay, Jamaica*

L. S. Hammond

Australian Institute of Marine Science, P. M. B. No. 3, Townsville, Queensland 4810, Australia

ABSTRACT: Concentrations of organic carbon and nitrogen, ATP, and total plant pigment (chlorophyll *a* + phaeophytin) were approximately twice as high in foregut contents of the deposit-feeding, aspidochirote holothuroids *Isostichopus badionotus* Selenka, *Holothuria mexicana* Ludwig and *H. arenicola* Forskal, and spatangoid echinoids *Meoma ventricosa* Lamarck and *Plagiobrissus grandis* Gmelin than in the adjacent sediments. This suggests that holothuroids and spatangoids selectively ingest nutrient-rich grains, contrary to the conventional view that they show poor chemical discrimination. The availability of the organic food resources did not vary consistently between different grain-size fractions of sediment. This obviates any *a priori* expectation that discrimination on the basis of grain quality, demonstrated here, will be coupled to discrimination according to grain size, previously shown not to occur in these species. Assimilation efficiency of the ingested carbon averaged 42 %. Plant carbon, calculated from pigment concentrations and probably derived from diatoms, represented a major carbon resource in the available sediments, but only a small proportion of that ingested was apparently assimilated. Meiofauna, a minor component of the available carbon (ca. 1 %), were ingested in lower numbers than those at which they occurred in the sediment, and were not digested or assimilated. Bacterial biomass was not determined, but other studies suggest that its contribution to the sedimentary carbon pool is low. It is likely that at least half of the carbon assimilated by these deposit feeders is of detrital origin. This result, which contrasts with present understanding of the nutrition of deposit feeders, may be indicative of qualitative differences between detritus of coral reefs and that of other shallow, coastal ecosystems.

INTRODUCTION

Reviews of the feeding biology of holothuroids and echinoids (Hyman, 1955; Anderson, 1966; Ferguson, 1973; Jangoux and Lawrence, 1982) reveal little advance in knowledge of the trophic requirements and nutrition of deposit-feeding forms over three decades. Although numerous early studies listed 'food' items, principally meiofauna and diatoms, present in the guts of various species (Hyman, 1955; Bakus, 1973) they provided no evidence that these items were assimilated by the deposit feeders. Other workers recognized that nutrition might be derived from more amorphous, detrital sources (e.g. Crozier, 1915; Chesher, 1969). Recent experimental studies suggest that, in common with the majority of deposit feeders (Fenchel and Blackburn, 1979), bacteria associated with detrital organic carbon, rather than the detritus itself, may be an important food resource for holothuroids (Sorokin, 1972; Yingst, 1976). No comparable data exist for spatangoid echinoids.

Tropical holothuroids and spatangoid echinoids occur at high densities in coral reef environments and grow to large sizes, while subsisting on sediments which contain only low concentrations of organic carbon (Chesher, 1969; Bakus, 1973). Of this, only a small proportion represents the bacterial biomass (Sorokin, 1973; Moriarty, 1982), implying that the importance of bacteria as food for deposit feeders may not be as great as in other environments. The present study investigated the ingestion and assimilation of various forms of organic carbon by the aspidochirote holothuroids *Isostichopus badionotus* Selenka, *Holothuria mexicana* Ludwig and *H. arenicola* Forskal, and the spatangoid echinods *Meoma ventricosa* Lamarck and *Plagiobris-*

* Contribution No. 179 from the Discovery Bay Marine Laboratory

0171-8630/83/0010/0297/$ 02.00

sus grandis Gmelin, in the shallow back-reef lagoon on the western side of Discovery Bay, Jamaica (Fig. 1). It is concerned only with nutrition derived from the ingested sediment, notwithstanding suggestions that direct uptake of dissolved organic substances (Ahearn and Townsley, 1975) and skin digestin (Pequignat, 1972) may comprise sources of nutrition for some species of these groups.

MATERIALS AND METHODS

Field Collections

Approximately 10 g dry weight of sediment were taken from the foreguts and hindguts (the first and last 10 cm or less) of dissected specimens of *Isostichopus badionotus, Holothuria mexicana* and *H. arenicola* from Site 1, and *Meoma ventricosa* and *Plagiobrissus grandis* from Site 2 (Fig. 1). Five specimens of each

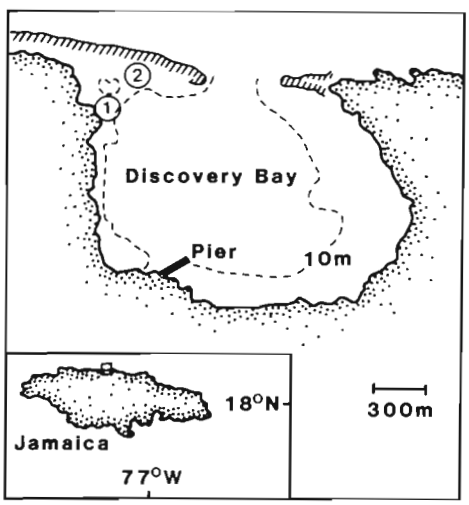

Fig. 1. Discovery Bay lagoon, behind fringing reef (cross hatched), bounded by the − 10 m contour (dotted line). Locations of the sampling sites are shown

species were used. Sampling was done in the late afternoon, when all species were actively feeding (Hammond, 1982a). Sediment samples were taken immediately adjacent to each individual of *I. badionotus* and *H. mexicana*, scraping only the top few millimetres of sediment. Samples were taken adjacent to each spatangoid at about 4 cm below the sediment surface, the level at which the animals feed (Chesher, 1969; Hammond, 1982a). Powell (1977) indicated that the funnel-feeding apodan holothuroid *Leptosynapta tenuis* derived most of its sediment intake from the top 3 cm of sediment, so samples for comparison with the foreguts of *H. arenicola*, also a funnel feeder, were taken to this depth beside each funnel. These procedures represented as closely as possible the feeding behaviour of the respective species.

To determine the distribution of food resources in different grain-size fractions of the available sediment, 3 fresh sediment samples from each location were hand-seived at 1 ∅ intervals from −1 to 4 ∅.

Fresh faeces were collected adjacent to each holothuroid, or from clean plastic containers in which *Plagiobrissus grandis* was placed. No faecal samples were obtained from *Meoma ventricosa*, which did not defecate after collection. (In the field, both spatangoids defecate below the sediment surface, rendering collection of faeces impossible). Other samples of fresh faeces from the 4 species, and of material removed from the posterior most part of the gut of dissected *M. ventricosa*, were retained in clean shallow glass containers in running seawater for 24 h. All the above samples were frozen immediately after collection, and each was subjected, within 3 wk, to the analyses described in the following section.

Foregut and hindgut contents and adjacent sediments were sampled from an additional 5 specimens of each species, and meiofaunal counts were made immediately on the fresh samples.

Laboratory Procedures

Total organic carbon and nitrogen were determined on a Colman Analyser by the two temperature method (Telek and Marshall, 1974), using 0.5 g of homogenized sediment, previously dried to a constant weight at 90 °C. Water content was thus established, for correction of the results of other assays which utilized wet sediment. The technique yields C and N determinations accurate to about ± 0.01 % (e.g. Culmo, 1974; Kepkay and Novitsky, 1980).

The cold H_2SO_4 method of Karl and LaRock (1975), incorporating the modifications recommended by Cooksey (1978) for carbonate sediments, was used for the extraction of ATP from ca. 2 g samples of wet sediment. A spike of 1000 ng ATP (Sigma Chemical Co.) was added to duplicates of five randomly chosen samples to evaluate extraction and assay efficiency. The luciferin-luciferase assay, utilizing firefly lantern extract (FIE-50, Sigma Chemical Co.) followed the procedures of Cooksey (1978). Light emission was measured on a JRB Inc. ATP Photometer.

Plant pigment, as chlorophyll *a* and phaeophytin, was determined from 0.2 g samples of wet sediment. Extraction followed the method of Tietjen (1968), and assay, on a Turner fluorometer, followed Strickland and Parsons (1972).

Meiofauna were extracted from 10 g wet weight samples of sediment and fore- and hindgut contents by

flotation, using a dilute sugar solution, and were then collected on a 125 μm mesh. The meiofauna so extracted, and any remaining in the sediment, were counted under a binocular microscope, recording live and dead animals.

Initially it was intended to use these assays, together with appropriate conversion factors, to partition the sedimentary organic carbon pool into its autotrophic, heterotrophic and non-living compartments. This ambition was thwarted by the incomplete recovery of ATP, although the same protocol has subsequently been applied by de Vaugelas (1981) to partition the organic carbon resource of reef sediment, purportedly with success.

RESULTS

The average levels of total organic C and N, total plant pigment, chlorophyll *a*, phaeophytin and ATP in each set of samples (sediment, foregut, hindgut, faeces, retained faeces) for the 5 species of deposit feeders are listed in Table 1.

The organic carbon content of the sediment was very low at both sites, in common with other reef sediments (e.g. Bunt et al., 1972; Webb et al., 1977; Sorokin, 1978; Moriarty, 1982). The organic nitrogen content was also very low, comparable to levels reported by Bunt et al. (1972) and Thomassin et al. (1976), but was an order of magnitude less than reported by Webb et al. (1977) at Enewetak Atoll. Both carbon and nitrogen levels were much lower at Site 2, where samples were taken about 5 cm below the sediment surface, than at Site 1, where superficial sediments were sampled. The average C:N ratios at each site was 10.5 and 12.8 respectively, but variation between samples was high. The coefficient of correlation (r) between C and N was = 0.64 and 0.38, at the two sites respectively. This may result in part from errors in the determination of N, since the resolution of the method was approximately ± 20 % of ambient levels.

Table 1. Mean and standard deviation of organic carbon (C), organic nitrogen (N), chlorophyll *a* (Chl *a*), phaeophytin (Php), total plant pigment (TPP = chlorophyll *a* ± phaeophytin) in μg g^{-1} dry weight of sediment, and ATP, in ng g^{-1} dry weight of sediment, in samples from the adjacent sediment (S), foregut (FG), hindgut (HG), faeces (F), and faeces retained for 24 h in running seawater (RF), for 3 holothuroid and 2 echinoid species. Sample size was 5 in all cases. Spaces indicate that samples were not taken

Species	Assay	S	FG	HG	F	RF
I. badionotus	C	5380,1750	10720,4190	5980,3780	6030,1230	5740,680
	N	600,120	1220,230	1000,140	800,160	640,280
	Chl *a*	65,24	54,35	103,48	75,46	102,30
	Php	0,0	78,50	29,18	45,34	23,6
	TPP	65,24	132,61	132,42	120,17	125,34
	ATP	128,37	157,71	107,26	105,27	110,21
H. mexicana	C	6420,2870	9060,1660	6660,2530	6440,2530	5920,3040
	N	480,430	920,190	760,720	500,290	650,190
	CHl *a*	46,21	31,22	52,29	50,10	116,27
	Php	3,3	78,40	54,29	34,11	42,17
	TPP	49,20	109,37	107,25	84,10	159,22
	ATP	97,40	166,56	107,40	99,29	102,59
H. arenicola	C	4210,1830	7930,2130	4260,1090	3000,1140	
	N	460,210	1400,590	460,110	440,50	
	Chl *a*	31,13	16,6	30,12	31,10	
	Php	1,1	27,10	13,8	6,2	
	TPP	32,12	43,14	43,20	37,11	
	ATP	87,39	161,59	103,42	66,17	
M. ventricosa	C	2990,580	5920,1890	3320,1460		5210,1020
	N	220,70	400,170	330,90		240,110
	Chl *a*	13,4	29,6	18,3		19,3
	Php	0,0	0,0	7,3		6,4
	TPP	13,4	29,6	25,4		25,5
	ATP	39,6	102,41	39,13		54,12
P. grandis	C	2880,260	5550,370	2900,1560	2850,690	3080,710
	N	240,50	440,210	380,130	180,180	260,150
	Chl *a*	13,3	29,8	19,5	23,8	26,9
	Php	2,0	1,0	6,5	3,0	2,0
	TPP	14,4	30,8	25,4	26,6	28,9
	ATP	61,10	150,27	53,5	48,9	61,14

There was an increase in both C and N content between the sediment and the foregut which was significant (one tailed Student's t, $p < .05$ is used here and in subsequent statements, except where a two-tailed test is indicated) in all cases except the C analysis for *Holothuria mexicana*. This species was also the only one in which C did not decrease significantly between the fore- and hindgut (Table 1). The sediment-foregut and foregut-hindgut changes in *H. mexicana* were significant at $K < 10\%$ probability level. The commensurate decrease in N between fore- and hindgut was not significant in any species except *H. arenicola*. Carbon content of the faeces was not significantly different (two-tailed test) from the hindgut levels in any species, and showed no significant change in faeces retained for 24 h. Nitrogen decreased significantly (two-tailed test) in the faeces of *Isostichopus badionotus* and *Plagiobrissus grandis*, but showed no significant change in the retained faeces of any species.

In all species except *Holothuria arenicola*, the total plant pigment concentration was significantly higher in the foregut than in the available sediment, but no species showed significant changes through the gut. The sediment pigment was almost exclusively chlorophyll *a* at both sites, at levels similar to those in other reef sands (Sournia, 1976; Roman, pers. comm.). A large proportion of the chlorophyll *a* ingested by the holothuroids was converted to phaeophytin, presumably as a result of the acid pH level in their foreguts (Hammond, 1981). In the spatangoids, which have an alkaline foregut (Hammond, 1981), this conversion was not evident.

The ATP levels found in all samples are indicative of a very low recovery, as they cannot account for even the plant biomass indicated by the pigment analyses. Loss of ATP probably occurred in storage, since recovery of the spike added prior to extraction and assay procedures was greater than 80%, comparable to that in other studies (e.g. Bancroft et al., 1976; Yingst, 1978). However, the ATP data show the same trends exhibited by the C, N and pigment data. There was a significant increase in ATP content of the foregut over that of the sediment, and a significant decrease in ATP in the hindgut compared to the foregut, in all species except *Isostichopus badionotus*. The latter trend undoubtedly reflects the death of organisms, and does not necessarily imply assimilation.

The low meiofaunal counts recorded for these sediments (Table 2) are typical of reef sands (Thomassin et al., 1976; Renaud-Mornant and Helléouet, 1977). As in most meiofaunal communities, from both temperate and tropical waters, nematodes and harpacticoid copepods dominated (McIntyre, 1969; Thomassin et al., 1976; Gerlach, 1978). Foraminiferans, which contribute much less to Caribbean reef sediments than to those of Indo-Pacific reefs (Orme, 1977), nevertheless may have been under-counted, due to the difficulty in distinguishing skeletons from live or recently dead animals. Table 2 shows there were fewer meiofauna in the foregut than in the sediment, and that numbers remained approximately the same through the gut, although the majority of animals were killed.

Table 2. Average number of meiofaunal individuals (all species) per g dry weight of sediment in samples from adjacent sediments (S), foreguts (FG) and hindguts (HG) of 3 holothuroid and 2 echinoid species. Percentage of dead animals, rounded to the nearest 10%, shown in brackets. Contribution of nematodes and copepods, as a percentage of all meiofauna recorded for each sample

Species	Category	S	FG	HG
I. badionotus	Total	11.1 (0)	6.2 (60)	6.0 (90)
	Nem %	80	69	83
	Cop %	11	11	15
H. mexicana	Total	12.6 (0)	4.2 (70)	5.1 (90)
	Nem %	61	65	81
	Cop %	19	21	12
H. arenicola	Total	6.4 (0)	2.9 (70)	3.4 (90)
	Nem %	57	81	76
	Cop %	24	12	12
M. ventricosa	Total	4.9 (0)	1.9 (40)	1.9 (80)
	Nem %	33	61	54
	Cop %	52	32	24
P. grandis	Total	5.1 (0)	2.2 (30)	1.9 (80)
	Nem %	65	55	57
	Cop %	16	19	24

The concentrations of organic carbon and nitrogen, total plant prigment and ATP in different size fractions of sediment from both sites are shown in Table 3. There was no consistent pattern of distribution of the food resource according to grain size. The total concentrations, corrected for the relative proportions of each grain-size fraction, indicate that some loss occurred during sieving. For example, for organic carbon the levels were about 65% of those in sediment samples taken adjacent to the test animals. In the absence of evidence to the contrary it is assumed that this loss occurred at an approximately equal rate in all size fractions. Therefore, in the subsequent discussion nutrient material is considered to be similarly distributed in all size fractions. Hammond (1981) cited additional evidence to support this assumption: in coral reef sands, the typically inverse, linear relationship between grain size and grain surface area (which in turn is directly related to available food occurring as a surface film on grains) does not hold, due to variation in shape of biogenic carbonate sand grains.

Table 3. Mean and standard deviation of organic carbon, organic nitrogen, total plant pigment, in μg g^{-1} dry weight of sediment, and ATP, in ng g^{-1} dry weight of sediment, in each size fraction of sediments from Sites 1 and 2. Three replicates were used in all cases except for TPP analysis, where 2 were used; where dashes occur only a single sample was analysed

Site	Assay	Phi Interval					
		−1 >2 mm	0 2–1 mm	1 1– .5 mm	2 .5– .25 mm	3 .25– .125 mm	4 .125– .063 mm
1	C	4600	3400	4900	3700	1400	1200
		1800	600	2000	1000	1000	–
	N	570	570	430	630	300	500
		300	290	60	120	100	–
	TPP	76	86	85	56	40	55
		7	16	6	1	17	–
	ATP	280	180	210	260	140	60
		110	30	20	100	90	70
2	C	2400	2100	3100	2000	1500	2300
		800	1000	1200	500	800	–
	N	270	400	270	400	430	300
		60	200	150	100	120	140
	TPP	15	16	12	16	17	21
		6	7	2	9	11	4
	ATP	90	90	80	80	90	260
		30	30	40	40	40	210

DISCUSSION

Table 4 demonstrates that, for all species and for all parameters assayed, there was on average a two-fold increase between the available sediments and the foreguts, which was statistically significant in almost all instances. Webb et al. (1977), Massin (1980) and Moriarty (1982) have also reported increases in organic C, by factors ranging from 1.2 to 3, in sediments ingested by holothuroids. Similar increases in organic N were noted by Tanaka (1958), Webb et al. (1977) and Moriarty (1982). Measurements of other parameters, such as proteins, carbohydrates and lipids (Massin, 1980) produced comparable trends.

The enhanced levels of these materials in the foreguts of deposit feeders is not likely to be due to the presence of digestive secretions. These might contribute carbon, nitrogen and even ATP (from amoebocytes; Trefz, 1958), but not chlorophyll *a* and phaeopigments. In all species, the moisture content of the foregut sediments increased by only a few percent, indicating that the volume of digestive juices was relatively small. Massin (1980) has shown that the digestive secretions of holothuroids are low in organic carbon.

The increases are also not likely to result from inappropriate sampling of the available sediments, as care was taken to closely mimic the feeding procedures of all species.

It is concluded, therefore, that the higher levels in the foregut result from active selection of nutrient-rich grains, or of particulate organic matter. The prevailing view that chemical discrimination by holothuroids is poor, and that particles are 'simply shovelled' into the

Table 4. Summary of differences in concentrations of organic carbon, nitrogen, total plant pigment and ATP between sediment and foregut samples, and of organic carbon and nitrogen between fore- and hindgut samples, in 3 holothuroid and 2 echinoid species. Each difference is expressed as a percentage. Abbreviations as in Table 1

Species	Assay	Foregut/ Sediment	Hindgut/ Foregut
I. badionotus	C	199	56
	N	203	82
	TPP	203	
	ATP	123	
H. mexicana	C	141	74
	N	192	83
	TPP	222	
	ATP	171	
H. arenicola	C	141	54
	N	304	33
	TPP	134	
	ATP	185	
M. ventricosa	C	198	56
	N	182	83
	TPP	226	
	ATP	261	
P. grandis	C	193	52
	N	183	86
	TPP	208	
	ATP	246	

mouth (e.g. Hyman, 1955; Trefz, 1958; Bakus, 1973) can no longer be sustained. The phenomenon of chemical discrimination, implied by observation by Massin and Jangoux (1976) that *Holothuria tubulosa* selectively ingested sand with an organic coating while rejecting clean sand, now appears to be established in holothuroids from a variety of habitats, including the deep sea (Khripounoff and Sibuet, 1980).

There are no previous data available to confirm the findings of the present study that carbon, nitrogen, plant pigments and ATP are more concentrated in the foregut contents of spatangoid echinoids. However, Buchanan (1966) reported anecdotal evidence of selection of nutrient-rich grains by *Echinocardium cordatum*.

The existence of this form of selective feeding, in the absence of any ability in all 5 species to discriminate between grains on the basis of size (Hammond, 1982b), is initially difficult to reconcile. Resolution of this apparent paradox will require elucidation of the processes of grain collection and gustatory discrimination, both of which are poorly known. However, there need be no *a priori* assumption, based on studies of other deposit-feeding taxa living in finer sediments, that grain-size selection and preference for nutrient-rich grains should be coupled, through the exponential increase in available food with decreasing particle size (e.g. Newell, 1965; Hylleberg and Gallucci, 1975). In these moderately sorted, medium sands, there is no evidence that nutritive value varies in a consistent manner among the different size fractions (Table 3), so that the adaptive advantage of selecting nutrient-rich grains may be gained independently of an ability to feed on a particular grain size. Probably, discrimination on the basis of food quality occurs, not at the level of individual grains, but by selectively placing the feeding podia on small patches with enhanced nutritional status. The carbon, nitrogen and pigment determinations (Tabel 1) provide much evidence for small-scale environmental patchiness which would facilitate such behaviour.

The independence of these 2 types of feeding selectivity highlights inadequacies in classifications of the trophic structure of the benthos (e.g. Walker and Bambach, 1974), since organisms may be selective or non-selective feeders depending on which parameters of the food resource are measured.

The changes in total organic carbon content between fore- and hindguts (Table 4) give an overall measure of assimilation. Conventionally, foregut-faeces differences are used, but in the present study, the age of the holothuroid faeces was not exactly known, and changes in the organic content after defecation were postulated, though not subsequently demonstrated. Webb et al. (1977) and Moriarty (1982) recognized that dissolution of $CaCO_3$ in the gut would result in lower estimates of assimilation efficiency using foregut-hindgut comparisons, but Hammond (1981) showed that dissolution was not significant. Assimilation averaged 39% for the 3 holothuroid species, very close to many values previously reported (Bakus, 1973; Webb et al., 1977). Lower average values have been reported by Yingst (1976), Hauksson (1979), Massin (1980), Moriarty (1982) and Khripounoff and Sibuet (1980), in the last instance for a deep-sea species. Assimilation of carbon by the spatangoids was slightly more efficient (46%). The statistical non-significance of the changes in N concentration through the gut parallels the findings of Webb et al. (1977), who attributed the result to sediment heterogeneity. The high variability of nitrogen levels at each site (Table 1) suggests that a similar explanation may be appropriate. The mobility of all species except *Holothuria arenicola* (Hammond, 1982a) would serve to amplify the effects of environmental heterogeneity. In studies of other holothuroids, Trefz (1956, in Bakus, 1973) and Tanaka (1958) reported N assimilation to be approximately 50%, while Moriarty (1982) gave a figure of 40% and Khripounoff and Sibuet (1980) recorded only 22% efficiency. The last 2 studies indicated that nitrogen is assimilated more efficiently than carbon.

Yingst (1976) proposed that meiofauna might be 'very important' as a food source for deposit feeders. Using average values of organic carbon content of meiofaunal individuals (Sikora et al., 1977; Gerlach, 1978; Yingst, 1978), it can be shown that the meiofauna contributed little more than 1% of the sedimentary cabon pool in the present study. Moriarty (1982) reported a similar value. Moreover, the failure of the deposit feeders to ingest the meiofauna in the numbers available (see also Renaud-Mornant and Helléouet, 1977; Hansen, 1978) and the apparent lack of assimilation in the gut both emphasize the insignificance of meiofauna as a carbon source. However, the death of the majority of ingested meiofauna during passage through the gut belies the importance attached by numerous workers to the occurrence of live meiofauna in the fresh faeces of holothuroids (e.g. Bertram, 1936; Trefz, 1958; Thorson, 1966). It suggests that at sufficiently high densities, holothuroids or spatangoids may effectively regulate the structure of meiofaunal communities (cf. Bell and Coull, 1978; Woodin, 1978).

The phytobenthos, principally diatoms, was a major component of the sedimentary organic carbon pool. Using a carbon: chlorophyll *a* ratio of 40 (Ferguson and Murdoch, 1975; Banse, 1977; De Jonge, 1980), the phytobenthos contributed about 40%, of the carbon in the surface sediments at Site 1 and about 18% of that in the subsurface sediments at Site 2. Higher ratios of ca. 61 ± 9 (95% C.I.) were found in some years in

mixed populations of benthic diatoms from a temperate estuary (De Jonge, 1980), but such values, even if applicable to the present study, do not appreciably alter the conclusions derived below. It is clear that much of the phytobenthos is not killed, digested or assimilated, since chlorophyll *a* levels in the fore- and hindgut were high, averaging 50 % and 86 % of the total plant pigment for the holothuriods and spatangoids, respectively (Table 1). The higher levels of chlorophyll *a* in the hindgut than in the foregut of the holothurians were not statistically significant except for *Holothuria arenicola,* and are interpreted as indicating an heterogeneous distribution in the available sediment (cf. Bunt et al., 1972). Where the chlorophyll *a* was converted to phaeophytin, the phytobenthos may well have been digested and assimilated, but this cannot be certain.

The inefficacy of the ATP extractions precludes any calculation of microfloral (bacterial, etc.) contribution to the sedimentary carbon pool. In other studies of reef sediments (Sorokin, 1978; de Vaugelas, 1981; Moriarty, 1982) bacteria constituted about 5 % of the carbon pool. Direct counting methods (Battey, pers. comm.) reveal lower bacterial populations in Discovery Bay sediments than reported by other authors using the same method (Sorokin, 1978) which suggests a similarly low contribution by bacteria to the sedimentary carbon pool. Notwithstanding evidence that bacteria are more strongly selected during feeding by holothuroids than are other organic components (Moriarty, 1982), and are also more efficiently assimilated (Yingst, 1976; Moriarty, 1982), they cannot be considered a major food source. Moriarty (1982) suggested that they may account for about 10 % of the carbon requirements of *Holothuria atra.*

It therefore appears likely that detrital (non-living) material is the major source of nutrition for the deposit-feeding holothuroids and spatangoids. The data on meiofauna and phytobenthos, and the inferred biomass of bacteria, imply that more than half of the sedimentary carbon pool is represented by detritus. Other workers have found the detritus to comprise 60 to 90 % of the total organic carbon in reef sediments (de Vaugelas, 1981; Moriarty, 1982). Even assuming complete assimilation of bacteria, meiofauna and killed phytobenthos, at least fifty percent of the ration of assimilated carbon must derive from detritus.

This finding contrasts with the results from studies of other deposit feeders, in which their failure to assimilate detritus has been attributed to the inability of their digestive enzymes to hydrolyze the structural carbohydrates which comprise the bulk of detritus in other ecosystems (Fenchel and Blackburn, 1979). It may signify a different enzyme complement in the holothuroids and spatangoids which permits them to degrade structural carbohydrates, but evidence for this, (e.g. cellulase activity) is equivocal (Coe, 1962; Yokoe and Yasumasu, 1964; Fish, 1967). Alternatively, it may indicate qualitative differences between detritus in coral reefs and that in other shallow coastal ecosystems. There is evidence that a significant amount of detritus entering coral reef lagoons occurs as organic aggregations derived from fore-reef and reef-flat communities (Marshall, 1965; Johannes, 1967; Qasim and Sankaranarayanan, 1970). These amorphous aggregations, consisting largely of coral mucus, flocculated organic substances and adherent particulate matter (Johannes, 1967; Coles and Strathman, 1973) may comprise half of the particulate organic carbon found in lagoonal waters; the remainder appears to be principally of algal origin (Marshall et al., 1975). The material is a source of energy for many organisms (Coles and Strathman, 1973; Gerber and Marshall, 1974; Benson and Muscatine, 1974), so may be readily assimilable by deposit feeders. The high carbon: nitrogen ratio of other detritus, which partially limits its utilization by depositfeeders (Briggs et al., 1979), is not characteristic of reef detritus, which may have C : N ratios much less than 10 : 1 (Coles and Strathmann, 1973; Gerber and Marshall, 1974). This removes one potential constraint on its utility as a food resource.

Sloan and von Bodungen (1980) proposed that *Isostichopus badionotus* faeces represent a potentially enriched food source for holothuroids. The faeces of *Holothuria tubulosa* also consistently had a higher organic content than the surrounding sediment (Massin, 1980). In the present study, the organic carbon content of the faeces was very similar to that of the sediment for all species, and there was no evidence of enrichment 24 h after defecation, even for N, which is generally indicative of microbial colonization. Holothuroid faecal masses do not retain their integrity much longer than 24 h, so it apears that the phenomenon of 'gardening' of the faeces (Hylleberg, 1975) is not significant for these deposit feeders.

Acknowledgements. This work was supported by a Jamaica Award under the Commonwealth Scholarship and Fellowship Plan. Dennis Taylor generously provided the facilities for most of the analyses at the Rosenstiel School of Marine and Atmospheric Sciences, University of Miami. Additional facilities were provided by the Discovery Bay Marine Laboratory and the Zoology Department, University of the West Indies. Assistance and advice from Keith Cooksey, Chris Miller, John Paul and Mike Roman were greatly appreciated. Jimmy Sammy performed most of the meiofauna counts. The manuscript was critically reviewed by Alastair Birtles, Russell Reichelt and Jeremy Woodley.

LITERATURE CITED

Ahearn, G. A., Townsley, S. J. (1975). Integumentary amino acid transport and metabolism in the apodous sea cucumber, *Chiridota rigida*. J. exp. Biol. 62: 733–752

Anderson, J. M. (1966). Aspects of nutritional physiology. In: Boolootian, R. A. (ed.) Physiology of Echinodermata. Interscience Publishers, New York, pp. 329–357

Bakus, G. J. (1973). The biology and ecology of tropical holothurians. In: Jones, O. A., Endean, R. (eds.) Biology and geology of coral reefs, Vol. 2. Academic Press, New York, pp. 325–367

Bancroft, K., Paul, E. A., Wiebe, W. J. (1976). The extraction and measurement of adenosine triphosphate from marine sediments. Limnol. Oceanogr. 21: 473–479

Banse, K. (1977). Determining the carbon-to-chlororphyll ratio of natural phytoplankton. Mar. Biol. 41: 199–212

Bell, S. S., Coull, B. C. (1978). Field evidence that shrimp predation regulates meiofauna. Oecologia 35: 141–148

Benson, A. A., Muscatine, L. (1974). Wax in coral mucus: energy transfer from corals to reef fishes. Limnol. Oceanogr. 19: 810–814

Bertram, G. C. L. (1936). Some aspects of the breakdown of coral at Ghardaqa, Red Sea. Proc. Zool. Soc. Lond. (1936): 1011–1026

Briggs, K. B., Tenore, K. R., Hanson, R. B. (1979). The role of microfauna in detrital utilization by the polychaete, *Nereis succinea* (Frey & Leuckhart). J. exp. mar. Biol. Ecol. 36: 225–234

Buchanan, J. B. (1966). The biology of *Echinocardium cordatum* (Echinodermata: Spatangoida) from different habitats. J. mar. biol. Ass. U. K. 46: 97–114

Bunt, J. S., Lee, C. C., Lee, E. (1972). Primary productivity and related data from tropical and subtropical marine sediments. Mar. Biol. 16: 28–36

Chesher, R. H. (1969). Contributions to the biology of *Meoma ventricosa* (Echinoidea: Spatangoida). Bull. mar. Sci. 19: 72–110

Choe, S. (1962). Biology of the Japanese common sea cucumber, *Stichopus japonicus* Selenka. Ph. D. thesis, Fisheries College, Pusan National University

Coles, S. L., Strathmann, R. (1973). Observations on coral mucus 'flocs' and their potential trophic significance. Limnol. Oceanogr. 18: 673–678

Cooksey, K. E. (1978). ATP determinations in the MAFLA Tract, 1977–1978. Third Quart. Report, Contract BLM AA550 CT7 34, University of Miami

Crozier, W. J. (1915). The sensory reactions of *Holothuria surinamensis* Ludwig. Zool. Jb. 35: 233–297

Culmo, R. F. (1974). A review of the performance of the Perkin-Elmer Model 240 in the elemental analysis of chemical compounds. ELAS-1, Perkin-Elmer Corporation

Fenchel, T., Blackburn, T. H. (1979). Bacteria and mineral recycling, Academic Press, London

Ferguson, J. C. (1973). Feeding, digestion and nutrition in Echinodermata. In: Florkin, M., Scheer, B. T (eds.) Chemical zoology, Vol. 3. Academic Press, New York, pp. 71–100

Ferguson, R. L., Murdoch, M. B. (1975). Microbial ATP and organic carbon in sediments of the Newport River estuary, North Carolina. In: Cronin, G. E. (ed.) Estuarine research, Vol. 1. Academic Press, New York, pp. 229–250

Fish, J. D. (1967). The digestive system of the holothurian, *Cucumaria elongata*. II. Distribution of the digestive enzymes. Biol. Bull. mar. biol. Lab., Woods Hole 132: 354–361

Gerber, R. P., Marshall, N. (1974). Ingestion of detritus by the lagoon pelagic community at Enewetak Atoll. Limnol. Oceanogr 19: 815–824

Gerlach, S. A. (1978). Food-chain relationships in subtidal silty sand marine sediments, and the role of meiofauna in stimulating bacterial productivity. Oecologia 33: 55–69

Hammond, L. S. (1981). An analysis of grain-size modification in biogenic carbonate sediments by deposit-feeding holothurians and echinoids (Echinodermata). Limnol. Oceanogr. 26: 898–906

Hammond, L. S. (1982a). Patterns of feeding and activity in deposit-feeding holothurians and echinoids (Echinodermata) from a shallow back-reef lagoon, Discovery Bay, Jamaica. Bull. mar. Sci. 32: 549–571

Hammond, L. S. (1982b). Analysis of grain-size selection by deposit-feeding holothurians and echinoids (Echinodermata) from a shallow reef lagoon, Discovery Bay, Jamaica. Mar. Ecol. Prog. Ser. 8: 25–36

Hansen, M. D. (1978). Nahrung und Freßverhalten bei Sedimentfressern dargestellt am Beispiel von Sipunculiden und Holothurien. Helgoländer. wiss. Meeresunters. 31: 191–221

Hauksson, E. (1979). Feeding biology of *Stichopus tremulus*, a deposit-feeding holothurian. Sarsia 64: 155–160

Hylleberg, J. (1975). Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. Ophelia 14: 113–137

Hylleberg, J., Gallucci, V. F. (1975). Selectivity in feeding by the deposit-feeding bivalve *Macoma nasuta*. Mar. Biol. 32: 167–178

Hyman, L. H. (1955). The invertebrates, Vol. IV, The Echinodermata, McGraw-Hill, New York

Jangoux, M., Lawrence, J. M. (eds.) (1982). Echinoderm nutrition, Balkema, Rotterdam

Johannes, R. E. (1967). Ecology of organic aggregates in the vicinity of a coral reef. Limnol. Oceanogr. 12: 189–195

Karl, D. M., LaRock, P. A. (1975). Adenosine triphosphate measurements in soil and marine sediments. J. Fish. Res. Bd Can. 32: 599–607

Kepkay, F. E., Novitsky, J. A. (1980). Microbial control of organic carbon in marine sediments: coupled chemoautotrophy and heterotrophy. Mar. Biol. 55: 261–266

Khripounoff, A., Sibuet, M. (1980). La nutrition d'echinodermes abyssaux. I. Alimentation des holothuries. Mar. Biol. 60: 17–26

McIntyre, A. D. (1969). Ecology of marine meiobenthos. Biol. Rev. 44: 245–290

Marshall, N. (1965). Observations on organic aggregates in the vicinity of coral reefs. Mar. Biol. 2: 50–53

Marshall, N., Durbin, A. G., Gerber, R., Telek, G. (1975). Observations on particulate and dissolved organic matter in coral reef areas. Int. Revue ges. Hydrobiol. 60: 335–345

Massin, C. (1980). The sediment ingested by *Holothuria tubulosa* Gmelin (Hothuroidea: Echinodermata). In: Jangoux, M. (ed.) Echinoderms present and past, Proceedings of the second European Colloquium on Echinoderms, Brussels. A. A. Balkema, Rotterdam, pp. 205–208

Massin, C., Jangoux, M. (1976). Observations ecologiques sur *Holothuria tubulosa, H. poli* et *H. forskali* (Echinodermata – Holothuroidea) et comportement alimentaire de *H. tubulosa*. Cah. Biol. mar. 17: 45–60

Moriarty, D. (1982). Feeding of *Holothuria atra* and *Stichopus chloronotus* on bacteria, organic carbon and organic nitrogen in sediments of the Great Barrier Reef. Aust. J. mar. Freshwat. Res. 33: 255–264

Newell, R. C. (1965). The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. Proc. Zool. Soc. Lond. 144: 25–45

Orme, G. R. (1977). Aspects of sedimentation in the coral reef environment. In: Jones, O. A., Endean, R. (eds.) Biology and geology of coral reefs, Vol. 2. Academic Press, New York, pp. 129–182

Pequignat, E. (1972). Some new data on skin-digestion and absorption in urchins and sea stars (*Asterias* and *Henricia*). Mar. Biol. 12: 28–41

Powell, E. N. (1977). Particle size selection and sediment reworking in a funnel feeder, *Leptosynapta tenuis* (Holothuroidea, Synaptidae). Int. Revue ges. Hydrobiol. 62: 385–408

Qasim, S. Z., Sankaranarayanan, V. N. (1970). Production of particulate organic matter by the reef on Kavaratti Atoll (Laccadives). Limnol. Oceanogr. 15: 574–578

Renaud-Mornant, J., Helléouet, M.-N. (1977). Rapport micromeiobenthos et *Halodeima atra* (Holothuroidea) dans un lagon Polynesien (Tiahura, Moorea, Ile de la Societe). Bull. Mus. Hist. nat., Paris, Serie 3, No. 474: 853–865

Sikora, J. P., Sikora, W. B., Erkenbrecher, C. W., Coull, B. C. (1977). Significance of ATP, carbon and caloric content of meiobenthic nemtodes in partitioning benthic biomass. Mar. Biol. 44: 7–14

Sloan, N. A., von Bodungen, B. (1980). The distribution and feeding of the sea cucumber *Isostichopus badionotus* in relation to shelter and certain sediment criteria of the Bermuda platform. Mar. Ecol. Prog. Ser. 2: 257–264

Sorokin, Yu. I. (1972). Bacteria as food for coral reef fauna. Okeanologiya 12: 195–204

Sorokin, Yu. I. (1973). Microbiological aspects of the productivity of coral reefs. In: Jones, O. A., Endean, R. (eds.) Biology and geology of coral reefs, Vol. 2. Academic Press, New York, pp. 17–45

Sorokin, Yu. I. (1978). Microbial production in the coral-reef community. Arch. Hydrobiol. 83: 281–323

Sournia, A. (1976). Primary production of sands in the lagoon of an atoll, and the role of foraminiferal symbionts. Mar. Biol. 37: 29–32

Strickland, J. D. H., Parsons, T. R. (1972). A practical handbook of seawater analysis (2nd ed.), Bull. Fish. Res. Bd Can. 167: 1–310

Tanaka, Y. (1958). Feeding and digestive processes of *Stichopus japonicus*. Bull. Fac. Fish. Hokkaido Univ. 9: 14–28

Telek, G., Marshall, N. (1974). Using a CHN analyser to reduce carbonate interference in particulate organic carbon analyses. Mar Biol. 24: 219–221

Thomassin, B. A., Vivier, M.-H., Vitiello, P. (1976). Distribution de la meiofauna et de la macrofaune des sables coralliens de la retenue d'eau epirecifale du Grand Recif de Tulear (Madagascar). J. exp. mar. Biol. Ecol. 22: 31–53

Thorson, G. (1966). Some factors influencing the recruitment and establishment of marine benthic communities. Neth. J. Sea Res. 3: 267–293

Tietjen, J. H. (1968). Chlorophyll and pheo-pigments in estuarine sediments. Limnol. Oceanogr. 13: 189–192

Trefz, S. M. (1958). The physiology of digestion of *Holothuria atra* Jager, with special reference to its role in the ecology of coral reefs. Ph. D. thesis, University of Hawaii

de Vaugelas, J. V. (1981). Distribution quantitative de la matiere organique total, vivante et detritique dans differents types de sediments coralliens de Polynesie francaise. C. r. hebd. Séanc. Acad. Sci. Paris, Serie 3, 292: 299–302

Walker, K. R., Bambach, R. K. (1975). Feeding by benthic invertebrates: classification and terminology for paleoecological analysis. Lethaia 7: 67–78

Webb, K. L., DuPaul, W. D., D'Elia, C. F. (1977). Biomass and nutrient flux measurements on *Holothuria atra* populations at Enewetak, Marshall Islands. Proc. 3rd. Int. Symp. Coral Reefs 2: 409–416

Woodin, S. A. (1978). Refuges, disturbance, and community structure: a marine soft bottom example. Ecology 59: 274–284

Yingst, J. Y. (1976). The utilization of organic matter in shallow marine sediments by an epibenthic deposit-feeding holothurian. J. exp. mar. Biol. Ecol. 23: 55–69

Yingst, J. Y. (1978). Patterns of micro- and meiofaunal abundance in marine sediments, measured with the adenosine triphosphate assay. Mar. Biol. 47: 41–54

Yokoe, Y., Yasumasu, I. (1964). The distribution of cellulase in invertebrates. Comp. Biochem. Physiol. 13: 323–338

This paper was presented by Dr. J. Bunt; it was accepted for printing on October 14, 1982