PALEOECOLOGIC INDICATORS AND TRACE FOSSILS

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Some of the potentially most useful information for paleoecologic and paleobathymetric analysis of marine sequences of any age involves variations of animal-sediment relationships and quantitative general faunal trends with depth in the modern ocean. Gross variations in the distribution of invertebrates across the littoral-to-abyssal gradient (fig. 8-1) commonly mirror bathymetrically significant variations of major physical parameters governed by the density stratified character of the world ocean. Some of these parameters (e.g. temperature) have varied with geologic time, latitude and depth but within predictable or measurable limits. However, other parameters (e.g., penetration of light in the open ocean) have likely remained constant at least through the Phanerozoic and later Proterozoic. Moreover, even an ice free globe will continue to exhibit pole-to-equater temperature gradients although atmospheric and oceanic transport rates would be much slower. Thus, even under the allowable maxima and minima many parameters can be expected to have remained in the relatively same depth-stratified sequence despite the fact that absolute depths associated with critical boundaries may have varied.

This particular lecture will focus on the variation of major faunal, bio-lithologic, and associated physical parameters with depth in the Recent ocean in a continental margin setting. Emphasis will be placed on recent data detailing useful quantitative or semi-quantitative macro and microfaunal parameters which can be readily measured or analyzed in a systematic way within ancient marine deposits. Additional discussions of these trends along with examples from the fossil record and a sumaary will be provided in a later lecture (Lecture 11). Consequently, references will be made to figures accompanying this lecture in notes for Lecture 11. Overall stress will be on interpretation of the Tertiary marine record, but many of the parameters discussed can be equally and readily applied to Mesozoic and Paleozoic sequences and some examples are drawn from these older horizons.

Benthonic Marine Environments

Classification of benthonic marine environments has experienced a somewhat confused history (23); however, the scheme used herein (fig. 8-1) represents a slightly modified version of a now relatively standardized classification (23) with the majority of zonal boundaries drawn at the top or base of one or more of the several significant water mass boundaries extant in the normal marine water column (fig. 8-1). In this way, depth terminology takes on some precision based on recognized physical phenomena rather than resting on vague and relative notions of "deep" or "shallow", in turn allowing paleodepth determinations to be utilized for hindcasting of estimated subsidence rates, paleobathymetric contours (7), or paleoenvironmental maps.

The water mass filling the irregular oceanic "bowl" is characteristically density-stratified due to variations in temperature and salinity with depth produced by latitudinal variations of surface temperature, evaporation, precipitation, zonal winds, and the production of relatively cold and dense bottom water in the polar regions (35). Additional layers can be recognized on the basis of the maximum penetration of light (photic zone), amounts of dissolved oxygen, selected nutrients, or undersaturation of calcium carbonate, etc. Each boundary ultimately impinges against the continental margin at a known depth forming in effect bathymetric datum levels which in many instances are clearly reflected in faunal boundaries or gradients. For example, the photo-aphotic boundary at 150 m is associated with a dramatic benthic macro and microfaunal boundary at the shelf edge (outer neritic zone) and can be utilized with some precision in Paleozoic as well as Teritiary sequences.

The *littoral zone* is that area of the bottom alternately exposed and covered during daily tidal fluctuations resulting in an especially biologically stressed environment. The *neritic* or *shelf* zone extends from tidal base to a depth of 150 m and is commonly but not invariably coincident with the structural edge of the shelf-to-slope transition. Importantly, this depth is associated with the base of the photic zone (150 m) and the base of the surface water layer (100 m), equivalent to the maximum depth of mixing due to wind stress and the Ekman spiral effect (sometimes termed the mixed layer). These two layers act together with upwelling and internal wave effects at the shelf edge as well as continental runoff and nepheloid layer transport to produce a dramatically rich benthonic habitat. Furthermore, the shelf can be divided into three subunits by noting that effective fairweather wave base is about 10-15 m along most open coasts with a zone of initial wave touch-down at about 50 m for average waves of 8 to 10 seconds. Both these latter wave boundaries create discrete differences in the character of the sediments and bottom currents across the shelf, in turn creating two biologically significant subdivisions of the inner shelf water mass in terms of turbulence, suspensates, substrate, sediment transport, and general physical stress.

The *upper bathyal* zone encompasses the shelf edge to a depth of 500 m and underlies an area of commonly vigorous upwelling and relatively high planktonic productivity. The base of the zone is usually coincident with the upper portion of the *oxygen minimum zone*, a layer of somewhat variable thickness characterized by marginal amounts of dissolved oxygen (0.1 to 0.5 ml/1) due to oxidation of abundant particulate organic matter produced in the mixed layer and within the near surface photic zone. The *upper middle bathyal zone* essentially encompasses the *oxygen minimum zone* although the upper and lower boundaries of this zone can range as shallow as 200 m and 1000 m respectively. This latter depth is also coincident with the base of the *permanent thermocline zone* (fig. 8-1) which may in turn have a relationship with the slow circulation associated with the oxygen minimum zone (42). Water below this depth is exceptionally stable in its characteristics, exhibiting extremely low temperature as a function of its high-latitude origin. Substrates within the *middle bathyal zone* generally suffer little bioturbation due to a marginal benthic megafauna beneath the oxygen deficient water mass (14, 36).

The boundary between the *lower middle bathyal* and *lower bathyal* zone is arbitrarily placed at 2500 m although there is some justification for placing it at 2000 m due to a possible bacterial "threshold" (38) which may in turn account for a sometimes pronounced microfaunal boundary at about this depth. The *lower bathyal* zone encompasses the top of the lysocline (LCD) at mid and low latitudes where the initial effects of deepsea carbonate dissolution are evident (11).

The *abyssal zone* begins at 4000 m and is essentially coincident with the top of the Recent *calcium carbonate compensation depth* (CCD) in mid and low latitudes (11). However, the effects of this chemical threshold as well as that

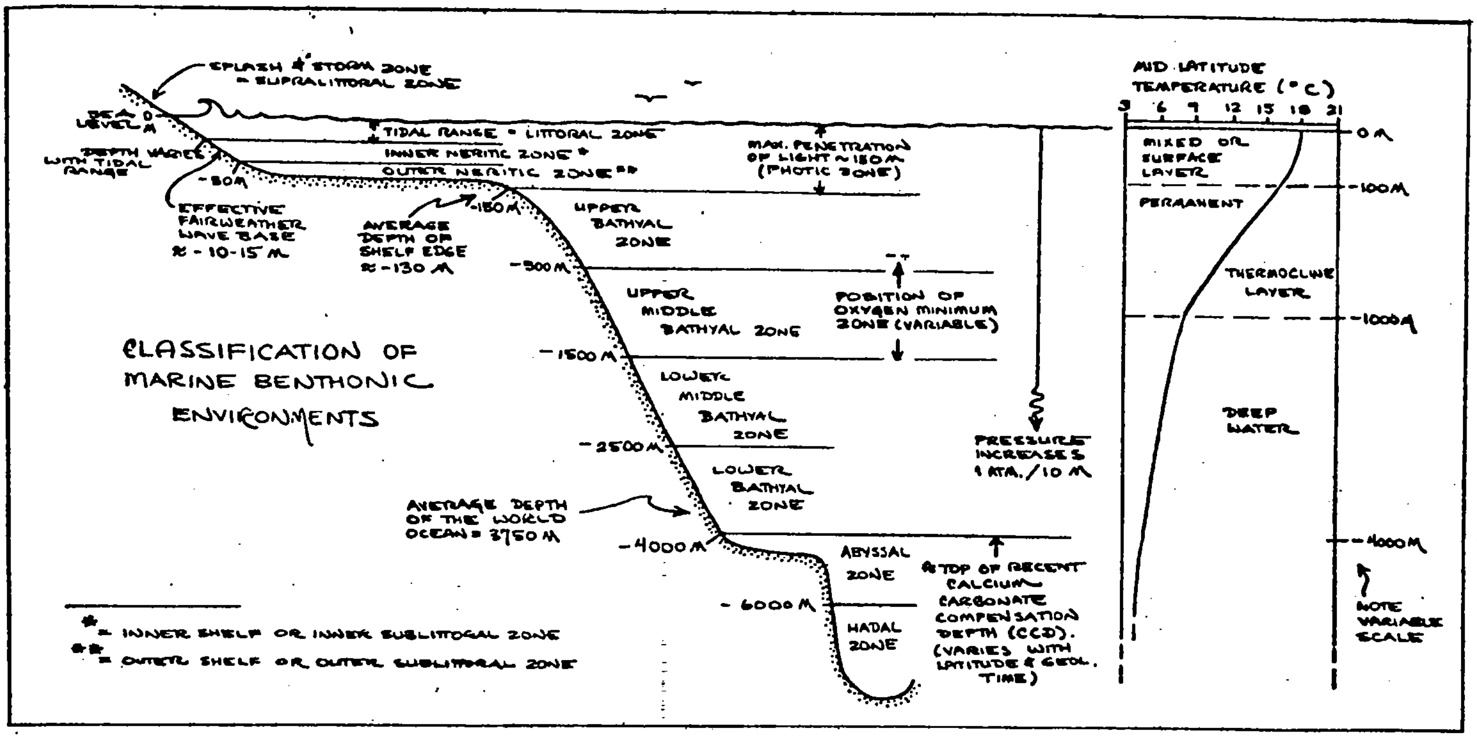

Fig. 8-1 Classification of benthonic marine environments in terms of depth and relationships with significant wave or water mass boundaries in the ocean; modified after H~~a~~edgpeth (23). Note that figure *is not* drawn to scale.

expressed at the LCD can be masked or modified by (a) high depositional rates of terrigenous debris in base-of-slope deposits and rise environments or (b) high rates of planktonic productivity causing depression of the CCD beneath equatorial currents and elsewhere (12). The *hadal zone* encompasses depths greater than 6000 m.

Abundance and Diversity of Macroinvertebrates

The principle controls on the distribution of benthic macroinvertebrates include temperature, salinity, oxygen, substrate, and in turn food-feeding relationships all of which vary both horizontally and vertically in the ocean. Greatest abundances of benthic invertebrates, both in terms of numbers of individuals per unit area as well as in terms of biomass, are associated with the photic zone and consequently the shelf environment, with a rapid decrease in water depths exceeding 100 m (figs. 8-2 and 8-3). Megafossil abundances can be routinely measured in stratigraphic sequences (number per unit area of outcrop, number per dry weight of sediment, etc.) with resulting trends pinpointing the dramatic shelf-slope abundance boundary in Phanerozoic marine sequences.

Variation in species diversity (total number of species) does not always exhibit a similar and straightforward trend with depth (fig. 8-4). Diversity of selected elements from the slope environment rivals the notoriously high diversity of shelf faunas due in part to the stability of this deeper environment with time (45). Moreover, there are significant differences in species diversity within shallow water environments across latitude due to changing physical and biological stress (fig. 8-4). For example, species diversity within boreal shallow water bivalve and polychaete communities is much lower than their tropical counterparts whereas the number of individuals in each case is comparable (fig. 8-4). However, biomass (as opposed to simple abundance) within these shallow water environments also varies with latitude (fig. 8-3) reflecting variations in productivity and ecologic efficiency in each system (49). Nevertheless, it has been estimated that ninety percent of all marine invertebrate species live on the shelf (49) due in large part to the heterogeneous and patchy nature of the macro and microhabitats characteristic of this zone, and the combination of favorable factors associated with both the photic zone and mixed layer at depths shallower than 150 m (fig. 8-1). Significantly, the abundance and diversity of paleontologically important groups (those commonly found as body fossils) generally reflect the larger scale faunal trends with depth (figs. 8-5 and 8-6) emphasizing the usefulness of the simple measurement of abundance in fossil marine sequences. Changes in abundance and diversity across the shelf-slope transition are not only pronounced (45) but also of critical geologic importance.

Shifting our attention from gross trends of macrobenthos with depth and latitude it is of interest to dissect these larger patterns and note trends among the major macrofauncal groups with depth. A traverse across the San Pedro shelf and basin off southern California provides clear evidence of one of the more startling facts of benthic life from the geologic point of view . . . the dominant elements among macroinvertebrate faunas on the shelf, slope, and basin are commonly composed of groups not ordinarily preserved as body fossils (fig. 8-7). Indeed, polychaete worms and crustaceans often comprise two of the dominant groups within almost all benthic marine communities[1] from shallow (32, 33, 41, 44) environments to abyssal depths (18, 25, 34, 45, 46), with mollusks and echinoderms of special importance on the shelf and holothurians increasing in abundance in abyssal and hadal settings (53). In fact, polychaetes and bivalves have been cited as commonly composing about 80 percent of most bathyal-abyssal faunal assemblages with bivalves commonly

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[1] An assemblage of organisms inhabiting a specific place (31).

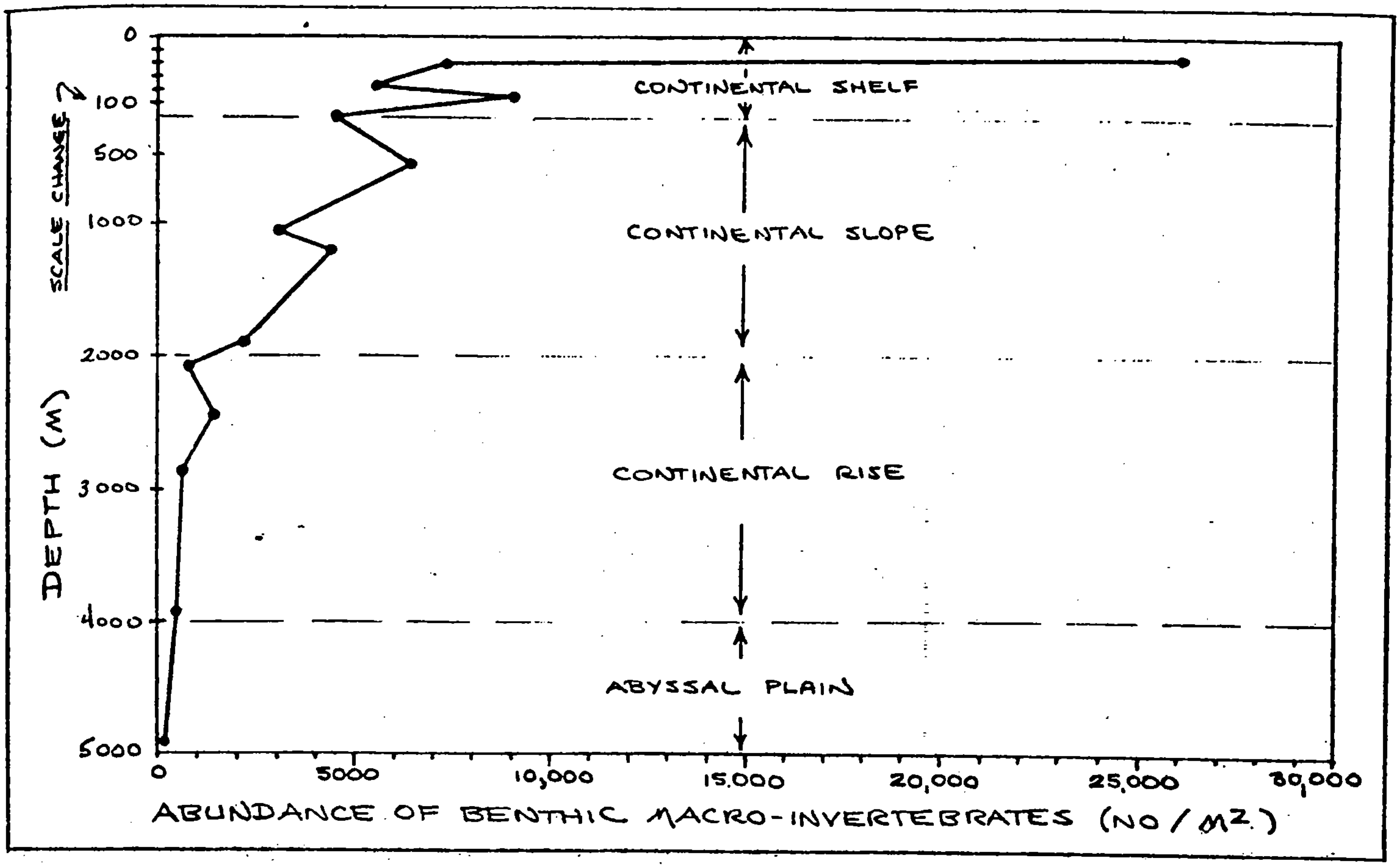

Fig. 8-2 Abundance of macro-invertebrates per square meter along a transect in the northwestern Atlantic Ocean from off Massachusetts to Bermuda (43). Samples were washed through a 0.42 mm sieve and counts include ostracods.

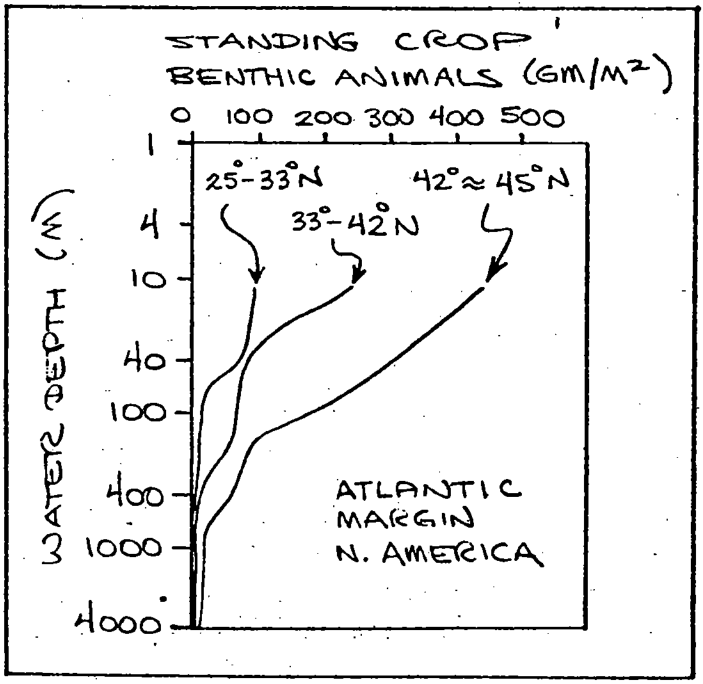

Fig. 8-3 Composite profiles illustrating general decrease of standing crop (biomass) of benthic animals with depth and with decreasing latitude based on 1800 samples taken off the Atlantic margin of North America (17).

several times less abundant than polychaetes. These patterns might seem momentarily grim in terms of producing a useful fossil record, but as it turns out crustaceans and especially polychaete worms leave a clear record of trace or ichnofossils in the form of dwelling tubes, burrows, crawling traces, etc. invariably representing *in situ* fossil evidence of their presence and abundance.

Expanding the San Pedro transect data even further it is apparent that additional paleontologically useful trends are exhibited among mollusks (fig. 8-8), with a general decrease of pelecypoda across the slope and a pronounced decrease in areas beneath the oxygen minimum zone accompanied by an increase in carnivorous gastropods. Thus, significant quantitative variations occur with this group with depth and environment even though they commonly compose less than 25 percent of the total benthic fauna. Moreover, recent studies have pointed to broad scale variations in molluscan taxonomic structure with depth (26) reflecting basic differences in feeding types as expressed by the general decrease in relative abundance of heterodont bivalves and an increase in pteriomorphs and protobranches going from shelf to abyssal depths. This trend is apparent in both Recent and Tertiary sequences (26) constituting one more useful paleoecologic - paleobathymetric tool in deposits of this age.

Substrates, Feeding Relationships and Potential Trace Fossils

It seems reasonable to expect that direct relationships exist between bottom dwelling animals and the nature of the

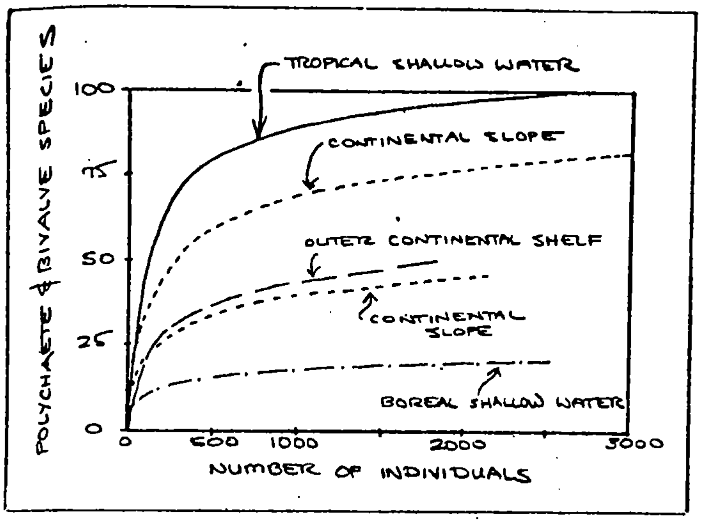

Fig. 8-4 Diversity curves for the number of species and individuals of polychaetes and bivalves (which generally amount to 80 percent of the total benthic fauna) in samples of different size from widely contrasting marine environments (45).

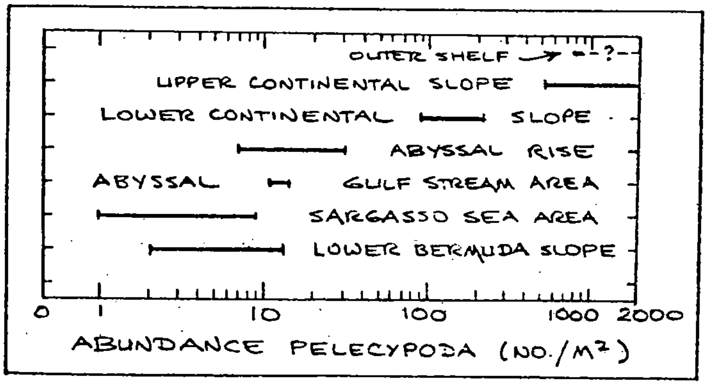

Fig. 8-5 Abundance of pelecypoda in various marine environments along a transect from off Massachusetts to Bermuda, northwestern Atlantic Ocean (46).

substrate on or in which they dwell, and research demonstrates this is indeed the case, especially in terms of food gathering techniques used by these animals (21, 36, 40). Indeed, a great deal of attention is currently being focused on the nature of feeding relationships or *trophic structure* within benthic communities because it allows functional comparison of ancient and Recent communities, emphasizes the detritus-eating bottom dwellers, and thus the dominant forms in each environment (51). These sorts of studies have shown that there is a stratification of feeding types in each community leading to efficiency and minimal competition in utilization of resources. Although emphasis has been placed on detritus eaters and how they feed (injest sediment, filter food from water, etc.) other feeding types can be included in this sort of overview leading to a standard array of trophic or feeding groups common to benthic marine communities of all ages (table 1). Generalizations emerging from these studies suggest that, (a) one trophic group dominates the biomass of each community, (b) one species dominates the biomass of each trophic group, and (c) each sucessively less abundant taxon in the community belongs to a different trophic group (51). This scheme of trophic structure has been repeatedly confirmed in both modern and fossil communities, (51) and because certain trophic groups and structures are specific certain marine environments it offers a relatively sophisticate means of establishing paleoenvironments. For exampl infaunal suspension feeders (table 1) tend to be predomina in many shallow environments whereas infaunal depos feeders dominate in lower bathyal-abyssal environments.

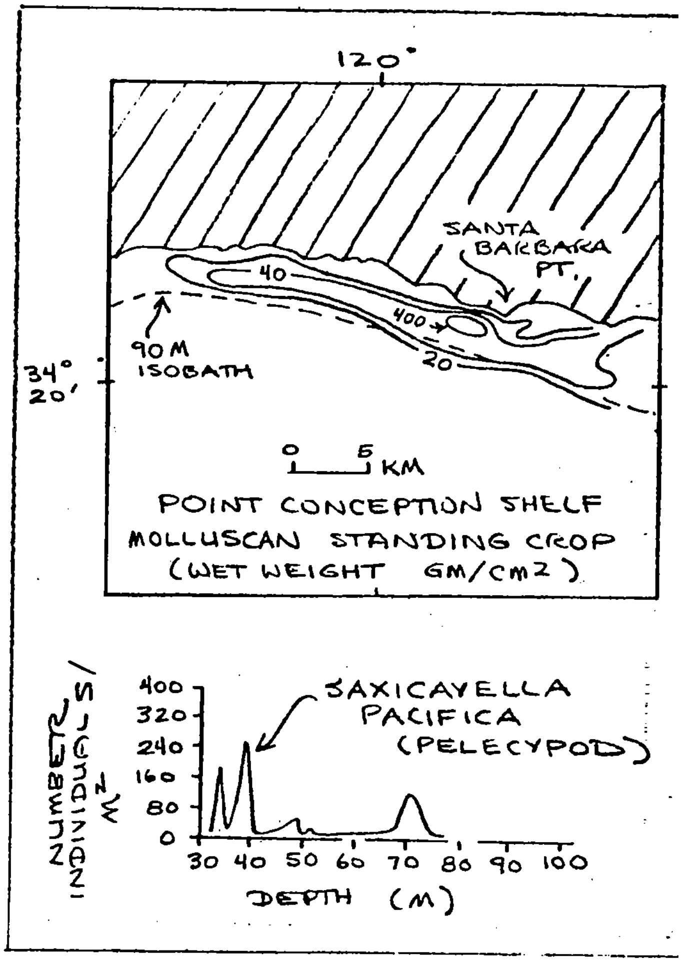

Fig. 8-6 Variation of molluscan standing crop (biomas and abundance of a single species of bivalve acro the continental shelf, Santa Barbara are California (33).

As was noted earlier, the dominant members of man Recent benthic macroinvertebrate communities a polychaetes and/or crustaceans which do not normally leave record in the form of body fossils but whose presence marked by dwelling tubes in the case of worms and b burrows, crawling traces, etc. in the case of crustaceans. The sorts of relationships between animals and potential trac fossils can be readily exploited when dealing with foss environments through the distinct association of certai feeding or trophic groups with specific benthic marin environments (36, 51, 53) and linked in turn with specifi trace fossil morphologies, orientations, and associations (tabl 1). Moreover, the combined use of trace fossils and bod fossils yields a far more complete and realistic picture c ancient marine communities and paleoenvironments than i possible using either group alone.

The growing interest in the study of trace fossils ha paralleled the similar growth in analysis of trophic structure with the two subdisciplines now essentially fused for purpose of paleoecology. Early studies of tracks, trails, burrows, etc

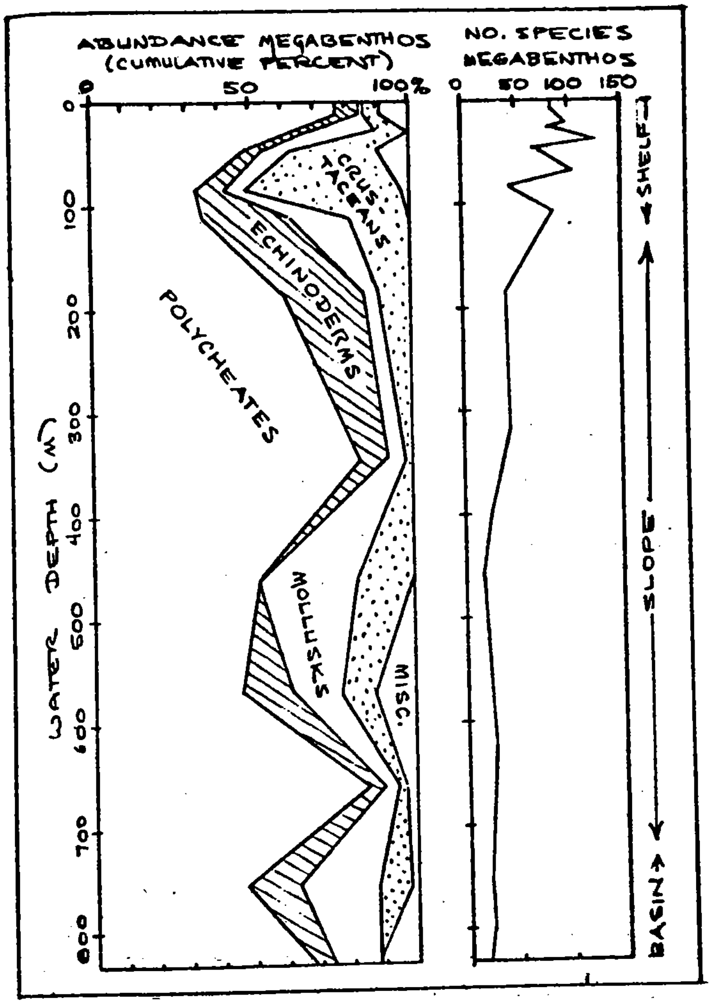

Fig. 8-7 Frequency distribution (cumulative percent) and diversity (number of species) of living mega-invertebrates, San Pedro shelf and basin, California (22).

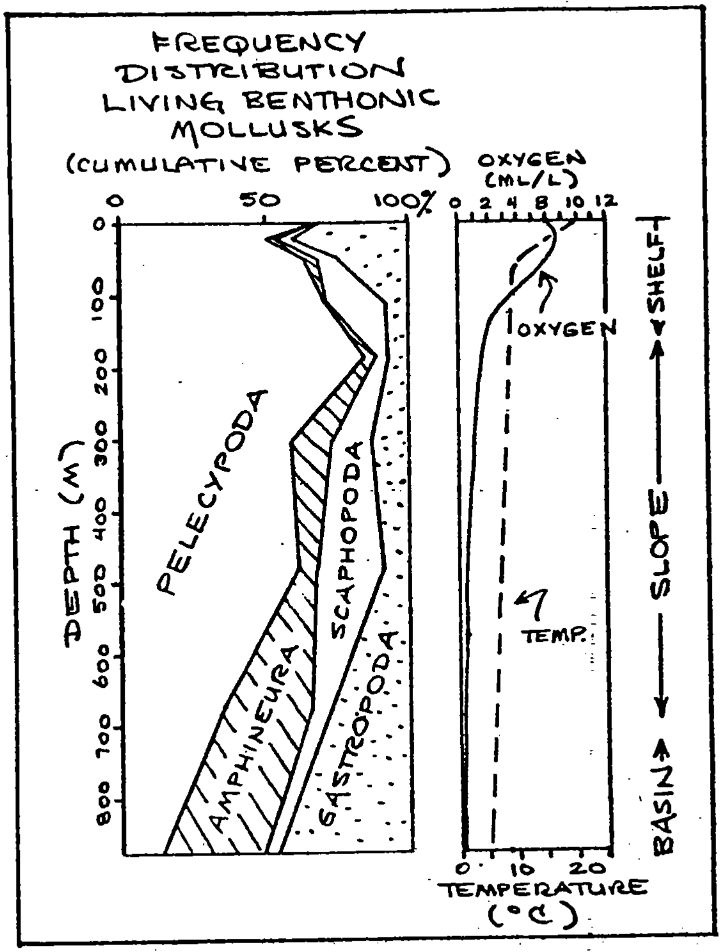

Fig. 8-8 Frequency distribution (cumulative percent) of living benthonic mollusks, San Pedro shelf and basin, California (2). Note marginal oxygen values below 400 m associated with oxygen minimum zone and basin-sill effect.

were viewed as curiosities but their value for paleoecology was ultimately recognized and increasingly exploited despite the general lack of information on formation of these forms in Recent environments (47). Moreover, the general lack or meagerness of body fossils (both in terms of natural distributions as well as removal through diagenic events) in many sedimentary sequences and the general ubiquity and abundance of trace fossils together with their recognized relationship with different trophic groups (table 1) have ultimately brought the subdiscipline of *ichnology*[2] to its current position of providing major input to most paleoecologic and paleobathymetric reconstructions (15, 20, 27, 47). Although myriad numbers of ichnofossils or trace fossils have been described and illustrated, only general trends will be noted in this lecture and Lecture 11, with the reader urged to consult some of the more recent references provided herein for an in-depth exploration of these features.

The environmental sensitivity of macroinvertebrates is clearly reflected by the distribution and patterns of well-preserved traces. For example, the distribution of crabs in lagoon and salt marsh estuaries appears to be closely tied to substrate character, salinity, and vegetation cover, with distinctive crab burrow patterns delineating the backshore and foreshore zones within these environments (1). Many other examples can be found of equally specific and sensitive trace fossil distributions, including microborings of filamentous fungi common in the photic zone (16) and combined trace fossil-sedimentologic models (28) but it is important to briefly review broader trends.

It has been recognized for some time that suspension-feeding macroinvertebrates are most common in shallow environments and deposit feeders are dominant in deeper environments (47, 53). Thus, the gross generalization can be made that burrows and tubes oriented normal to the sediment surface are characteristic of shallow water environments (littoral through shelf depths), whereas horizontal burrowing and "mining" traces oblique to the sediment-water interface characterize bathyal and abyssal environments (47). An excellent example demonstrating the general validity of this generalization is provided by the distribution of deposit and filter (suspension) feeders in the wide spectrum of benthic environments present in the Gulf of California and silled anaerobic deep basins off southern California (fig. 8-9). The general trend noted above is not only confirmed by this illustration but in addition other significant trends are apparent. For example, there is a noticeable peak in abundance of filter feeders within low salinity lagoons and

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[2] The study of fossil and Recent traces of organisms.

TABLE 1 - ABBREVIATED CLASSIFICATION OF FEEDING IN BENTHIC MARINE INVERTEBRATES AND POTENTIAL TRACE FOSSILS (LEBENSSPUREN)[7]

FEEDING CATEGORY (Trophic Group)	GENERAL DEFINITION	LIFE SITE	LOCATION OF FOOD UTILIZED	POTENTIAL TRACE FOSSILS	
				Structure or Trace	Character
1. Suspension Feeders (Filter Feeders)	Remove food from suspension in water mass without need to subdue or dismember particles	1a. Epifaunal[5]	High water mass[1] Low water mass[1]	(e) Dwelling structures	(a) Resting Traces (Cubichnia) shallow depressions with bowl or trough-like relief
		1b. Infaunal[4] (burrowers)	Sediment-water[2] interface	(b) Crawling traces (c) Grazing Traces	(b) Crawling Traces (Repichnia) Trackways and trails (intra or epistratal); elongated, sinuous, continuous, linear; some branching, commonly annulated.
			In sediment[3] (shallow)	(d) Feeding structures	(c) Grazing Traces (Pascichinia) Grooves, pits, furrows made at substrata surface; unbranched, non-overlapping; curved to tightly coiled patterns; complex patterns.
2. Deposit Feeders	Remove food from sediment either selectively or non-selectively without need to subdue or dismember particles	2a. Epifaunal[6]	Sediment-water interface	(c) Grazing traces	(d) Feeding Structures (Fodinichnia) Temporary burrows; single, branched or un-branched; cylindrical to sinuous shafts or u-shaped burrows; oriented at various angles.
			Shallow (in sediment)	(b) Crawling traces	(e) Dwelling Structures (Domichnia) Burrows or dwelling tubes usually forming permanent homes; simple, bifurcated or u-shaped structures perpendicular or inclined to bedding; intricate burrow systems.
		2b. Infaunal[4] (burrowers)	Deep (in sediment)	(d) Feeding structures	
3. Browsers	Acquire food by scraping plant material from environmental surfaces or chewing or rasping larger plants.	Epifaunal[6]	Sediment-water interface	(c) Grazing traces	
4. Carnivores	Capture live prey	4a. Epifaunal[6]	Sediment-water interface	(a) Resting traces	
		4b. Nectobenthic[6]	Sediment-water interface	(b) Crawling traces	
		4c. Infaunal[4]	In sediment	(d) Grazing traces	
5. Scavengers	Eat larger particles of dead organisms.	5a. Epifaunal[6] 5b. Infaunal[6]	Sediment-water interface	(a) Resting traces (b) Crawling traces	
			In sediment	(c) Grazing traces	
6. Parasites	Use Fluids or tissues of host organism	Same as host	Same as host	Dissolution patterns and/or borings in host body fossil	

[1] Organic concentration low compared with sediment-water interface but large volumes of material pass a given point over time.

[2] Sediment-water interface has highest instantaneous concentrations of organic material; location of benthic epifauna and all benthic flora.

[3] High concentrations of nutrient organic material in sediment within 5 cm of sediment-water interface. Decreasing organic content with depth due to bacterial decomposition. Anaerobic bacteria increase with depth. Below 75 cm organic material is refractory and not a food resource.

[4] Normally mobile

[5] Mobile and immobile forms

[6] Mobile forms

[7] Adapted from Frey (1973) and Walker and Bambach (1974) with additions and modifications.

inner shelf environments coincident with areas of highest concentrations of suspensates. A striking increase in abundance of deposit feeders is also apparent in silled basin environments. Thus, a simple tabulation of dwelling and burrow orientation within a given stratigraphic sequence plotted in terms of cumulative percent of total trace-fossil assemblage per unit thickness might be expected to yield useful paleobathymetric patterns in light of this Recent model (fig. 8-9). Additional examples from the fossil record are provided in Lecture 11.

Significant Microfaunal Trends

The recent strides in paleoecologic and paleobathymetric analysis of macro-invertebrates using body fossils, trace fossils, concepts of trophic structure, and community analysis have, for the most part, been concentrated in Paleozoic marine sequences whereas similar analysis of the late Mesozoic and Tertiary sequences have been based primarily on scrutiny of microfossils, primarily foraminifera. Although microfossils, including foraminifera, are plentiful in many Paleozoic and Mesozoic deposits, the increasingly modern aspect of late Mesozoic and Tertiary faunas together with an exponential increase in knowledge concerning the ecology and distribution of Recent foraminiferal faunas have focused attention on these younger faunas. In fact, many of the Tertiary biofacies-lithofacies packages appear to be direct analogs of many well-studied modern littoral through lower bathyal continental margin environments.

The test compositions, ubiquity, abundance, and dual planktonic-benthonic habit of foraminifera have combined t make them the premier paleoecologic tool in late Mesozoi through Recent marine sediments, although other group including ostracods, radiolarians, and diatoms are also o significant use. Foraminiferal abundance and diversity i modern marine sediments have also made them one of th most useful biologic indicators in marine geologic an environmental studies (9, 38), with a sensitivity exceedin mechanical measurements. Although we are still in the initia throes of investigating the many physical and biologi complexities bearing on the distribution of benthonic an planktonic foraminifers, a large number of quantitativ investigations have illustrated that well-establishe distributional patterns exist, clearly reflecting some of th significant physical boundaries in the marine environment (fi 8-1) with major faunal changes occuring with increasing dept and distance from the strandline (4, 38). In additio composition, structure, and morphology of benthon foraminifera exhibit convergent environmental adaption evolutionary trends through time (3), allowing use homeomorphs in recognition of paleoecologically importa species.

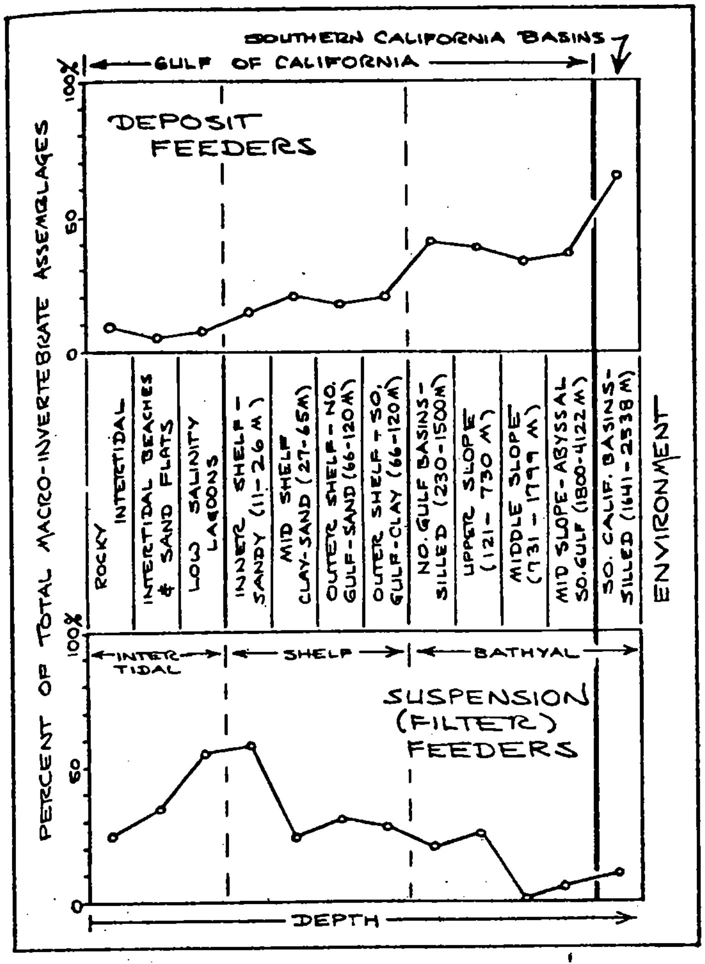

Fig. 8-9 Distribution of living macro-invertebrate deposit and suspension feeding types in various intertidal through abyssal environments of the Gulf of California and comparison with silled basins off southern California (36).

Modern foraminiferal faunas have been analyzed from a wide spectrum of Recent marine environments along with associated distributional trends of ostracods and radiolarians, and a number of useful and repetitive trends have emerged which have direct and general application to paleobathymetric interpretation in ancient marine sequences.

The general abundance of any microfossil can be analyzed in terms of number of the specimens per gram of dry sediment, yielding a foraminiferal number, radiolarian number, etc. For a given sample (fig. 8-10 and 8-11), *foraminiferal number* can vary as a function of rate of productivity and/or rate of sedimentation; however, trends in abundance as measured with this index exhibit trends similar to mega-invertebrates in continental margin settings with foraminiferal number increasing with depth to a maximum at the shelf-slope transition (fig. 8-10). Deeper continental margin environments usually are characterized by decreasing foraminiferal numbers with increasing depth; however, isolated high numbers can occur in turbidite layers due to displacement and redeposition from shallower depths. Radiolarian tests commonly increase in abundance (relative and absolute) with increasing bathyal water depths becoming generally more abundant then foraminifera at depths exceeding 2000 m (fig. 8-10 and 8-11). The calcium carbonate compensation depth (CCD) is also responsible for the relative increase in rediolarian abundance at depths exceeding 3000 m due to dissolution of calcareous foraminiferal tests. This later effect is also responsible for the relative abundance of arenaceous foraminifera in deeper environments (fig. 8-10), although the effective depths of the LCD and CCD vary with latitude (11) and local water mass characteristics. Alternately, decreasing ratios of foraminifers to ostracods clearly delineate open marine environments from barred paralic environments such as lagoons and marshes (5). Diversity of benthonic foraminifera also increases to a maximum in the outer shelf-upper bathyal zone (30), although downslope displacement of shallow species commonly creates artifically high species numbers in deeper environments.

One of the most useful trends exhibited by Recent foraminifera is the general lack of planktonic specimens in shelf and littoral sediments, an abrupt increase in both abundance and diversity at the shelf edge in response to the presence of more normal open ocean water, and a relative increase in productivity induced by upwelling of nutrient-rich water at the shelf break (fig. 8-12). In fact, the abrupt increase in planktonic specimens can be used to map the shelf-slope juncture both in surface and subsurface fossil sequence.

Many studies have illustrated the systematic variations of benthonic foraminiferal faunas, with increasing depth recorded as variation of dominant biofacies with depth. Modern benthonic foraminiferal biofacies established in the Gulf of California (4) serve as an excellent example of this sort of analysis as well as illustrating a number of associated trends commonly recorded in Tertiary basins of the Pacific Coast and elsewhere (fig. 8-12). Biofacies analysis involves arranging benthonic species exhibiting similar *upper* depth limits into groups ultimately indicative of major depth increments or environments. Use of upper depth limits in defining these groups is of critical importance because of continual downslope displacement and redeposition of specimens from shallower depths. In many instances displaced specimens constitute well over 50 per cent of specimens found in bathyal environments (fig. 8-14), which demonstrates the fallacy of using the most abundant species in a sample for paleobathymetric interpretation in fossil sequences. This same phenomenon also accounts for the artificial extension of shallow biofacies into deeper water (fig. 8-13). Paleobathymetric curves are consequently constructed *using the deepest dwelling forms* present in any given sample yielding estimated *minimum depths of deposition*; correct paleodepths are not found by "integrating" the depth aspect of the entire fauna to arrive at a "mean" paleodepth.

The upper depth limits of some modern species are known to vary from place to place in response to variation in bottom temperature, etc., and some fossil species can be expected to have exhibited similar variations. However, a significantly large group of modern cosmopolitan bathyal species exhibit constant upper depth limits regardless of major differences in temperature, substrate, etc. (8). Use of these isobathyal species together with homeomorphic relationships, emphasis on depth restricted genera, statistical analysis of recurrent species associations, and overall variations in faunal diversity and abundance have allowed this sort of biofacies analysis to be successfully applied to sediments of Tertiary through Cretaceous age (48).

A number of specific trends within broad foraminiferal biofacies patterns have special interest, such as the effect of the oxygen minimum zone on faunal composition, productivity (39), and sedimentation (14). Moreover, certain species such as *Suggrunda eckisi* are apparently restricted to this critical zone and have homeomorphic counterparts in Tertiary sediments (29, 30). Other paleoecologically important

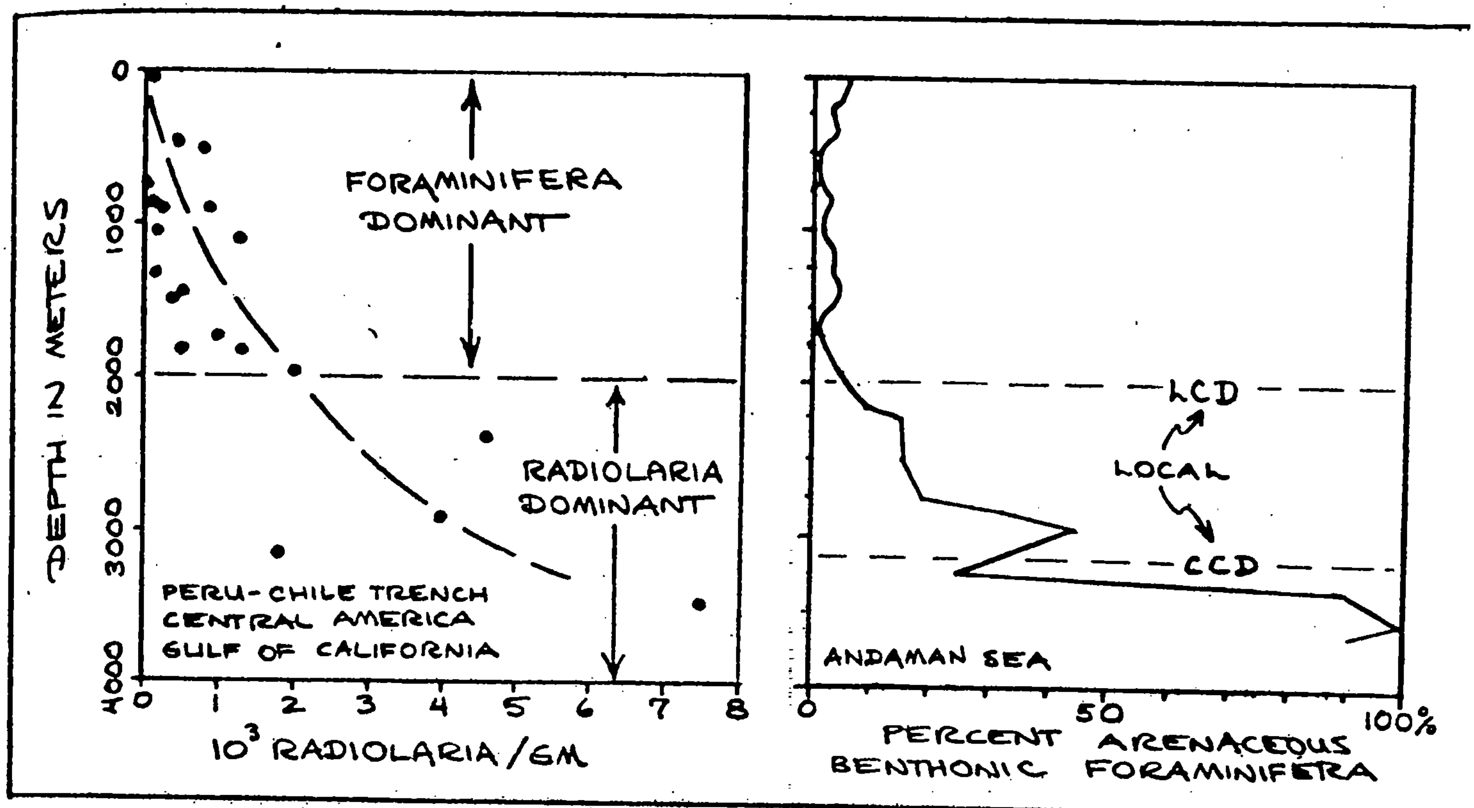

Fig. 8-10 Abundance of radiolarian tests with depth in the eastern Pacific Ocean (4, 10, 7) and abundance of benthonic arenaceous foraminifera in the Andaman Sea (19) along with relationship to a locally-elevated lysocline (LCD) and calcium carbonate compensation depth (CCD).

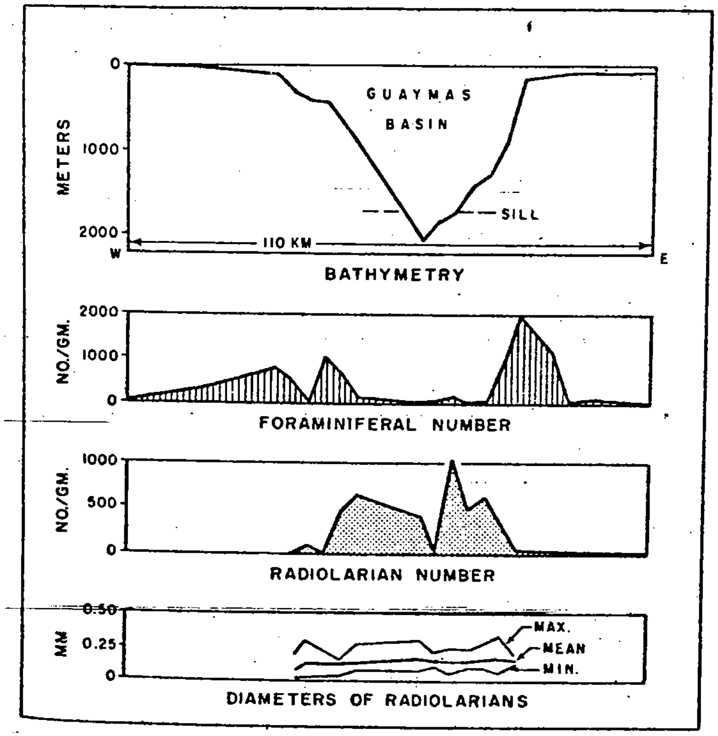

Fig. 8-11 Abundance of foraminiferal tests, radiolarian tests and variations in radiolarian diameter across the Guaymas Basin, Gulf of California (30).

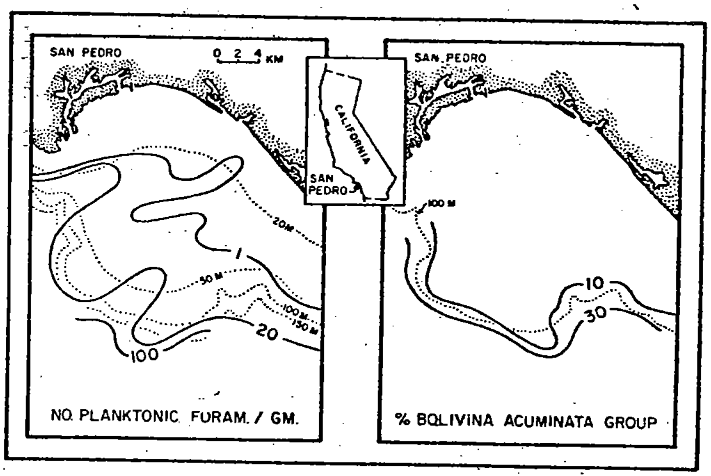

Fig. 8-12 Abundance of planktonic foraminifera *Bolivina acuminata* group (biofacies) in relationship to the edge of the San Pedro shelf, California (9).

trends include systematic and repetitive changes in size or ornamentation of certain genera with depth, such as the well-established gradient from striate to papillate ornamentation with increasing depth exhibited by the uvigerinds (3, 30).

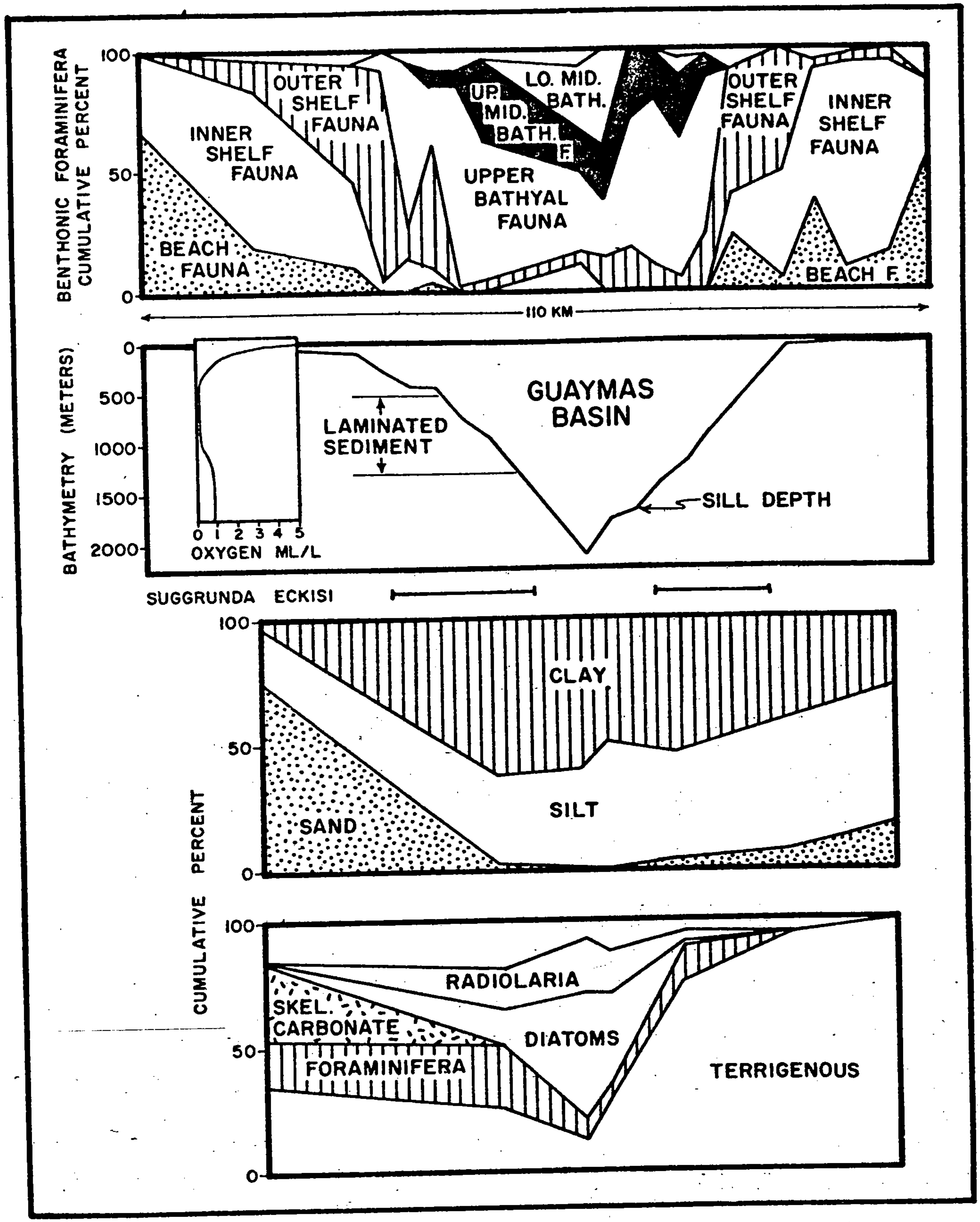

Fig. 8-13 Cumulative distribution of benthonic foraminiferal biofacies, Recent sediment type, lithologic constituents, and bathymetry across Guaymas Basin, Gulf of California (30). Note that limits of oxygen minimum zone in this basin coincide with the distribution of *laminated* diatomaceous sediments. The benthic species *Suggranda eckisi* Natland serves as an index to the low oxygen conditions. Differences in the amount of terrigenous material and foraminifera on the east and west flanks of the basin reflect the difference in rate of influx of sediment from each coast and the presence of a deep-sea fan on the east flank.

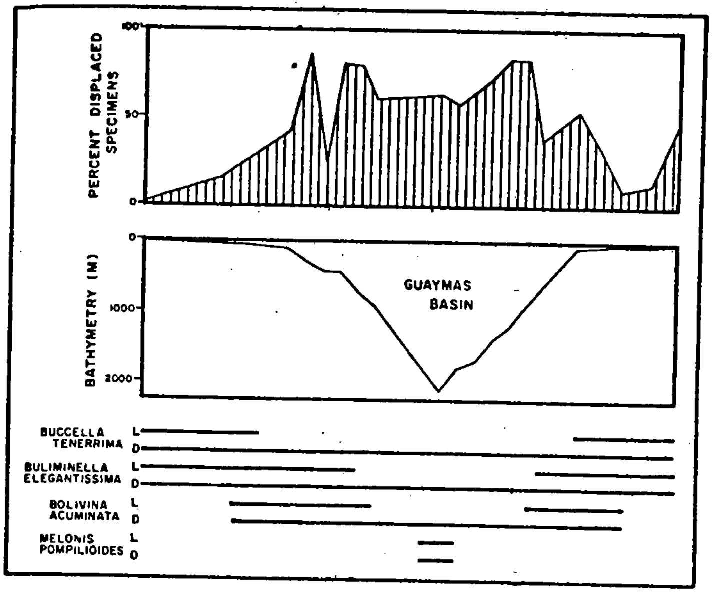

Fig. 8-14 Percentage of displaced (redeposited) benthonic foraminifers, distribution of both live and dead specimens of selected species: of benthonic foraminifers, and bathymetry along on east-west traverse across Guaymas Basin, Gulf of California (30).

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