

Deposit feeding by some deep-sea megabenthos from the Venezuela Basin: selective or non-selective

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ABSTRACT: Food sources and feeding selectivity of numerically dominant asteroids and holothurians collected with trawls from the Venezuela Basin, Caribbean Sea, were investigated by means of gut analysis. Particle-size distributions of gut contents of *Thoracaster cylindratus*, *Styracaster horridus*, *Psychropotes semperiana*, and *Pseudostichopus atlanticus* and of sediments were compared from 3 different sedimentary provinces in the Venezuela Basin (3,410–5,062 m depth). Megabenthic echinoderms (megabenthos) from the 2 shallower provinces had gut contents with particle-size distributions almost identical to that of the top 5 mm of sediment and conspicuously coarser than sediment below 5 mm depth. Gut contents of echinoderms from the deepest province had a higher percent of coarse and medium sand-size foraminiferan tests than that of surrounding sediment. Microscopic examination of the coarse fractions revealed intact pelagic foraminiferan tests in the guts of megabenthos collected from 5,000 m depth whereas pelagic foraminiferan tests from surrounding surface sediments were fragmented and eroded. The possibility of recently settled fecal pellets from the pelagic realm as a food source is suggested. These data suggest that some bulk deposit feeders skim the surface of the sea bottom feeding on the uppermost layer of sediment; thus, they selectively ingest the more nutritive, uppermost layer of sediment in the deep sea without modifying feeding behavior *per se*.

INTRODUCTION

Understanding of feeding behavior and food sources of deep-sea megabenthos is based on information inferred by sea-floor photographs, observations from manned submersibles, and studies of gut contents from animals collected from the sea floor (Sokolova, 1959; Schoener and Rowe, 1970; Heezen and Hollister, 1971; Carey, 1972; Pawson, 1976, 1982; Khripounoff and Sibuet, 1980; Hickman, 1981). Although the information suggests that deposit feeding predominates among deep-sea megabenthos, the record is not clear as to what feeding strategies and food resources might be used in this resource-poor realm.

Feeding selectivity, an aspect of deposit-feeding strategy that links feeding behavior to food source, has been investigated for several deep-sea megabenthic species. Some species selectively feed on specific sizes or types of particles; others are non-selective, feeding instead on bulk sediment. Such studies necessarily involved comparison of gut contents with sediment from where the animals were collected (Khripounoff

and Sibuet, 1980; Hickman, 1981; Shick et al., 1981). Although only limited inferences on selectivity are drawn from data of this type, almost insurmountable difficulties of live animal collection and experimentation at great depths make most other approaches infeasible.

The occurrence of 3 different sedimentary provinces in 1 zoogeographical area (i.e. the Venezuela Basin) created a natural setting for a unique investigation. The pelagic sedimentary province was characterized by a foraminifera ooze (64 to 76 % carbonate); the turbidite sedimentary province was below the lysocline and characterized by a carbonate-depleted pelagic layer overlying a turbidite deposit; the hemipelagic sedimentary province was characterized by a carbonate sediment (20 to 29 %) with a smaller accumulation of foraminiferan tests than the pelagic province (Briggs and Richardson, 1984). All 3 stations were low energy benthic boundary layer environments where hydrodynamic processes are not effective in transport of surface sediments (Richardson, 1983a). Uniformity of substrate within a sedimentary province,

combined with a diversity of natural particle sizes between sedimentary provinces, provided an opportunity to investigate *in situ* deposit-feeding selectivity in the same megabenthic species collected at all provinces.

Two species of asteroids and 2 species of holothurians were collected from every sedimentary province. In terms of both abundance and extent to which they rework sediment, asteroids and holothurians constitute a significant portion of deep-sea deposit-feeding megabenthos (Heezen and Hollister, 1971; Rowe, 1971, 1974; Haedrich et al., 1980; Carney and Carey, 1982).

Particle-size distributions of sediment from guts of megabenthic asteroids and holothurians were compared with particle-size distributions of undisturbed, finely-sectioned (with depth) sediment cores from the collection area. These data were used to determine whether the asteroids and holothurians from the Venezuela Basin feed selectively or non-selectively and at what depth they feed in the sediment.

MATERIALS AND METHODS

Sample collection. The asteroids *Thoracaster cylindricus* Sladen and *Styracaster horridus* Sladen, and the holothurians *Psychropotes semperiana* Theel and *Pseudostichopus atlanticus* Theel were numerically dominant among echinoderms collected in 23 benthic trawls at 3 sedimentary provinces in the Venezuela Basin, Caribbean Sea, during Cruise 1301-82 of USNS BARTLETT, 14 October-8 December 1981 (Fig. 1; Table 1). Distances over which the 41-foot (12.5 m) shrimp trawls (see Haedrich et al., 1980) were hauled averaged 11.0 km in Province 1, 15.6 km in Province 2,

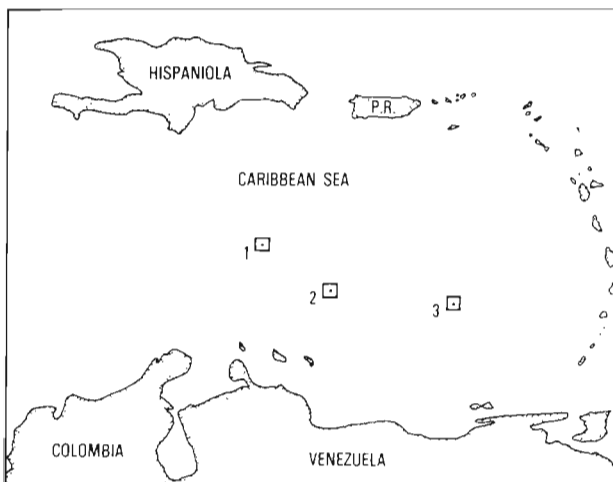


Fig. 1. Map of the eastern Caribbean Sea showing the 3 province locations

Table 1. Data characterizing the 3 provinces sampled in the Venezuela Basin. Organic carbon values represent the mean of 3 cores (with duplicates) at each province. Latitude and longitude define the approximate center of the sampling area

	PROVINCE 1	PROVINCE 2	PROVINCE 3
LATITUDE	15°08'N	13°45'N	13°30'N
LONGITUDE	69°12'W	67°45'W	64°45'W
DEPTH (M)	3935-4063	4949-5062	3410-3549
SEDIMENT TYPE	PELAGIC (foram ooze)	TURBIDITE (at 14 and 37 cm)	HEMIPELAGIC
ORGANIC CARBON (%)	0.33	0.80	0.59
NO OF TRAWLS	6	10	7
NO OF MEGAFUNA	1009	1529	1368
ECHINODERMS	315	454	768
DECAPODS	88	109	141
FISH	262	63	192

and 17.1 km in Province 3. Bottom collection distances were estimated from ship's speed and Benthos® time-depth recorder traces. Asteroids were preserved in 70 % ethanol and holothurians were preserved in 5 % formalin buffered with sodium borate. Buffered formalin was injected by syringe into the guts of holothurians. Table 2 presents the numbers collected per hour trawling for the echinoderms under investigation for each of the provinces.

Sediments from the same 3 provinces were collected with a 0.25-m² box corer (Hessler and Jumars, 1974). Nineteen box cores from Province 1, 20 box cores from Province 2 and 18 box cores from Province 3 were collected. Thirty-five box cores were subcored with short sections of 6.1 cm (inside diameter) piston core liner to determine sediment physical and acoustic properties (Briggs and Richardson, 1984); the remaining box cores were used for macrofauna analysis (Richardson, 1983b). The subcores were sealed at both ends, remaining undisturbed, upright and refrigerated during transportation and storage. Subcores for organic carbon analysis were collected and frozen, 1 from each of 3 box cores collected at each province.

Sediment analysis. Forty-seven asteroid and holothurian specimens were selected at random for gut analysis from 14 trawl catches representing 3 sediment provinces. The contents of cardiac stomachs of asteroids were removed by first cutting the organisms open along the ambulacral grooves, then scraping out the sediment and thoroughly rinsing the stomachs with distilled water. Intact guts of holothurians were removed, split open, and rinsed thoroughly with distilled water. When guts of holothurians contained copious quantities of sediment, material from the foregut and hindgut was divided for separate analysis. Sediment from 2 or 3 organisms of the same species and province were combined for analysis when the amount of material was very small.

Four subcores collected from 3 box cores in Pro-

Table 2. Catch rates (numbers h⁻¹ hauled \pm SE) of echinoderm species studied in the 3 provinces of the Venezuela Basin

Species	Province 1	Province 2	Province 3
<i>Thoracaster cylindratus</i>	4.36 \pm .70	.72 \pm .27	2.66 \pm .31
<i>Styracaster horridus</i>	1.50 \pm .30	.45 \pm .36	.34 \pm .10
<i>Psychropotes semperiana</i>	5.56 \pm 1.6	3.34 \pm .53	9.50 \pm 1.4
<i>Pseudostichopus atlanticus</i>	.10 \pm .10	1.96 \pm 1.9	.93 \pm .34

vince 1, 6 subcores collected from 5 box cores in Province 2, and 4 subcores collected from 3 box cores in Province 3 were used to determine particle-size distributions. Sediment from subcores was extruded and sectioned at 2 cm intervals after the overlying water was carefully siphoned off. Additional subcores (3 each from Provinces 1 and 2, and 2 from Province 3) were sectioned at 0.5 cm intervals down to a depth of 2 cm to determine the particle-size gradient at the sediment surface with greater resolution.

All gut-derived and core-derived sediments remained in distilled water for 3 to 4 d while material settled and preservatives from the gut-derived sediment were diluted by evaporation and decantation. After the samples had remained in a deflocculent solution (2.5 g l⁻¹ sodium hexametaphosphate) overnight, the samples were sieved gently to separate the coarse fraction (> 62 μ m, or 4 ϕ) from the fine fraction (< 62 μ m, or 4 ϕ). In this way, fragile foraminiferan tests were separated from the sediment sample before ultrasonic disaggregation. Sediment particle-size distribution was determined with an ATM Sonic Sifter for sand-sized particles and with a Micromeritics® Sedi-

graph Model 5000 and pipette method for silt- and clay-sized particles (Briggs and Richardson, 1984). This method was determined in preliminary analyses of foraminiferan ooze to be successful in avoiding destruction of the coarse fractions: successive treatments of a sediment sample did not significantly change mean grain size (ϕ) or particle-size distribution (histograms). All coarse fractions were retained for microscopic study.

Sediment organic carbon determinations were performed with a Perkin-Elmer Model 240 CHN Analyzer after treating the samples to remove calcium carbonate.

RESULTS

Many asteroids and holothurians had gut contents (wet weight) that weighed as much as the animal itself. Ingested prey were not observed in gut contents except for 2 mollusks collected in 2 specimens of *Thoracaster cylindratus*.

Sediments were quite uniform in particle-size distribution with depth within each province. Fig. 2 illus-

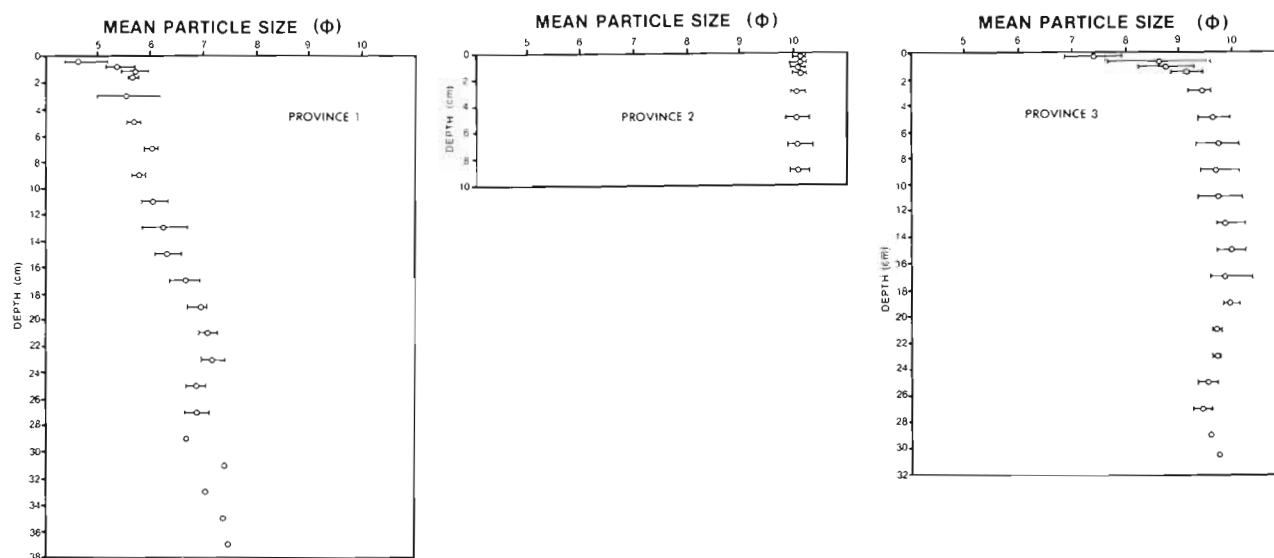


Fig. 2. Depth profiles of sediment-particle size in Provinces 1, 2 and 3 depicted as averages of the mean phi (ϕ) values at depth intervals sampled. Horizontal bars: ranges in values from the subcores

trates the relatively small ranges in mean particle size (mean ϕ) with depth for all subcores within each province. Particle size units (ϕ) are expressed on a logarithmic scale where particle diameter (mm) = $2^{-\phi}$. Particle-size distribution data beyond conventional feeding depths of asteroids and holothurians were included to reinforce the case for sediment homogeneity within a sedimentary province.

However, particle-size distributions of sediment were notably different between sedimentary provinces (Fig. 2 to 5). Province 1 had the coarsest sediment (smallest mean ϕ values) of the 3 provinces, reflecting the large number of sand-size carbonate tests of Foraminifera. Province 2 had the finest sediment (greatest mean ϕ values) of the 3 provinces, owing to the dearth of biogenic carbonate in the sediment. Province 3 was intermediate in mean particle size in comparison to the other provinces.

Sediments with large amounts of biogenic carbonate (Provinces 1 and 3) displayed generally decreasing particle sizes (increasing mean ϕ values) with increasing depth in the sediment. Moreover, the greatest change in mean particle size with depth occurred within the top 2 cm of sediment in these provinces. These data confirm the preservation of the thinly-stratified surface sediments in subcores needed to ascertain feeding selectivity. By contrast, Province 2 had a very fine-grained sediment that was virtually unchanged in its particle-size distribution down to a depth of 10 cm (Fig. 2). A turbidite deposit containing much coarser, terrigenous particles was found below 10 cm. Because the turbidite layer was undisturbed by bioturbation (Richardson, pers. comm.) and none of the

distinctively terrigenous material was found in the gut contents of the megafauna studied, data below 10 cm in Province 2 were omitted from consideration in this paper.

The Wilcoxon 2-sample test was used to determine within each province whether the sediment from tops of subcore samples and the sediment from guts of megabenthos had the same particle-size distribution (null hypothesis). The data were ranked according to mean particle size. Only in Province 2 was the null hypothesis rejected for all megabenthic specimens. Moreover, graphical comparisons between particle sizes of sediment from subcores and guts of megabenthos were as conclusive as statistical analysis (Fig. 3 to 5). Mean particle size (ϕ) of gut-derived sediments varied little for deposit feeders collected in the same province and was always coarser than mean particle size of subcore-derived sediment below 2 cm in the same province (Fig. 3). Although specimens from Provinces 1 and 3 did exhibit a predilection toward coarser sediments, only the specimens from Province 2 had gut contents that were notably coarser than the top 5 mm of sediment as determined by the analysis of thinly-sectioned tops of subcores.

Particle-size distributions of sediment from subcores and guts of megabenthos were separated onto size-class percentages of sand, silt and clay in Fig. 4. Comparisons between size-class percentages of sediments from tops of subcores and from guts of megabenthos (asteroids and holothurians combined) corroborated results from comparisons of mean particle sizes (Fig. 3). In Provinces 1 and 3 percentage sand in gut-derived sediment was the same as found in the top

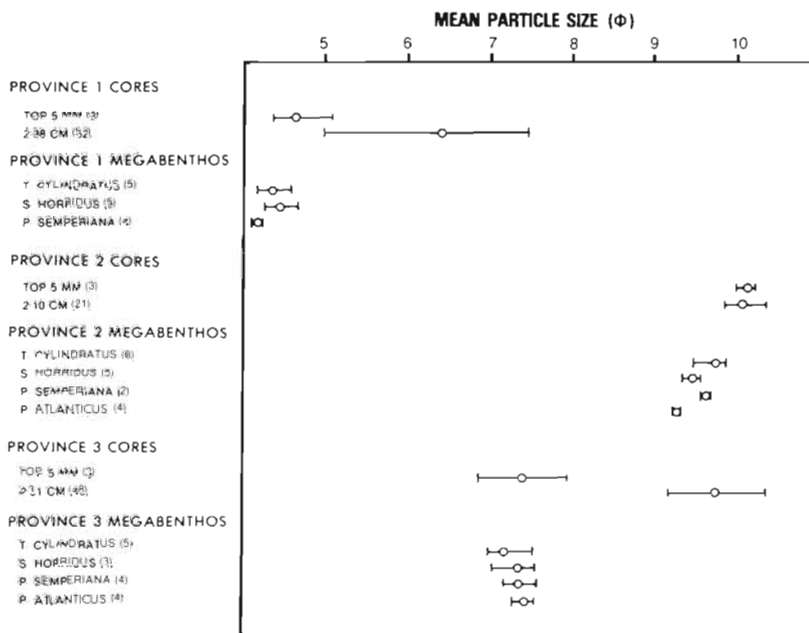


Fig. 3. Comparison of mean particle size in sediments from the top 5 mm of subcores, below 2 cm depth in subcores, and guts of megabenthos from Provinces 1, 2 and 3. Points: averages of mean ϕ values. Bars: ranges in values from all determinations. Numbers of samples listed in parentheses

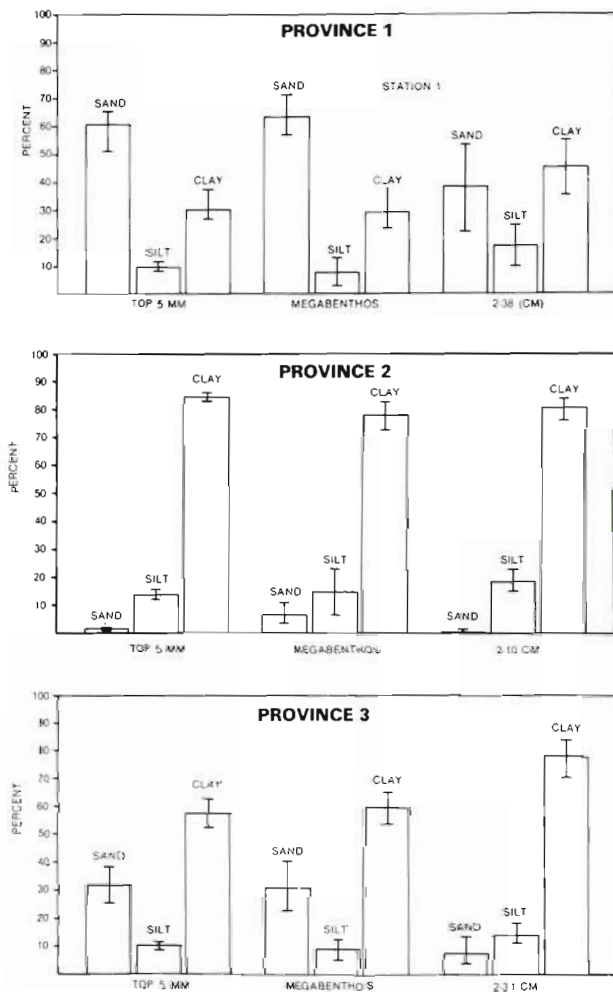


Fig. 4. Percentages of sand-silt-clay in the top 5 mm of sediment in subcores, gut sediment from the megabenthos, and sediment below 2 cm in depth from Provinces 1, 2 and 3. Vertical bars: ranges in values from all determinations

5 mm of sediment and notably higher than the remainder of the core (Fig. 4). There was no notable difference in percentages of sand, silt, and clay between surface sediment and deeper sediments in Province 2. Sand-sized particles, however, were definitely more numerous in gut-derived sediment in that province.

Particle-size frequency histograms of representative sediment samples from top 5 mm of subcores, guts of megabenthos, and 2 to 4 cm-deep sections of subcores separated particle-size distributions into individual ϕ (ϕ) intervals for more intricate comparisons. Frequency histograms of sediment particle size show the higher percent sand-sized particles in ingested sediments and surface sediments were concentrated in 0 to 1 and 1 to 2 ϕ (ϕ) intervals in Provinces 1 and 3 (Fig. 5). Moreover, ratios of coarse sand-sized (0 to 1 ϕ) particles to medium sand-sized (1 to 2 ϕ) particles were approximately the same in surface sediment and gut-

derived sediment from Provinces 1 and 3. Sediment in Province 2 was composed predominantly of clay-sized particles ($< 4 \mu\text{m}$). All guts of megabenthos from Province 2, however, contained pelagic foraminiferan tests ranging from coarse sand-size to very fine sand-size which did not occur as frequently in surface or deeper sediments (Fig. 5).

Microscopic examination of the sand-sized fractions from all provinces revealed the coarse sand-sized particles to be chiefly the tests of the planktonic foraminifera *Orbulina universa*, *Globorotalia* spp., and *Globigerinoides* spp. Other items making up the sand fractions included radiolarian tests, sponge spicules, echinoderm spines, and various arenaceous benthic Foraminifera. The relative proportions of individual sand-sized fraction components varied in relation to one another only with regard to benthic Foraminifera. A larger proportion of benthic foraminiferans was found in the surface-collected and gut-derived sediment in Provinces 2 and 3. The benthic foraminiferans, however, were conspicuously less evident at depths in the sediment below 5 mm.

In Province 2, in addition to more sand-sized material in the gut-derived sediment than in the sediment cores, the gut contained some intact planktonic foraminiferan tests. Sediment cores, in contrast, contained only extremely fragmented and dissolved tests. Because both gut-derived and core-derived sediments received the same care in the sieving process, this difference in the condition of the foraminiferan tests was probably not an artifact.

Sediment mean particle size was slightly coarser in the foregut than the hindgut (9.24 ϕ vs. 9.26 ϕ ; 9.18 ϕ vs. 9.24 ϕ) in 2 specimens of *Pseudostichopus atlanticus* collected in Province 2. This difference, however, is within the range of variability for the sediments and may not represent a physical modification of sediment by digestive processes.

The amount of organic carbon in the sediment in all 3 provinces was low (Table 1). The highest values (0.80 %) were found in Province 2; the lowest values (0.33 %) were found in Province 1. As with the sediment particle size and other physical and acoustic measurements, there was little variability between values of organic carbon within each sedimentary province.

DISCUSSION

The analyses of gut contents from *Thoracaster cylindricus*, *Styracaster horridus*, *Psychropotes semperiana*, and *Pseudostichopus atlanticus* can only provoke speculation as to what actual food sources are being exploited by deposit feeders in the Venezuela Basin. Food sources available to deposit-feeding megaben-

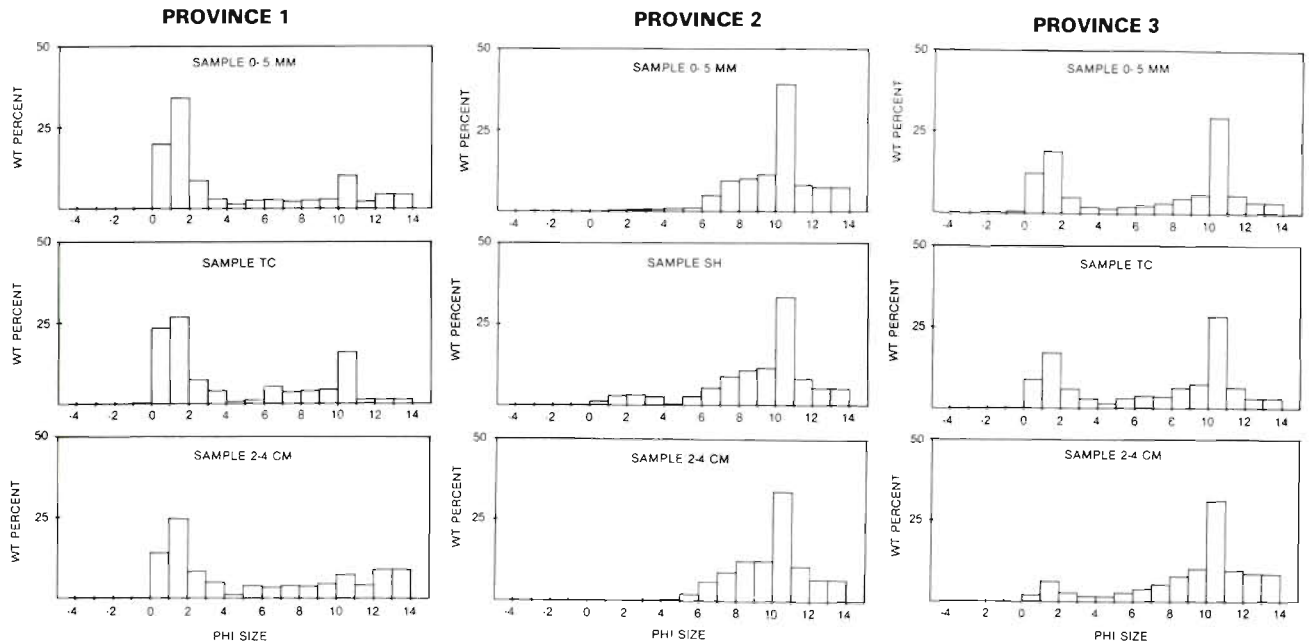


Fig. 5. Representative examples of particle-size frequency histograms of sediments from the top 5 mm of subcores, guts of megabenthos (SH = *Styrcaster horridus*; TC = *Thoracaster cylindratu*), and the 2 to 4 cm section of subcores collected in Provinces 1, 2 and 3

thos in the deep sea include organic detritus, bacteria, and macrofauna (Sanders and Hessler, 1969; Dayton and Hessler, 1972; Sokolova, 1972; Jannasch and Wirsén, 1977; Morita, 1979; Deming and Colwell, 1982). The recovery of 1 gastropod and 1 bivalve from the guts of 47 megabenthic specimens supports the idea of living carbon only complementing non-living carbon in the diet of the deposit feeders. In addition to these hard-bodied species, some soft-bodied invertebrates may have been ingested. These specimens would be indiscernible in the gut contents after sediment analysis. Indeed, the presence of sediment in the gut does not exclude the possibility of foraging for living prey (Ankar and Sigvaldadottir, 1981). Potential prey organisms (macro-, meio- and microfauna) attain their maximum abundance in surface sediments at all 3 provinces (Richardson, 1983b; Woods, 1983; Harvey et al., 1984). Organic carbon values similarly reach a maximum in surface sediments (Briggs and Richardson, 1984). However, based on estimates of carbon content of shallow water nematodes by Sikora et al. (1977), deep-sea meiofauna contribute at most only about 1% of surface sediment organic carbon in any province. These data, together with findings from Khripounoff and Sibuet (1980) and Hammond (1983) showing a lack of preference for meiofauna by holothurians, suggest that they are not selectively feeding on this component of the infauna. Although ingested meiofauna would represent a small portion of the carbon, the living organic matter nevertheless

might be of greater nutritional value than non-living organic matter. Certainly, benthic foraminiferans should also not be dismissed from consideration as a food source (Buzas, 1978). Bacteria and other microfauna may contribute a significant portion of available organic matter in the deep sea (Morita, 1979; Burnett, 1981).

The gut analyses provide more evidence on feeding behavior than on food resources. Graphical comparisons of particle-size distributions of sediment from the top 5 mm of subcores and guts of megabenthos demonstrate that the dominant echinoderms from the Venezuela Basin feed non-selectively on surface sediment in Provinces 1 and 3. Outwardly, the evidence does not support non-selective feeding in the same megabenthos species in Province 2. The data suggest that asteroids and holothurians in Province 2 may be selectively feeding on sand-sized particles in the sediment. Some shallow-water and deep-sea species of asteroids and holothurians possess the capability to discriminate between particles on the basis of size (Rhoads and Young, 1971; Pawson, 1976; Hauksson, 1979; Khripounoff and Sibuet, 1980; Sloan, 1980).

Some evidence suggests that asteroids and holothurians may discriminate on the basis of nutritive quality instead of size (Pawson, 1976; Hauksson, 1979; Khripounoff and Sibuet, 1980; Hammond, 1983). Sources, and hence quality, of detrital food reaching the sea floor is presumably the same in all provinces in the basin. In fact, carbon/nitrogen ratios of sediment

organic matter are similar for surface sediments throughout the Venezuela Basin (Briggs, unpubl.). The amount of organic carbon in Province 2 was determined to be the highest of the 3 provinces. Quantitative differences in organic matter may have induced the megabenthos to modify their feeding strategy in Province 2, but not enough is known about energy requirements of deep-sea deposit feeders to pursue this possibility further. Nevertheless, it is not clear what nutritive advantage exists in selectively ingesting sand-size foraminiferan tests.

Concentration of planktonic foraminiferan tests in the guts of megabenthos from Province 2 may not be evidence of selective deposit-feeding. Particle sorting in the gut of a deposit feeder can result in higher concentrations of indigestible particles in the gut contents than in sediment immediately ingested (Self and Jumars, 1978). Conceivably, particle sorting in the gut could produce the retention of carbonate tests within the guts of holothurians. Yet, it is not clear why such a difference between environmental and gut sediments should occur only in Province 2 and why there is no evidence of sorting from separate analysis of foreguts and hindguts in holothurians from Province 2.

An intriguing possibility for the source of the sand-size particles in the guts of megabenthos at Province 2 is recently deposited fecal pellets from the overlying water column. The nutritional value of fecal pellets to deposit feeders in general has been discussed (Newell, 1965; Frankenberg and Smith, 1967; Johannes and Satomi, 1967) and these pellets are available as a source of food for deep-sea deposit feeders (Wiebe et al., 1976; Honjo, 1978). The amount of organic matter in fecal pellets is generally higher than in the surrounding sediment, thereby encouraging some deposit feeders to feed by skimming fecal pellets off the surface of the sediment (Hylleberg and Gallucci, 1975; Hauksson, 1979). Honjo et al. (1982) demonstrated that carbonate tests are a major constituent of settling fecal pellets in the deep sea. In this way, foraminiferan tests may arrive intact on the sea floor without having suffered dissolution from deep oceanic water that is undersaturated with respect to calcium carbonate. In fact, the presence of well-preserved foraminiferan tests was observed in gut sediment of megabenthos collected at Province 2 which is the deepest province sampled and below the lysocline. If the deposit feeders are skimming large areas of the surface of the sea bottom and non-selectively feeding on the uppermost layer of sediment, then they are also selectively ingesting recently deposited fecal pellets. That a non-selective, surface deposit feeder would appear to behave as a selective deposit feeder without modifying feeding behavior *per se*, makes this possibility an intriguing one. Conceivably, the megabenthos at all 3 provinces

are feeding on recently settled fecal material. However, this feeding strategy would be obvious only at water depths where settling pelagic carbonate rapidly dissolves. Accumulations of foraminiferan tests at shallower provinces preclude the use of carbonate tests, in effect, as a natural tracer of a food chain pathway. Sea-floor photographs of the provinces corroborate evidence of surface feeding from gut analysis (Young and Jahn, 1983). Minimal sediment disturbance in the paths immediately behind specimens of *Psychropotes* implies that this species, at least, is a surface feeder.

Comparisons between particle-size distributions of environmental and gut sediments strongly suggest that dominant asteroids and holothurians in the Venezuela Basin are non-selective, bulk deposit feeders. The presence of coarser sediment in the guts of megabenthos need not indicate that the same species of deposit feeders presented with different substrates would modify feeding behavior. Non-selective feeding on surface sediments selects, in effect, for recently deposited fecal material (and potentially for living prey) concentrated in the surface sediment.

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