Feeding and Metabolism

Between-Community Contrasts in Successful Polychaete Feeding Strategies

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ABSTRACT

Benthic marine polychaetes are herein classified on the basis of several feeding strategy parameters, notably degree of motility and feeding stratum (suspension, surface deposit, subsurface deposit). Along a depth transect from the Southern California coast (2.4 m) to the central North Pacific (5600 m), the relative abundance of sessile individuals increases ($P < 0.00001$) with depth to at least 400 m and then decreases at greater bathyal and abyssal depths. The increase is postulated to be a response to increasing sediment stability, while the subsequent decrease may be attributable to the relation between optimal foraging area and food availability. Variation in sediment mobility and food input might similarly account for many other biogeographic patterns.

> *For thou dost fear the soft and tender fork of a poor worm.*
>
> -- Shakespeare
> *Measure for Measure*
> Act III, Scene 1

The proportional contributions of various taxa to benthic standing stocks change markedly from shallow water to the abyss (e.g., Sanders et al. 1965; Menzies et al. 1973). Although decreasing food supply (implied by decreasing standing stock and decreasing community respiration rate) with increasing depth and increasing distance from shore has been implicated in this change (e.g., Belyaev et al. 1973; Rex 1973), the characteristics which determine successful species at particular depths remain largely unidentified. As Hessler and Jumars

(1974) noted, most of the taxa are largely deposit feeding at all the depths considered, "so the cause of the shift must be at a more subtle level." Several observations suggest what this more subtle level might be. Hessler and Jumars (1974) noted that the vast majority of polychaete individuals in the extremely food-poor abyssal benthos of the central North Pacific are creeping or burrowing deposit feeders. At the other end of the depth spectrum, along exposed coasts, sessile species fare poorly on soft substrates owing to sediment instability (e.g., Purdy 1964; Swedmark 1964). The dearth of sessile polychaetes in the physically stable North Pacific abyss, however, must have a different explanation. To aid in formulating some cogent hypotheses regarding these observations, we attempted to assess changes in feeding strategy (sensu Schoener 1971) along a gradient in depth.

The available data are inadequate to parameterize most of the components of foraging strategy, but the Polychaeta provide some hope of a consistent classification dealing with some aspects of feeding patterns. In particular, classes of motility and feeding modes may be distinguished. We confine our present consideration strictly to the marine soft-bottom (sand-silt-clay) habitat, where Polychaeta are typically numerically dominant among macrofaunal taxa at all depths, usually constituting from 50 to 80 percent of the total macrofaunal numbers. Polychaeta are Precambrian in origin (Glaessner and Daily 1959), and their major radiations have taken place some considerable time in the past (Fauchald 1974). We therefore hope that a view of the benthic world through polychaete feeding strategies will reveal a steady state--that the absence of a major feeding type from any extensive area is probably not a function of limited dispersal time.

Our work was supported by NSF grant GA42754. We must also express thanks for the late Dr. Olga Hartman's identifications of the polychaetes in most of the samples. Our hypotheses are guided by one of her favorite sayings, "The only way to avoid mistakes is to do nothing." Some mistakes were avoided, however, through thoughtful reviews by K. Banse, B. C. Coull, J. T. Enright, R. Feller, R. R. Hessler, and M. L. Jones. Contribution No. 925 from the Department of Oceanography, University of Washington, Seattle, Washington 98195.

METHODS AND MATERIALS

We first attempted to classify all benthic, soft-substrate polychaetes on the basis of as many feeding-related parameters as consistently possible. The predominantly morphological data at hand were inadequate to deal with two groups, carnivores and the family Sphaerodoridae. The former category displays a range of behavioral complexity (e.g., Ockelmann and Vahl 1970) which cannot be readily deduced from morphological features, and the latter group's source(s) of nutrition remains unknown. Sphaerodorids typically have a strongly papillated body surface and no apparent gut contents, a condition which is suggestive of carnivory (Hunt 1925) or assimilation of dissolved organics (Stephens 1972) but which gives little firm grounds for dealing with the family under our approach. In the remaining polychaetes, we deal only with adults. This disclaimer is necessary because larvae of detritivores may be carnivorous (e.g., Kühl 1974).

Among the remaining polychaetes, three mobility categories can be recognized: sessile, discretely motile, and motile. We use these terms to refer specifically to feeding strategies. "Sessile" implies that members show no evidence of post-settlement movement away from one feeding location. "Discretely motile" indicates that individuals must be stationary or very slowly moving for efficient operation of their primary feeding mode. The term is used here to imply that the motion is likely to be a discrete or recognizable event, separated from other such events by periods of apparent sessility. This concept corresponds in some respects to Remane's (1940) "semi-sessile" grouping. Finally, by "motile" we mean that the major feeding mode does not require any "setting up" period, and that movement from place to place is relatively frequent, if not continuous.

Similarly, three feeding strata can be recognized. Species which feed on suspended matter may be called "filter feeders." Groups feeding specifically on deposits at the sediment-water interface may be called "surface deposit feeders," and polychaetes feedon buried sediments may be named "burrowers." The latter category might more accurately be termed subsurface deposit feeders, but doing so would interfere with our scheme of abbreviations in tables and figures. In addition to motility classes and feeding strata, the structures which are used in feeding can be recognized. For example, it is relatively easy to note whether an animal feeds with tentacles or jaws.

Space restrictions make it impossible to document fully our reasons for each classification. However, Table 1 gives a complete listing of the results of our literature search and our functional morphological inferences (Jumars and Fauchald, in preparation). We stress the provisional nature of this scheme and our willingness to relocate taxa on the basis of further evidence. Figures 1-3 illustrate the intended differences between categories, but some subjectivity is inevitable. For example, Dragoli's (1960, 1961) observation that *Melinna palmata* (Ampharetidae) may leave its tube under the stress of hydrogen sulfide poisoning does not, in our opinion, compromise our consideration of *Melinna* as a sessile group, but we recognize that alternative interpretations are possible.

Three groups of polychaetes complicate our classification somewhat. *Phyllochaetopterus* (Chaetopteridae) retains the morphological capability to both "surface deposit feed" (with palps) and to "filter feed" (by pumping), accounting for the complex abbreviation F-SST-P. We were unable to assign the Onuphidae (excluding *Hyalinoecia* and

Table 1. Feeding strategy classification of benthic marine polychaetes, excluding predominantly carnivorous species and the family Sphaerodoridae

FST - Filtering, Sessile, Tentaculate
  Sabellariidae
  Sabellinae
  Serpulidae
  Spirorbidae

FSP - Filtering, Sessile, Pumping
  Chaetopteridae (except *Phyllochaetopterus*)

FDT - Filtering, Discretely motile, Tentaculate
  Fabriciinae
  Owenia

FDP - Filtering, Discretely motile, Pumping
  Arenicolidae

FDJ-P - Filtering, Discretely motile, Jawed and Pumping
  Neanthes diversicolor
  Nereis zonata
  Platynereis
  Rhamphobrachium

F-SST-P - Filtering and Surface deposit feeding, Sessile, Tentaculate and Pumping
  Phyllochaetopterus

SST - Surface deposit feeding, Sessile, Tentaculate
  Ampharetidae
  Boccardia
  Dodecaceria
  Polydora
  Pygospio
  Terebellidae (with exceptions below)
  Tharyx (some species only)
  Trichobranchidae

SS-DJ - Surface deposit feeding, Sessile or Discretely motile, Jawed
  Onuphidae (except *Hyalinoecia* and *Onuphis conchylega*)

SDT - Surface deposit feeding, Discretely motile, Tentaculate
  Acrocirridae (with exceptions below)
  Apistobranchidae
  Artacaminae
  Cirratulidae (except some *Tharyx*)
  Flabelligeridae
  Longosomidae
  Magelonidae
  Myriowenia
  Nicolea
  Polycirrinae
  Sabellongidae
  Spionidae (with exceptions above)
  Trochochaetidae

SMJ - Surface deposit feeding, Motile, Jawed
  Dorvilleidae (except *Meiodorvillea*)
  Eunicidae
  Hesionidae (some without jaws)
  Hyalinoecia
  Nereidae (with exceptions above)
  Onuphis conchylega

BSE - Burrowing, Sessile, Eversible proboscis
  Fauveliopsis glabra
  Maldanidae
  Myriochele

BMJ - Burrowing, Motile, Jawed
  Lumbrineridae
  Meiodorvillea
  Nephtys incisa
  Nephtys picta

BMX - Burrowing, Motile, various other modes (X)
  Aphroditidae
  Bogueidae
  Capitellidae
  Cossuridae
  Fauveliopsis (except *F. glabra*)
  Flabelligella (except palpate species)
  Lacydoniidae
  Opheliidae
  Orbiniidae
  Paraonidae
  Pectinariidae
  Scalibregmidae
  Sternaspidae

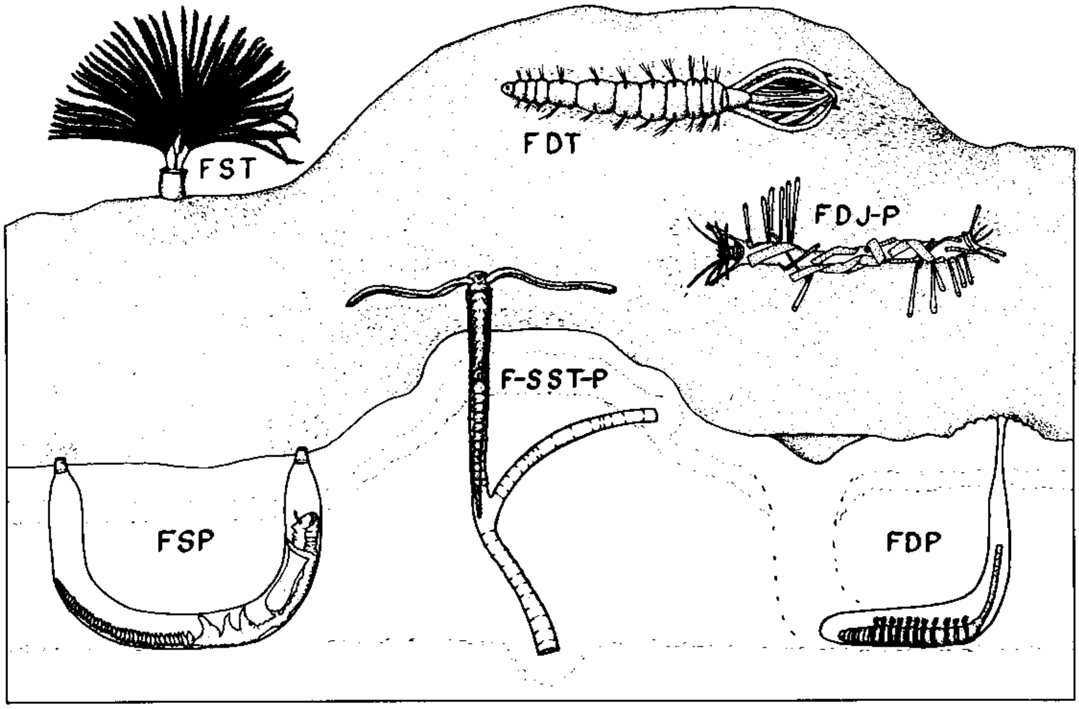

Fig. 1. Examples of filtering strategies (see Table 1). FST: Sabellinae; FDT: Fabriciinae; FDJ-P: *Platynereis* (Nereidae); FSP: *Chaetopterus* (Chaetopteridae); F-SST-P: *Phyllochaetopterus* (Chaetopteridae); FDP: *Arenicola* (Arenicolidae).

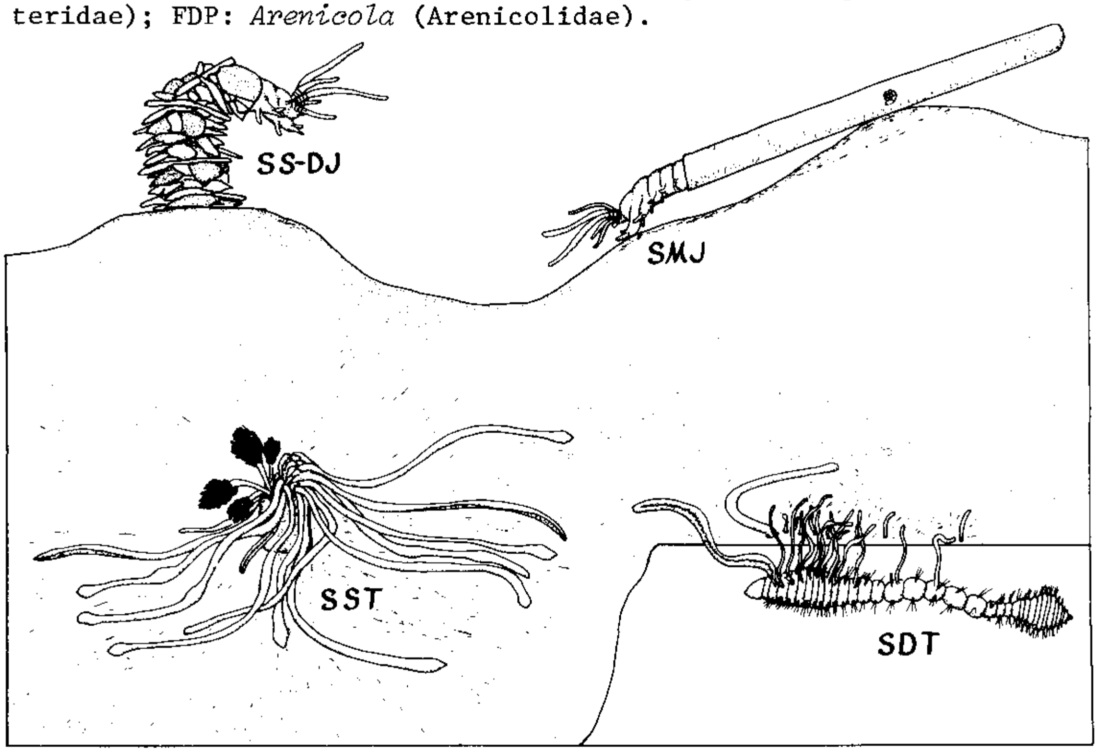

Fig. 2. Examples of surface deposit feeding strategies (see Table 1). SS-DJ: *Diopatra* (Onuphidae); SMJ: *Hyalinoecia* (Onuphidae); SST: *Pista* (Terebellidae); SDT: *Tharyx* (Cirratulidae).

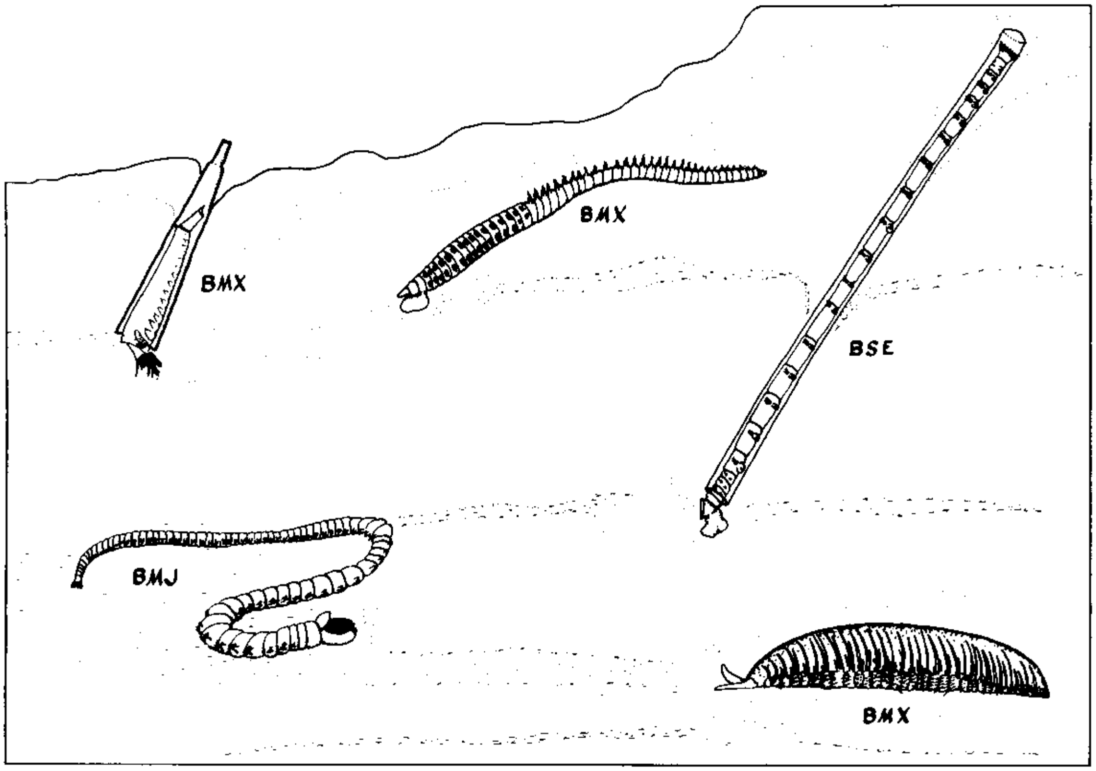

Fig. 3. Examples of burrowing strategies (see Table 1). BMX, upper left: *Pectinaria* (Pectinariidae); BMX, upper middle: Orbiniidae; BSE: Maldanidae; BMJ: Lumbrineridae, jaws everted; BMX, lower right: Aphroditidae.

Onuphis conchylega) with any degree of confidence to either the sessile or discretely motile category, producing the abbreviation SS-DJ. The compound abbreviation FD-JP refers to those nereids which have been observed to filter feed by pumping water through a mucus net. In subsequent analyses, we divided individuals falling into these categories equally between the classes they straddle. For example, in considering feeding strata, if four *Phyllochaetopterus* were sampled, two would be assigned as filter feeders and two, as surface deposit feeders. Without added information, this procedure was the least biased we could devise for dealing with these borderline or compromise cases. In all other instances where the literature gave no information or conflicting information, we were able to make a firm (not necessarily correct) decision to assign taxa to a single category.

We used the multinomial distribution for an analysis of the relative degree of success of the resulting categories. The symbol p_i represents the observed proportion of individuals belonging to the category i, and π_i is used for the corresponding theoretical population parameter (just as $\bar{x}_i$ and μ_i might, respectively, be used for a set of observed or sample, and theoretical or population, means). Proportions sometimes find disfavor because a change in any one p_i produces a complementary change in all other p_j (where $i \neq j$). Snee (1974), however, circumvented some of these objections in an attractive graphical approach. He detailed a principal components procedure to be used when more than three proportions are considered simultaneously, but we limited ourselves to three proportions and a triangular plot, to which our tripartite classifications are suited. Note in Figure 4 that the categories responsible for some changes may be easily identified. Geologists will recognize this format in their familiar sand-silt-clay diagram, and geneticists may recognize it as a convenient means of displaying relative homozygote-heterozygote frequencies (e.g., Schaffer and Mettler 1970). Methods of establishing confidence regions for π_i about the observed proportion p_i were also reviewed by Snee (1974).

We wished to restrict classification errors due to unfamiliarity with the local fauna to a minimum and to have a large body of data from which to draw. The California State Water Quality Control Board (Allan Hancock Foundation, University of Southern California, 1965) has published such data from benthic samples taken along the entire Southern California coast. Hereafter we refer to these samples as belonging to the "state survey." We eliminated those stations not completely sorted and identified (by Dr. Olga Hartman) from consideration, leaving 316 samples ranging in water depth from 2.4 to 397 m. To reduce this number to a manageable size for desk calculator manipulation, with relatively little loss of generality, we stratified the depth range of the 316 samples into ten equal logarithmic intervals and selected three stations at random from each of these intervals. We used a logarithmic stratification because most features we could conceive to exert effects on feeding

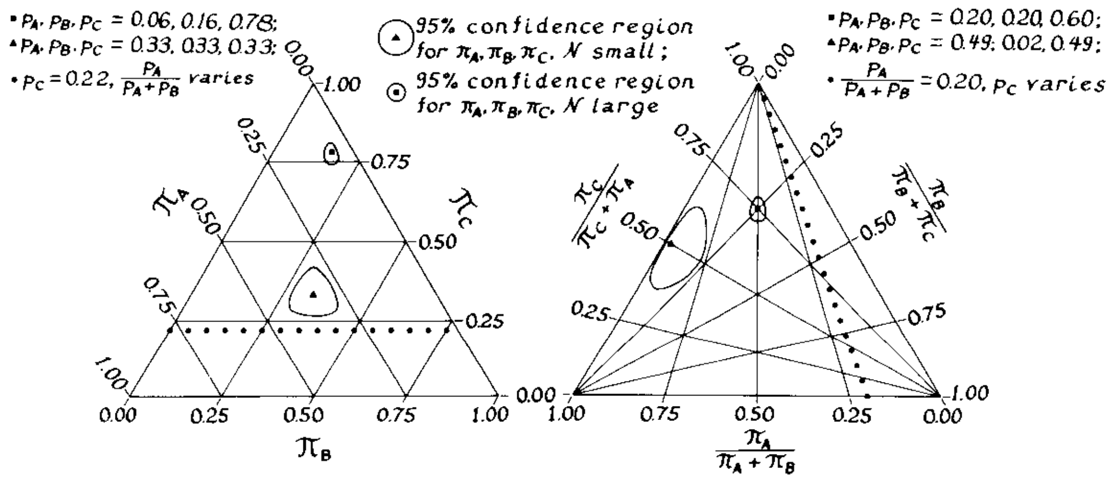

Fig. 4. Two interpretations of triangular charts. Left chart: isolines show constant proportions of each of A, B, and C; right chart: isolines show constant ratios of A, B, and C to each other, in pairs as indicated. Relative utilities of the two interpretations are determined by the patterns of variation observed. Compare with Figures 5 and 6.

strategies vary exponentially with depth (viz. Rowe et al. 1974). A closer spacing (on a linear scale) is thus warranted in shallower water, where a greater rate of change is expected. In subsequent analyses of the state survey material, we are thus dealing with a total of 30 samples unless otherwise stated.

Excluding carnivores and Sphaerodoridae, we then classified the polychaete faunas of each sample according to the scheme of Table 1. Also classified in this manner were polychaetes from the Santa Catalina Basin (five 0.25-m^2 box cores at approximately 1130-m depth), from the San Diego Trough (five 0.25-m^2 box cores at approximately 1230-m depth), and from the central North Pacific (twelve 0.25-m^2 box cores at approximately 5600 m). The bathyal samples came from studies of species' dispersion patterns in the Southern California Continental Borderland (Jumars 1974, 1975a, b), and the abyssal cores were part of a program of quantitative community analysis (Hessler and Jumars 1974). For our preliminary discussion of depth-correlated variation, only the three feeding strata and the three motility classes are considered in detail.

RESULTS

Results of calculating p_i for the strata and the motility classes are presented separately for the state survey (Fig. 5) and for the deep-sea samples (Fig. 6). Confidence regions were drawn in the latter case because sufficient data exist to establish that the animal dispersion patterns do not grossly violate the assumption of random sampling from a multinomial distribution (see Johnson and Kotz 1969). Species' dispersion patterns over small areas in these

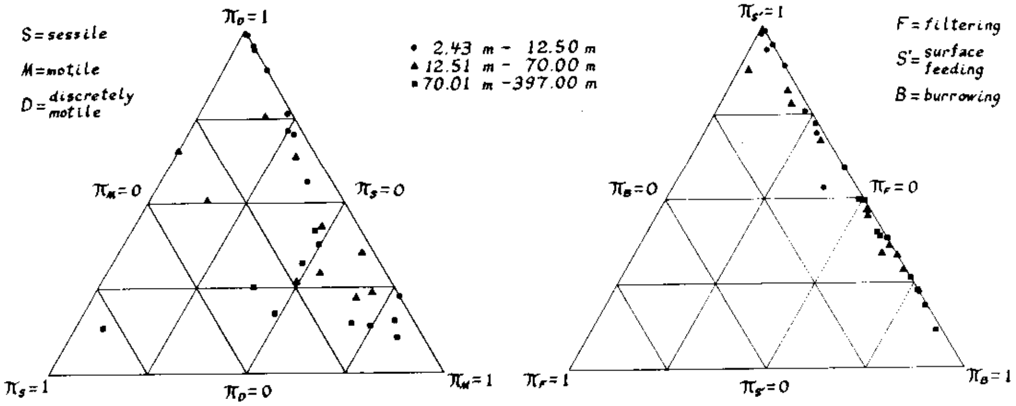

Fig. 5. Triangular chart presentation of feeding strategy variation with depth for state survey samples. Only the values $\pi = 0$ (sides of triangle) and $\pi = 1$ (vertices of triangle) are labeled, but isolines correspond to those of Figure 4 (left).

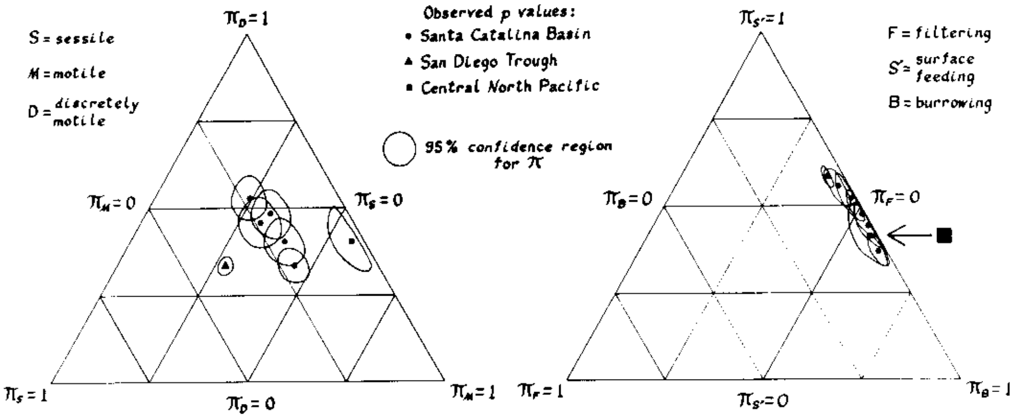

Fig. 6. Triangular chart presentation of feeding strategy variation by location for the deep-sea samples. Only the values $\pi = 0$ (sides of triangle) and $\pi = 1$ (vertices of triangle) are labeled, but isolines correspond to those of Figure 4 (left).

deep-sea regions are not markedly patchy (Hessler and Jumars 1974; Jumars 1974, 1975b). For the San Diego Trough and the central North Pacific, the between-sample results of the classifications are homogeneous enough to permit grouping of all cores, as shown in Figure 6. In the Santa Catalina Basin cores, however, heterogeneity (non-overlap of some pairs of 95 percent confidence regions for π_i) was observed, so that confidence regions for the contents of each of the cores are figured. As Snee (1974) pointed out, this plot is a graphical analogue of the heterogeneity chi-square procedure.

The trends seen in Figure 5 are then analyzed with the nonparametric rank-difference correlation statistic, selected because it is insensitive to the obvious nonlinearities of the figure (Tate and Clelland 1957). If some particular trend were of *a priori* interest, it would be unwise to engage in multiple testing but, in order to facilitate hypothesis formulation, all the possible correlations with depth suggested by Figure 4 are assessed. The data upon which Figure 5 is based show a trend of increasing proportion of motile species with depth, followed, at greater depths, by a decreasing proportion. Because this relationship is not monotonic, the rank-difference correlation coefficient of depth with the proportion of motile individuals underestimates its strength (Tate and Clelland 1957). The probabilities assigned in Table 2 do not reflect this problem or the degree of multiple testing involved and should be interpreted accordingly.

Even after giving appropriate weight to these problems, however, interpretation is not safe. The state survey samples were taken with an orange peel grab (those samples from 10-m depth or greater) or a van Veen grab (the shallower stations). Such grab samplers cannot be expected to penetrate to equal depths in the entire range of sediment types encountered. Specifically, they tend to take a deeper "bite" in softer sediments. One might expect, therefore, a larger

Table 2. Rank-difference correlation coefficients (r) of sample depth with the indicated covariables. Covariable subscripts correspond to the legend of Figure 5, and r^2 gives the approximate portion of variability in one variable "explained" by covariation in the other. P is the probability of obtaining the observed coefficient by chance when the variables are in fact independent (N = 30). See also Figure 4

Motility Analysis				Feeding Stratum Analysis			
Covariable	r	r^2	P	Covariable	r	r^2	P
P_S	0.77	0.59	<0.0001	P_F	-0.22	0.05	>0.20
P_D	-0.78	0.61	<0.0001	$P_S{}'$	-0.61	0.37	<0.001
P_M	0.48	0.23	<0.01	P_B	0.59	0.35	≃0.001
$\frac{P_S}{P_S + P_M}$	0.50	0.25	<0.01	$\frac{P_F}{P_F + P_B}$	-0.37	0.14	<0.05
$\frac{P_D}{P_D + P_S}$	-0.86	0.75	<0.00001	$\frac{P_S{}'}{P_S{}' + P_F}$	0.06	0.00	>0.70
$\frac{P_M}{P_M + P_D}$	0.61	0.38	<0.001	$\frac{P_B}{P_B + P_S{}'}$	0.59	0.35	≃0.001

proportion of burrowers in volumetrically larger samples. For the 20 orange peel grab samples in which a sample volume was recorded, our suspicions were, unfortunately, confirmed. The correlation of water depth with sample volume (r=0.42, one-tailed $P < 0.05$) was of the same sign and magnitude as the correlation of depth with the proportion of burrowers (r=0.39, $P < 0.05$). Any possible real trend of increasing porportion of burrowers with increasing water depth was therefore confounded with this apparent sampling bias, and further, the same bias would be expected to affect the proportion of motile individuals because most burrowers were motile in all the samples. Furthermore, grab samplers generally do not enclose the same area for their full depth of bite. This area generally decreases with depth in the sediment (Holme and McIntyre 1971). The proportion of burrowers is thus likely to be an underestimate at all water depths, but, a more serious underestimate at shallower stations. For these reasons, we concentrate on one aspect of the analysis which is not severely affected by these biases, namely the numerical ratio of sessile to discretely motile individuals. Some confounding is still possible because the maldanids are not thereby excluded. We believe their exclusion would be unrealistically conservative, although the ratio of sessile to discretely motile individuals would still correlate very strongly with depth (r=0.69, $P \simeq 0.0002$), even with all burrowers excluded.

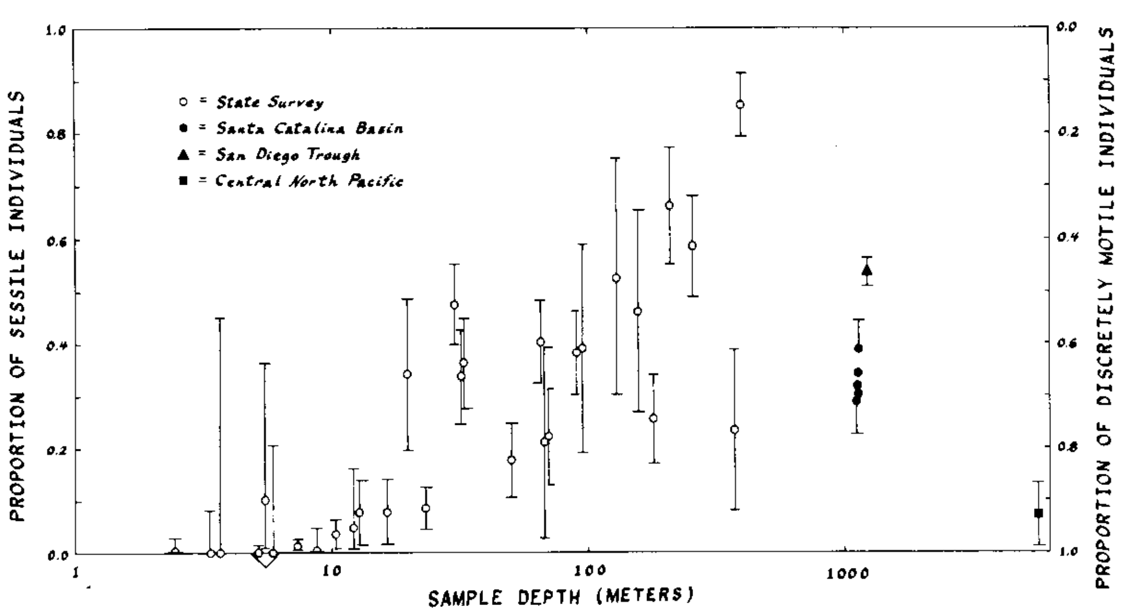

Fig. 7. The ratio of sessile individuals to discretely motile individuals versus sample depths (logarithmic scale). Bars show 95% confidence intervals for the ratio (binomial distribution model). The triangle under the abscissa indicates that the three bracketed samples all fell at the same depth.

Figure 7 combines the data on the ratio of sessile to discretely motile individuals from Figures 5 and 6. The data need not be recalculated, but can be generated graphically by projecting a vector from the vertex, $P_M=1$, through the point of interest onto the axis joining $P_S=1$ and $P_D=1$ to obtain the desired ratio. From the values so obtained, it is obvious that the strong positive correlation between water depth and the proportion of sessile individuals (Table 2) does not extend into the abyss. Figure 7 suggests instead that a maximum in the proportion of sessile individuals might occur between 400 and 1000 m. The 95% confidence limits for the proportions are shown, and, by the above arguments, these limits are probably fairly accurate for the deep-sea samples. For the state survey stations, on the other hand, these error-bars probably represent minimum estimates because dispersion patterns in shallow water tend to show aggregation. They are useful, however, in giving a rough indication of the relative sample sizes involved, smaller error-bars representing larger samples. Most of the following discussion is based on Figure 7.

DISCUSSION

When cross-classified according to our analyses, the classification itself is of some ecological interest. As noted in Table 3, several combinations have not been observed among the world's

Table 3. A cross-classification of the feeding strategies from Table 1. Φ: combination not yet documented; i: apparently incompatible combination; ε: energetically unlikely; ?: problem in the classification. (See text.)

		Sessile	Discretely Motile	Motile
Filter Feeding	Tentaculate	FST	FDT	Φ_i
	Pumping, Jawed	Φ_ε	FDJ-P	Φ_i
	Pumping, no jaws	FSP	FDP	Φ_i
		F-SST-P		
Surface Deposit Feeding	Tentaculate	SST	SDT	Φ_i
	Jawed	SS-DJ		SMJ
Burrowing	Jawed	Φ_ε	Φ_ε	BMJ
	Eversible proboscis or other means (X)	BSE	?	BMX

non-carnivorous, non-sphaerodorid, marine benthic polychaetes. These "null sets" (Φ) seem to fall into one of two categories: functionally incompatible combinations, and energetically unlikely strategies. In the former category, movement on or in the sediment appears incompatible with simultaneous (though not subsequent) filter feeding or with feeding by means of ciliated tentacles. In the latter category, there probably have not been enough large food particles suspended in the oceans to have made the evolution of a jawed, sessile filter feeder a likely event.

One apparent problem with our classification is indicated by the question mark in the table. No species are classified as discretely motile burrowers. Some of the central North Pacific and bathyal maldanids have fragile tubes which are long and geometrically complex. Some maldanids might conceivably add to a tube as they work laterally through the sediments, but, lacking firmer evidence, we currently leave all maldanids in the sessile category.

The magnitudes of the correlation coefficients nevertheless leave no doubt ($P \simeq 0.9998$, even with all burrowers excluded) that we have found a strong pattern which demands explanation. However, there is no limit to the number of possible causes which might be invoked to explain the pattern in Figure 7. Rather than compiling long lists of alternative hypotheses which would be useful in some ways (Platt 1964), we deal with a few that appear to make the most intuitive sense. Our major effort in this discussion will be to devise suitable tests of these few.

First and foremost, the observed correlations of the numerical ratio of sessile to discretely motile individuals probably have little to do with depth per se. We propose that the two depth covariables of primary importance in producing the correlations are (1) sediment stability, and (2) flux of organic matter. On an open, or exposed, coastline, sediment stability generally increases with water depth. Along the Southern California coast in particular, sediment motion is usually appreciable to depths of 30 m or more (Drake et al. 1972). Some such motion is indicated to depths of 100 m (Gorsline and Grant 1972), but infrequent storm surges might be expected occasionally to effect sediment instability in even greater depths (e.g., Draper 1967). Sediment mobility would seem to place a premium on animal motility. Most obvious is the problem of burial, particularly in shallow water (Fager 1968). Less obviously, sediment motion alters local sediment characteristics, probably giving an advantage to those individuals which can move to locally optimum conditions. The characteristics of bivalves found in high-energy (physical energy) environments (e.g., Stanley 1970) support these arguments. We hypothesize (Hypothesis 1) that decreasing intensity and frequency of disturbance with increasing depth accounts for the depth-sessility correlations in the state survey samples.

Although it may (Rowe et al. 1974) or may not (Carey 1972) be reflected in standing stock of macrofauna, community metabolism appears, in general, to decrease in rate with increasing depth and distance from shore, presumably due to a concommitant decrease in the flux of organic matter to the sea bed (Pamatmat 1973). Foraging area, in turn, has been demonstrated to be inversely proportional to food supply in a number of vertebrate species (e.g., Birdsell 1958; Schoener 1968; Smith 1968). For our next hypothesis, however, Bernstein's (1975) study is most pertinent. In examining foraging radii of ants under conditions of varying food supply, she also found an inverse relationship. Foraging radius was relatively constant within species, though, so that species replacement occurred along a gradient in food abundance. We propose that a similar phenomenon may account for the observed decrease in relative abundance of sessile individuals with increasing depth greater than 400 m (Fig. 7). Sessile individuals have a feeding radius limited by the length of feeding appendages or, in the case of maldanids, by the area from which fresh sediment will cave in as the animal feeds. (For the moment, we are not considering filter feeders.) The foraging areas of discretely motile or motile individuals do not have such obvious limits. We hypothesize, then, that (Hypothesis 2) the foraging radius required for adequate nutrition exceeds the reach of most sessile individuals at greater bathyal and abyssal depths.

The apparent maximum in relative abundance of sessile individuals at intermediate depths in Figure 7 would thus result from the interaction of our two hypothesized causes, as will become more apparent when we formulate some predictions (below). It is probably useful at this point to emphasize that we are not redescribing the relatively well-documented reduction in relative importance of filter feeding with increasing depth (Sanders et al. 1965; Jørgensen 1966;

Riedl 1971). Although the arguments for such a reduction parallel ours for the replacement of sessile individuals (albeit filter feeders are usually replaced at considerably shallower depths), suspension feeders are not numerically important in any of the samples we treat (Figs. 5 and 6).

One pattern which cannot be clearly extracted from our present data but which should be mentioned in passing is that of the variation of the relative abundances of the various feeding strata (suspension, surface, subsurface) with water depth. In our deep-sea samples, individuals are divided roughly equally between surface deposit feeders and burrowers (Fig. 6). In grab samples (Fig. 5) from the state survey, burrowers often comprise well over half the individuals. Unless the bow wave of the grabs were quite severe, it is difficult to imagine that grab samplers, which often retain a proportionately smaller area with increasing depth in the sediment (Holme and McIntyre 1971), could unrealistically inflate the proportion of burrowers. Therefore, the proportion of burrowers probably is lower in the deep-sea areas sampled than at some shelf depths. The pattern could be elucidated with further box core samples at shelf depths.

Our two basic hypotheses can more readily be used to generate disprovable predictions (see Platt 1964) if they are stated in more general terms. The first hypothesis may be generalized to state that increasing magnitude and frequency of sediment motion decreases the relative fitness of sessile life styles (Purdy 1964). The second hypothesis may be generalized to state that decreasing food supply increases the relative fitness of foraging strategies utilizing larger foraging areas (Schoener 1968, 1971). Clearly, these general hypotheses are not original, but some of the following predictions based on them appear not to have been made before.

According to these hypotheses, species replacements should occur over short distances where gradients in sediment mobility or food abundance are steep. In Table 4, we propose several "natural experiments" (Diamond 1973) to perform the desired tests. As presented, the hypotheses are easier to discuss separately.

Uniformity in temperature with depth is often cited as a reason for broad species' depth ranges in the Antarctic (e.g., Menzies et al. 1973; Arnaud 1974). We propose in addition, as some of Arnaud's (1974) data substantiate, that the existence of convective mechanisms for food transport to the bottom, coupled with high surface productivity, provides a generally similar amount of food over a broad depth range, thus permitting broad depth distribution of single feeding strategies. We predict much narrower ranges in the Arctic Ocean due to the general nearshore limitation of high productivity (Matheke and Horner 1974). Benthic studies of the Alaskan North Slope fauna (Carey, personal communication) could be used to test this prediction.

Where food input is relatively low over wide depth ranges, we also would expect single feeding strategies to be eurybathic. Eurybathy of species would thus be expected in the poorly productive

Table 4. Predicted rates of change in species composition with depth and distance from shore for various regions, except that the equatorial predictions concern directed distances along similar depth contours. (See text.)

Cause	Rate of Species Replacement With Distance	
	Rapid	Slow
Variations in flux of energy-rich fixed carbon	Arctic Nile Delta S. California Across Equator	Antarctic E. Mediterranean Red Sea Along Equator
Variations in input of turbulent energy	Open Coasts	Sheltered Coasts

regions of the eastern Mediterranean and Red Seas. Contrastingly rapid species (feeding strategy) replacements would be expected near the Nile Delta.

In the deep sea, rapid species replacement would be expected across the equatorial region due to rapid changes in surface productivity with latitude. Conversely lower rates of change would be expected in transects along the equator. Among the polychaetes, we predict a relatively high proportion of sessile species will be found along the equator because of high surface productivity. This hypothesis will soon be tested with samples collected at approximately 3°N, 125°W by Hessler (personal communication) and with samples to be processed during the preparation of an environmental impact statement concerning the effects of manganese nodule mining in the central Pacific (Environmental Research Laboratories, National Oceanic and Atmospheric Administration, in preparation). Similarly, shifting regions of high and low productivity over geologic time might provide a mechanism for geographic isolation and speciation of benthic populations, just as we propose the faunas of the North and South Pacific gyres are separated by a region containing species adapted to the relatively higher food input under the equator.

Although the relationships of various species to sediment mobility have often been noted (e.g., Purdy 1964), we propose the relationship is stronger and of wider application than heretofore realized. Recent interest in the bearing of sediment stability on community composition has been kindled by the hypothesis of trophic group amensalism (Rhoads and Young 1970), which has been largely verified in subsequent investigations (e.g., Aller and Dodge 1974). According to this hypothesis, suspension feeders are not abundant on reworked (by deposit feeders) and unstable sediments. Our results (Fig. 7) suggest that degree of sediment stability also determines the kind of deposit feeder which will predominate (sessile or not).

If our results are indicative, this relationship might be expected at least to the deepest shelf depths of exposed coasts, where storm surges are a normal winter occurrence (Draper 1967).

Another test of the stability-sessility relationship is possible by examination of faunas in sheltered bodies of water. In these cases, if food supply is sufficient, sessile species would be expected to show high relative abundance in shallow water. Day (1974) observed a strong correlation of shelter with species composition in estuaries, but the species were not categorized by sessility. For both the sessility-sediment stability and the sessility-food supply relations it would be useful to examine taxa other than Polychaeta as well. Again, if direct measures of foraging area or sessility could not be obtained, a classificatory scheme might prove useful.

So far our discussion has been limited to community composition, but the characteristics of individuals may also vary. The robustness of animals living in unstable sedimentary regimes is well known (e.g., Stanley 1970). The fragile nature of deep-sea animals from stable regions is also commonly recognized (e.g., Hartman and Fauchald 1971). Morphologies may also be expected to vary with changing food supply. In particular, our hypothesized relation between food supply and foraging area would suggest that individuals existing under low food fluxes may have relatively long or extensible feeding appendages. Polychaeta constitute a poor test of this prediction because feeding appendages are often greatly extensible and are often lost upon preservation. To some extent, the prediction has been confirmed by Allen and Sanders (1966), who observed that the relative weight of feeding palps increases with depth of collection for some closely related protobranch bivalve species. The prediction might be more easily tested, however, by measuring the relative lengths of ampeliscid or corophiid (amphipod) feeding antennae with increasing water depth.

If these predictions are not disproven, the present hypotheses also have implications for species diversity arguments. Structural heterogeneity and species diversity often correspond (e.g., MacArthur and MacArthur 1961). Rhoads (1974) convincingly demonstrated with some recent photographs that soft-bottom communities do exhibit structural heterogeneity, and there are several reasons to believe such heterogeneity should be maximal where sessile species dominate. First, according to our previous arguments, an area dominated by sessile individuals is not physically disturbed or homogenized. Second, with relatively few motile individuals, such an area is probably not quickly biologically homogenized, either. Third, unless the sediment modifications (e.g., tubes) common to sessile animals are so abundant as to abut; these modifications, interspersed with less or differently modified sediment, would be expected to add to the heterogeneity. Not only is environmental heterogeneity effected by sessile species, but such species are most likely to be affected by it as well. As argued in greater detail by Jumars (1975a, b), animals with small areas of activity or ambits (Lloyd 1967) are most likely to experience a coarse-grained, heterogeneous environment.

If all else were equal, one might then expect species diversity to reach a maximum at the depth with a maximum percentage of sessile individuals. An intermediate-depth diversity maximum has been documented for the gastropods (Rex 1973). However, all else is not equal. In particular, hypsographic curves (e.g., Menard and Smith 1966) reveal that little of the ocean bottom falls at such intermediate depths. Hence, the effective "island size" (MacArthur and Wilson 1967) for species limited to such depths is small relative to the effective island size for species of abyssal regions. Despite this disclaimer and the fact that manganese nodules and abyssal hills (D. A. Johnson 1972) also contribute to deep-sea benthic environmental heterogeneity, the effects of sessile species sometimes appear to dominate (Jumars 1975b).

Perhaps the most salutary prediction arising from the present hypotheses is more painfully obvious: easily measured parameters and biologically important parameters may bear little relation. R. G. Johnson (1974) clearly illustrated this maxim in searching for biologically meaningful sediment descriptions and in contrasting these new appraisals with the standard sedimentary parameters employed by geologists. Our hypotheses point to the desirability of assessing directly such intractable features as individual foraging areas, local fluxes of foods, and frequencies and intensities of sediment motion. Until such observations are made, the importance of easily measured community covariables, such as temperature and mineral grain size, will continue to be overrated, and causes will be difficult to extract.

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NOTE:

The reader wishing to apply a trophic classification to either Arenicolidae of Flabelligeridae would do well to consult references published since this manuscript was submitted, i.e.,

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