

Interpreting long-term changes in benthic community structure: a new protocol

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Abstract

Documentation of long-term change in benthic ecosystems is important for assessing and managing the effects of such change on: 1) secondary production, particularly leading to commercially important food webs, 2) pollutant transfer within the food web, 3) the ability of the 'new' assemblage to metabolically burn-off labile detritus that might otherwise accumulate, contributing to long-term hypoxia, and 4) recycling of nutrients from the seafloor back to primary producers.

Organism-sediment relationships which accompany benthic disturbances have predictable features. Although participating species may vary regionally or seasonally, their life-history attributes and functional relationships to the associated sediment appear to be universal. Pioneering seres are near-surface dwelling, productive, and are readily available to demersal predators. However, these taxa may be potential pollutant vectors. Dense tube mats may promote the deposition and retention of high BOD organic matter. Late successional stage seres are represented by deeply bioturbating 'head-down' deposit feeders. The deep cryptic infaunal habitat of these species may make them less important as prey for epifaunal predators. Sediments populated by these equilibrium assemblages are characteristically low in labile organic matter, sedimentary sulphides, and oxygen demand. Nutrients (N, P, Si) are returned to primary producers by biogenic irrigation of sediment pore water.

Mapping of successional mosaics is important for documenting major long-term change in benthic community structure and associated biogenic processes. Our mapping tool consists of a vessel-deployed sediment-profile camera; organism-sediment relationships can be imaged *in situ* with this instrument. Such a mapping protocol is not intended to replace traditional sampling. Rather, the successional maps are used to efficiently detect change in a system, design a cost-efficient sampling grid for obtaining geochemical and biological ground-truth samples, and to construct hypotheses about how the change might answer the four outlined management questions.

Introduction

The majority of environmental monitoring or assessment work over the last few decades has consisted of short-term research (i.e., less than one or two years) to provide short-term answers to problems recognized as 'urgent' at the time of the study. This is particularly true with marine studies, where costs associated with field sampling operations are fairly significant. History has shown that long-

term, irreversible changes affect man most seriously; even the structure seen in natural, undisturbed communities is usually controlled by infrequent severe events that disrupt the community and return the successional process to an earlier stage (Green, 1984). Long-term studies are needed to obtain reliable estimates of both natural variation in undisturbed systems as well as interpreting the long-term effects of impacts on complex systems.

Four management issues are raised regarding the

significance of long-term change in benthic community structure on: 1) secondary production and its importance for commercially important species, 2) pollutant transfer within the food web, 3) the ability of the 'new' benthic assemblage to metabolically burn-off labile detritus that might otherwise accumulate contributing to long-term hypoxia, and 4) recycling of nutrients from the seafloor back to primary producers. It is our opinion that existing monitoring methods do not provide much useful information regarding these management questions.

It is our purpose to draw attention to the shortcomings of existing approaches to benthic monitoring and to offer an alternative approach which may provide more useful information to those charged with the responsibility of making management decisions about changes in benthic community structure. It is becoming increasingly clear that unless managers are provided with more useful paradigms and efficient monitoring methods, traditional monitoring approaches will be curtailed. This trend is already apparent in the United States and has had a serious effect on both pure and applied benthic research. In fact, the inadequacy of the type of information gained from traditional benthic sampling methods for use by environmental managers coupled with the associated expense and slow data return have most likely been responsible for the lack of long-term benthic monitoring efforts to date.

Our perspective will be focused on fine-grained subtidal sediments for three reasons: 1) this is the dominant facies in many estuaries and embayments; 2) particle-bound pollutants are often associated with muds; and, 3) this facies may be associated with hypoxia and methanogenesis.

Critique of existing methods

Over the past 15 years, a great deal of applied benthic work has been done in the context of environmental baseline studies, impact assessment, and monitoring. Most of this work, including our own, involved traditional benthic sampling methods, i.e. grab or box-core sampling followed by removal of the organisms from the sediment by sieving. The resulting samples are used to generate species abundance lists, diversity and faunal similarity indices, and community dendrograms. The resulting base-

line statistics are then mapped in space or compared over time in order to characterize the range of natural variation. With these baseline data in hand, investigators attempt to infer pollution or disturbance events at those stations where a change in diversity (or other measure of structure) has occurred at a selected level of significance.

Two major problems with the above traditional approach have prompted us to abandon this type of monitoring. The first problem stems from the kind of information that is provided. For the last three decades, benthic investigators have been searching for means of extracting ecological information from species lists, attempting to convert descriptive, natural history observations into a format that would convey the impression of a 'hard' science (what Gould, 1981, has appropriately described as 'physics envy'). The calculation of species diversity indices popularized in the 1960's has persisted within the community of benthic ecologists, even though most terrestrial ecologists have abandoned their use years ago. Peet (1974) has pointed out that one of the strongest objections to using a diversity index for comparing a variety of habitats is that there is no valid basis for comparing the richness of a series of communities using a single index unless one can assume that the underlying species-individuals relationships are similar. A variety of other investigators have pointed out the many shortcomings of diversity indices (e.g., Green, 1979; Routledge, 1980; Wolda, 1981).

With the increased use of computers and application of multivariate techniques, benthic ecologists are now attempting to interpret changing patterns of species distributions in time as well as space, trying to extract ecologically meaningful information from the large volume of data that a benthic survey typically produces by using techniques such as factor and cluster analyses. Gould (1981) has pointed out that the decision to use techniques like these as the primary method to analyze large data sets implies a deep ignorance of principles and causes, in reality an elegant method of grasping for straws; these methods should be applied with the hope that they might provide suggestions for more fruitful lines of inquiry. Unfortunately, large scale benthic surveys rarely, if ever, progress beyond this, viewing the dendrograms and resolution of principal components as the end result.

Information statistics, per se, commonly provide little ecological insight. Beyond documenting that a change has occurred in benthic population structure, these data do not provide information that can be used by a manager to make judgements as to whether the documented change is desirable or will have a negative impact on the system in terms of resource management objectives.

Other than saying that diversity has changed, what other information can be provided to an environmental manager? In a management context, the definition of a desirable or negative impact is usually judged in terms of how a long-term change might ultimately effect man. The problem can be reduced to the question of what is intrinsically positive or negative (in an ecosystem sense) about a relatively high or low diversity facies or a system that experiences periodic change in diversity? The only unequivocal answer would be related to an event which resulted in a high or low diversity system reverting to an azoic state (zero diversity). This dramatic change would clearly result in a non-productive system (and would not require the calculation of diversity indices to illustrate the point). If maintenance or enhancement of production is the management goal, this change is clearly a negative one. However, this extreme case is a rare example; most monitoring involves the detection of more subtle gradients in species abundances, number of species, and biomass. The manager is then faced with the inevitable 'So what?' question once a change in population structure is demonstrated. This problem has also been noted by Gray (1976), who cites the inadequacy of existing theoretical frameworks for interpreting the significance of change in benthic community structure.

The second problem concerns techniques for sampling the benthos in order to detect long-term change. Sampling tools for large scale surveys traditionally have been limited to grab or box-core samplers. This method of sampling the bottom and associated on-deck processing results in various degrees of destruction of important *in situ* ecological information which is contained in the spatial and structural relationships of benthic organisms to one another and to the associated sedimentary matrix. This destruction can occur in a variety of ways, either from the pressure wave which precedes the instrument as it approaches the bottom, from water passing through the sampler and washing

away the sediment surface during recovery, or from the final process of sieving the sample, which destroys any remaining organism-sediment information. The ensuing sorting and faunal identification is extremely labor-intensive and expensive; there is characteristically a long time-lag between field collection and data return or final interpretation. While grabs and box corers will always be important for quantitative sampling, sampling technology needs to be advanced so that benthic gradients can be more rapidly and efficiently mapped *in situ* by remote methods. Reconnaissance mapping techniques can then be used to detect major changes in benthic communities; once a change has been detected, reconnaissance maps can serve to locate station positions for efficient sampling with traditional quantitative methods.

An organism-sediment successional paradigm

Organism-sediment relationships which accompany benthic disturbances have predictable features. The term disturbance is used here to define natural processes, such as seafloor erosion, changes in seafloor chemistry, foraging disturbances which cause major reorganization of the resident benthos, or anthropogenic impacts, such as dredged material or sewage sludge dumping, thermal effluents from power plants, deposition of drilling muds and cuttings, pollution impacts from industrial discharge, etc. Because the perspective of this paper is to address long-term change, these disturbances must be extraordinary, i.e. beyond the ability of the resident benthos to regulate or accommodate the perturbation. Infaunal succession in shallow nearshore clastic sediments commonly takes between 1 and 10 years: '... it appears that over a wide range of communities many successions take about as long as the average longevity of the dominants of the infrequently disturbed or "climax" community' (McCall & Tevesz, 1983).

Figure 1 shows the progressive development of the infaunal community over time following deposition of dredged materials (1A) and the shallow to deep spatial tiering of infauna along a pollution gradient (1B). Although these examples show different taxa participating in various stages of infaunalization, the organism-sediment relationships appear to be similar (see Rhoads & Germano, 1982, for details). This primary succession is defined as

'the predictable appearance of macrobenthic invertebrates belonging to specific functional types following a benthic disturbance. These invertebrates interact with the sediment in specific ways. Because functional types are the biological units of interest, our definition does not demand a sequential appearance of particular invertebrate species or genera.' (Rhoads & Boyer, 1982).

An important aspect of using this successional approach to interpret benthic monitoring results is relating organism-sediment relationships to the dy-

namical aspects of end-member seres. This involves deducing dynamics from structure, a technique pioneered by R. G. Johnson (1972) for marine soft-bottom habitats. The application of an inverse methods approach to benthic monitoring involves making *in situ* measurements of salient structural features of the organism-sediment relationships shown in Fig. 1. This can be accomplished with sediment profile photography (Rhoads & Cande, 1971; Rhoads & Germano, 1982). The organism-sediment relationships illustrated in Fig. 1 can be

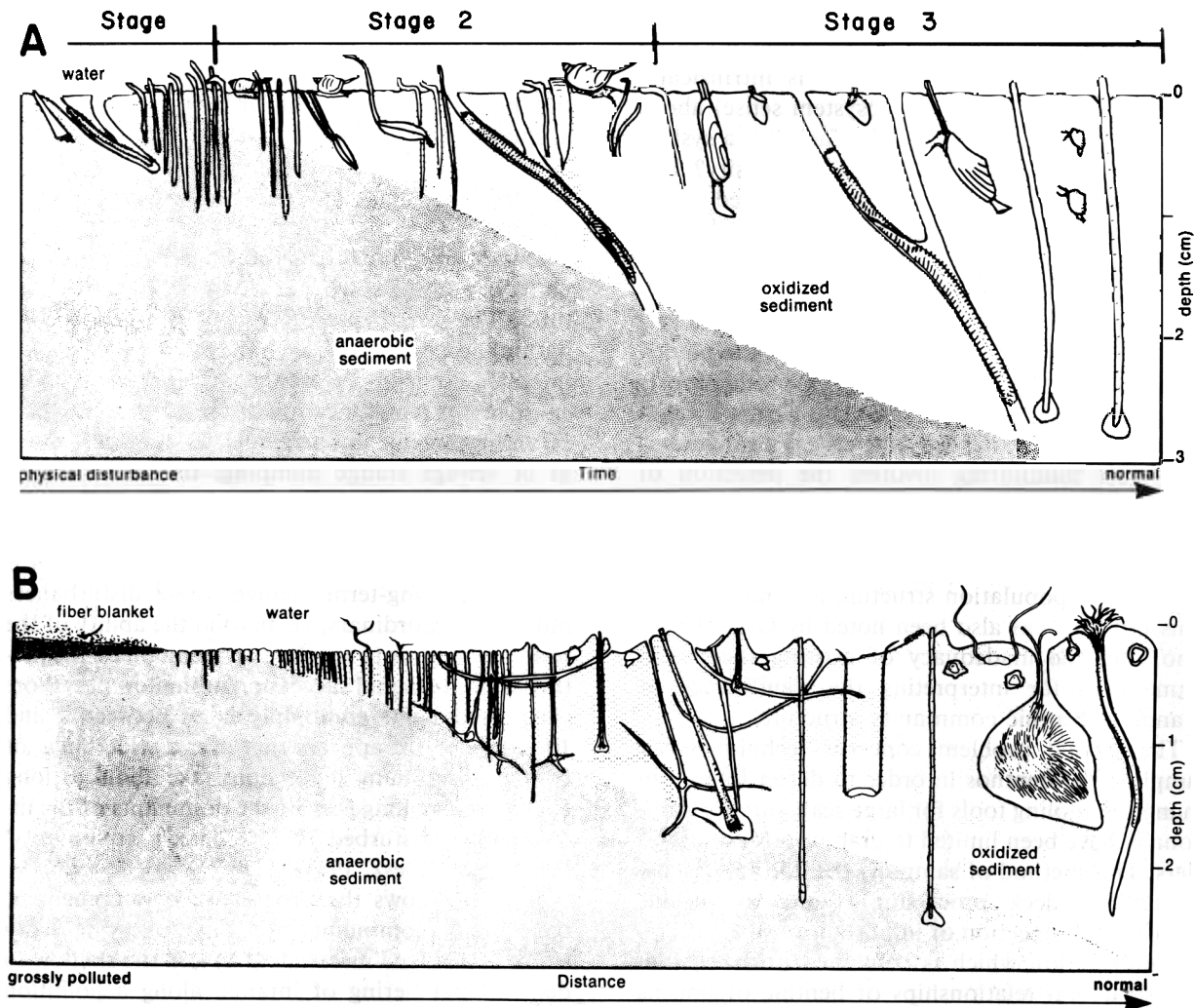


Fig. 1. (A) Development of organism-sediment relationships over time following a physical disturbance in Long Island Sound, USA. Subsequent mapping experience shows that the values on the depth axis also vary seasonally and with the dominant bioturbating taxa in the Stage III sere. Later work has also shown that in environments rich in labile detritus, Stage I polychaetes can co-exist with Stage II and Stage III seres. (B) Organism-sediment relationships associated with a pollution gradient associated with a pulp-mill effluent. Modified from Pearson and Rosenberg (1978). This figure is from Rhoads and Germano (1982). See text for additional discussion.

imaged *in situ* using this technique.

Long-term degradation of the benthic environment frequently involves the loss of equilibrium species (shown at the right-hand side of Fig. 1). These high-order seres are then replaced by pioneering seres (left-hand side of Fig. 1). Changes in organism-sediment relations and population dynamics accompanying this change are summarized below with examples (for a more complete discussion, the reader is referred to reviews by Pearson & Rosenberg, 1978; Rhoads & Germano, 1982; Rhoads & Boyer, 1982).

Many representatives of high-order seres (subsequently referred to as Stage III seres) are deeply burrowing errant or tube-dwelling infauna which feed head-down (conveyor-belt species *sensu* Rhoads, 1967). These infauna advect particles over vertical dimensions of several centimeters. The areas of subsurface feeding are recognized as water-filled pockets (feeding voids) which contain coarse sediment which apparently has been rejected in the feeding process. Dominants in these Stage III assemblages include, for example, maldanid, pectinid, and orbinid polychaetes, caudate holothurians, protobranch bivalves, some infaunal ophiuroids and irregular urchins (see above reviews for further discussion). These taxa typically have larger body sizes and longer mean life spans than early successional seres. The *in situ* mapping of Stage III seres requires the recognition of subsurface feeding pockets which identify the presence of these conveyor-belt species. Examples of Stage III seres from a wide geographic range of near-shore environments are shown in sediment-profile images in Fig. 2.

These stages are also associated with a thick near-surface zone of high-reflectance sediment related to deep bioturbation. This high reflectance layer is related both to the presence of ferric hydroxide coatings on particles and to low concentrations of pore-water sulphides. Although the presence of ferric hydroxide coatings on particles indicates that at some time these particles have been in a positive redox environment, one may not assume that pore waters are aerobic at the time of sampling from their presence alone unless microprobe redox measurements have been made (Revsbech *et al.*, 1979). Nevertheless, we have found measurements of the thickness of the apparent positive redox zone (as manifested in high sediment

reflectance) to be correlated with the depth of infaunal bioturbation and useful in reconnaissance mapping of physical and biological disturbance gradients on the seafloor. The thickness of this zone can be expected to change seasonally in benthic environments where changing water temperatures affect rates of bioturbation. For this reason, maximum information from this reconnaissance mapping technique can be obtained during the summer and early autumn when bioturbation rates are high. Pearson & Stanley (1979) have also mapped redox depths as an efficient means of detecting pollution gradients.

The mapping of early or low-order successional stages, subsequently referred to as Stage I seres, requires the recognition of small tubicolous polychaetes or oligochaetes at the sediment surface. These may be very densely aggregated, particularly in eutrophic environments (Fig. 3). Stage I assemblages commonly are not quantitatively sampled in most benthic monitoring studies, particularly if the sieve mesh diameter that is used for processing samples is greater than 0.3 mm (Germano, 1983b). This successional sere is dominated by tubicolous worms that feed on labile detritus located at, or near, the sediment surface. Capitellid and spionid polychaetes are the commonly encountered members of this sere (Pearson & Rosenberg, 1978; Rhoads *et al.*, 1978); meiofauna may also dominate (Rudnick *et al.*, 1985). Because the exploited resources are located near the sediment surface, the feeding and bioturbation zone is thin. The thickness of the apparent redox zone therefore is also thin or may even be absent in habitats where dissolved oxygen is low in concentration (Fig. 3B).

The long-term recovery of a benthic habitat, starting at an azoic or Stage I sere, may involve a transitional stage (Stage II sere) before a Stage III (equilibrium) system is established. This may involve the appearance of a diverse assemblage of tubicolous amphipods, molluscs, and polychaetes. Some head-down feeders may appear at this stage, but a major fraction of the colonizing assemblage will tend to feed at, or near, the sediment-water interface. The thickness of the apparent positive redox layer is typically transitional between an early pioneering polychaete Stage I and a Stage III assemblage (Fig. 1). In our experience, Stage I taxa can persist and are commonly associated with Stage III seres. In the retrograde transition of

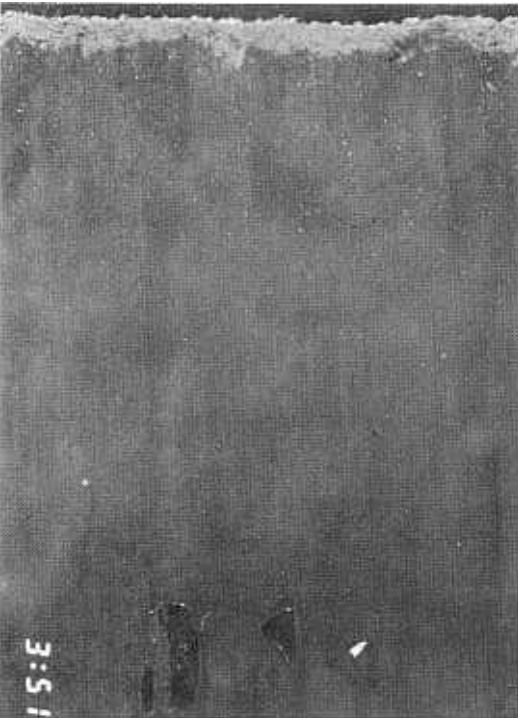
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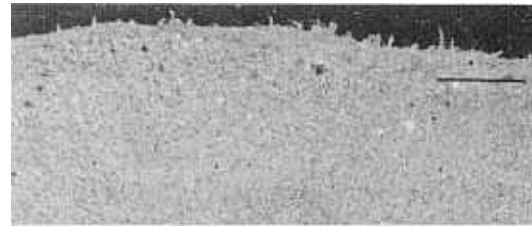
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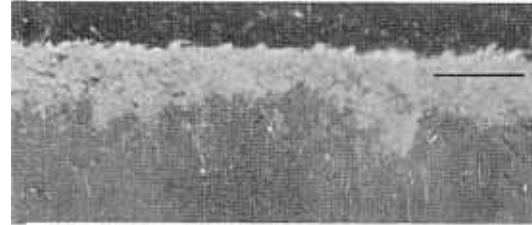
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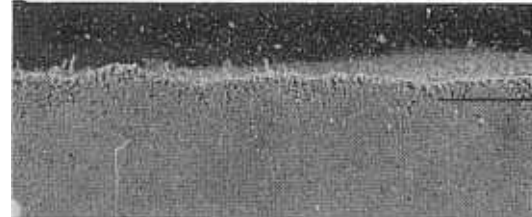


Fig. 3. Examples of Stage I seres from a wide range of subtidal sediments. Figures 3 A-C are 15 cm in width. Bar scales in D-F equal 1 cm. (A) A Stage I sere populating a sandy layer overlying mud on the inner continental shelf of the Gulf of Mexico. An enlarged view of these polychaetes is shown in (D). (B) A Stage I sere from western Long Island Sound showing a shallow apparent redox boundary, sulphidic sediment, and methane gas bubbles at the bottom of the photograph. An enlarged view of the surface is shown in (E). The profile camera was fitted with a dissolved oxygen probe located near the top of the optical window with a digital readout in the window. When this image was taken, the instantaneous dissolved oxygen reading 2 cm above the bottom was 2.9 mg/l. (C) A late Stage I sere from central Long Island Sound showing that the apparent redox boundary can be depressed to over 4 cm with this assemblage. An enlarged view is shown in (F).

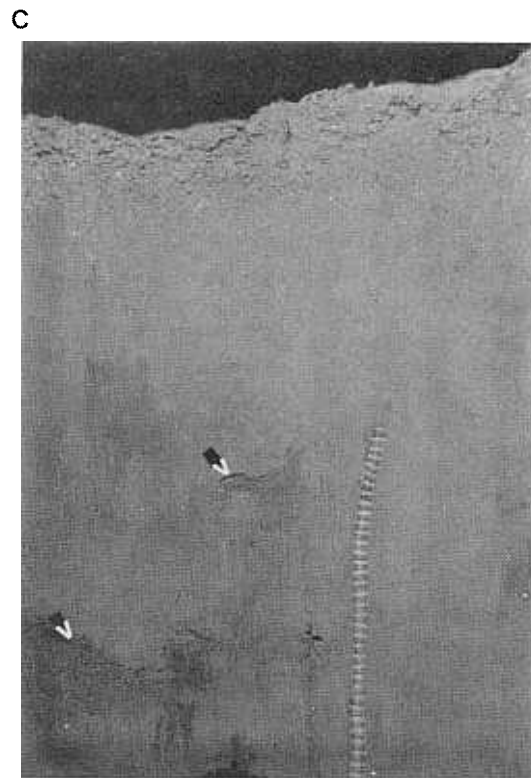
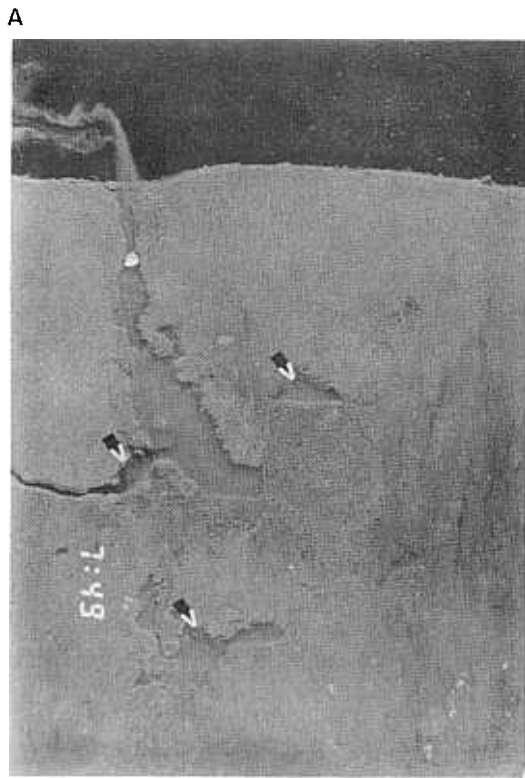


Fig. 2. Examples of Stage III seres from a wide range of subtidal muds. Arrows identify the presence of active feeding voids (i.e., open feeding pockets) produced by head-down conveyor-belt deposit feeders. The width of each photograph is 15 cm. (A) Subsurface feeding by maldanid polychaetes in the lower Chesapeake Bay. (B) A Stage III sere from the inner continental shelf of the Gulf of Mexico. Note Stage I taxa at the sediment surface. Species producing the subsurface feeding voids is not known. (C) Stage III feeding voids from the mouth of the Bay of Fundy. (D) A stage III community consisting of the bioturbating caudate holothurian *Molpadia oolitica* and maldanid polychaetes from Cape Cod Bay, Massachusetts. Note the presence of Stage I polychaetes at the surface (*Euchone incolor*). (D) has been reproduced from Rhoads & Young (1971).

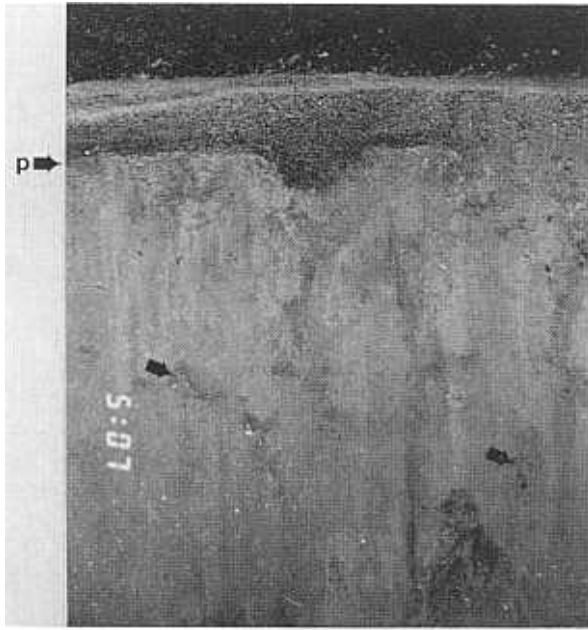


Fig. 4. A sediment profile image showing the record of a retrograde succession in the upper Chesapeake Bay. The symbol 'P' identifies the interface between a prehypoxic interval (below) and a hypoxic interval (above). The prehypoxic interval consists of high reflectance sediment (low pore-water sulphides) and the remnants of relict, i.e. collapsed and inactive, feeding zones for Stage III taxa (arrows). The hypoxic interval consists of reduced fecal pellets of Stage I taxa.

Stage III to Stage I, it is sometimes possible to recognize the presence of relict (i.e. collapsed and inactive) feeding voids (Fig. 4).

Deducing dynamics from structure

The structural and spatial relationships of organisms to their sedimentary habitat, as described above, can be used to infer dynamical aspects about benthic secondary production, food web contamination, bottom water hypoxia, sediment reworking, and nutrient recycling. These structure-process relationships are summarized in Table 1.

Secondary Production: The relationship of the successional paradigm to secondary production is based on field work which has shown that populations of pioneering species have very high intrinsic rates of increase, and that annual or subannual disturbances may enhance secondary production by stimulating repopulation of newly opened space (Odum, 1969; Rhoads *et al.*, 1978; McCall & Tevesz, 1983). There is also some preliminary evidence that disturbances which promote the diffusion of hydrogen sulphide from bottom sediments into the water column may attract pioneering species to such disturbance sites (Cuomo, 1985). Because the biomass of pioneering seres is concentrated at, or near, the sediment surface, this productive stage

Table 1. Benthic ecosystem attributes associated with pioneering and late stage seres.

System attribute	Successional stage		Selected references
	<i>Early (Stage I)</i>	<i>Late (Stage III)</i>	
Secondary production	High potential for r-selected taxa	Lower potential for K-selected taxa	Odum (1969); Rhoads <i>et al.</i> (1978); McCall & Tevesz (1983).
Prey availability	High as prey are concentrated near the surface	Lower as infauna are deep burrowing*	Becker & Chew (1983); Smith (1985).
Potential for food-web contamination	Highest for suspended or recently sedimented particulates. Body burdens may be low related to short mean life-spans(?)	Highest for deeply buried contaminants. Longer mean life spans may lead to significant body burdens(?)	Bryan (1985); Lee & Swartz (1980); Swartz & Lee (1980); Phelps (1967).
Nutrient recycling	Limited to solutes in ≤ 3 cm	Solutes exchanged over distances to 20 cm or deeper	Aller (1978), (1980), (1982), (1985); Lee & Swartz (1980); Rice (1986).
Potential for bottom water hypoxia	High, storage systems for labile detritus	Low, a recycling or 'purging' system	Untested hypothesis

* Non-lethal predation of distal ends of siphons or caudal segments may be important for some predator species (DeVlas, (1979); Trevallion *et al.* (1970); Woodin (1982), (1984)).

may provide food for commercially important secondary consumers (Rhoads *et al.*, 1978; Becker & Chew, 1983).

Stage III seres, in contrast, are populated by species having relatively low ontogenetic and population growth rates. These infaunal species live cryptically within the sediment and commonly do not show significant seasonal changes in abundance or biomass (McCall & Tevesz, 1983). Stage III taxa may therefore prove to be less important as prey than Stage I species. However, Woodin (1985) has shown that non-lethal predation (presumably by demersal fish) of the caudal ends of maldanid polychaetes (a common Stage III taxon) can occur.

Once successional mosaics have been mapped, questions involving the importance of each sere to commercial fin-fisheries and potential pollutant transfer within the benthic food web can be investigated employing a Benthic Resources Assessment Technique (BRAT) (Lunz & Kendall, 1982). This involves quantitative sampling of demersal fish and potential invertebrate prey species from the different infaunal successional stages that are mapped. The size-class distribution of major taxa of ingested prey is determined from stomach contents and is compared with the size-class distribution of prey species as a function of depth in the sediment for each type of successional assemblage sampled. This is accomplished by separately sieving strata removed from vertically partitioned box cores (Fig. 5). Identification of the available zone or maximum feeding depth in the sediments used by a specific demersal predator can be accomplished by comparing relative prey size distribution patterns in a predator's diet with environmental size-depth patterns from the box core samples. These data can then be used to identify a subset of species for subsequent tissue analysis of both predators and their prey relative to the range of pollutants in local sediments that may be of concern. The success of such a BRAT analysis depends on the investigator's ability to establish the food spectrum of different year-classes of fish and seasonal or diel differences in foraging and prey availability.

Food Web Contamination: Because the feeding and bioturbation depths of Stage I pioneering seres are not as great as Stage III seres, pioneering taxa are exposed to contaminants associated with the near sediment surface zone. Phelps (1967) showed that partitioning of stable elements (Fe, Zn, Sc, and

BENTHIC RESOURCES ASSESSMENT TECHNIQUE (BRAT)

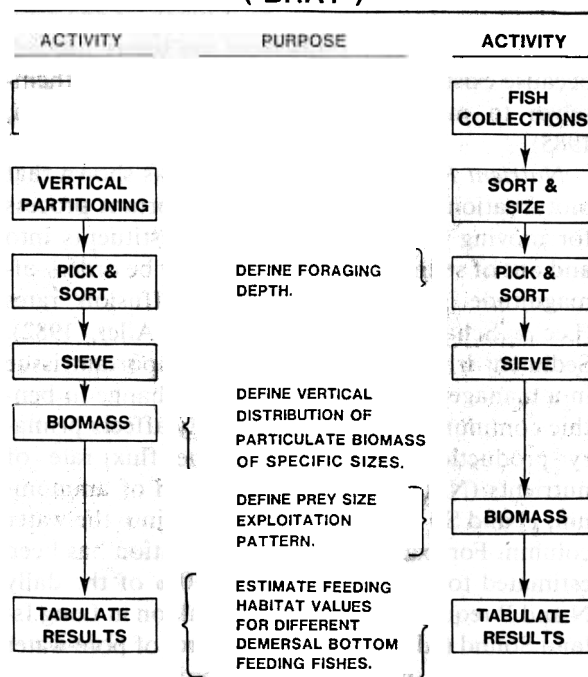


Fig. 5. A flow chart showing the operational procedures involved in relating the resource value of different benthic successional stages to commercially important predators through the BRAT technique; see Lunz & Kendall (1982) for additional details.

Sm) within a benthic community could be related to the vertical stratification of feeding. Iron is preferentially partitioned into tissues of near surface feeders while Zn is concentrated in deep burrowers. Partitioning of toxic metals, radionuclides, and organic toxins may also be related to feeding depths, local redox conditions and quality of organic substrates.

The difference in mean life-spans between Stage I and Stage III taxa suggests that bioaccumulation of some pollutants may be less of a problem with early successional stages than with late stages. This hypothesis has not been adequately tested, because the small polychaetes or oligochaetes associated with disturbed habitats are commonly not sampled. In those studies where they have been sampled, tissue analysis has not been done because of the small size of individuals. Nevertheless, a general appreciation of these rela-

tionships is leading to the practice of capping polluted dredged materials with a clean layer of sediment that exceeds the mean bioturbation depth of local Stage III taxa (Sumeri, 1984). Additional field data concerning this issue are sorely needed, because existing laboratory data do not lend themselves to making long-term predictions (Bryan, 1985).

Nutrient Recycling: Recent work has shown that bioturbation is a quantitatively important process for moving water and dissolved constituents into and out of sediments; this process may be orders-of-magnitude greater than simple diffusion rates (Lee & Scharz, 1980; Aller, 1980; Aller, 1982). Sediment irrigation can be a very important issue in a management context when the change in benthic community structure ultimately affects primary production by controlling the flux rate of nutrients (N, particularly in the form of ammonium, P, and Si) from the bottom back into the water column. For example, sediment irrigation has been estimated to provide from 10 to 30% of the daily N and P requirements of phytoplankton in Long Island Sound (Aller, 1980). The control of pore-water chemistry by macrofaunal colonizers has been shown in detailed studies of early chemical diagenesis of disposed dredged material (Rhoads *et al.*, 1977). The early colonization phase is characterized by diffusional profiles of pore-water sulphate, ammonium, and phosphate. Near-surface regions of these profiles are progressively influenced by biogenic irrigation as colonization progresses. The flux rate of pore-water solutes is not only a function of the cumulative pumping rate of infauna, but the flux and reaction rates are also affected by three-dimensional diffusion geometry (Aller, 1982). Detailed descriptions of this phenomenon has been described for protobranch bivalves (Aller, 1978), and maldanid (Aller, 1978), capitellid (Aller & Yingst, 1985), orbiniid (Rice, 1986), and terebellid polychaetes (Aller & Yingst, 1978). Burrows and tubes effectively increase the three-dimensional surface area of diffusion boundaries. This geometry is best developed in Stage III seres and can be quantitatively important for recycling nutrients back to primary producers.

The relative importance of Stage I successional seres in nutrient cycling is not well documented. However, many pioneering polychaetes live in short, cylindrical tubes which may have composi-

tional properties that serve to decrease diffusion coefficients across the tube wall (Tenore *et al.*, 1982: 747). The biogenically mixed zone is relatively shallow. Although sediments populated by pioneering seres may contain large inventories of nutrients, the return of these nutrients to the water column will be largely controlled by molecular diffusion rates. In this sense, sediments associated with pioneering seres have the potential to be storage systems, while those populated with Stage III seres may be considered as purging or recycling systems. From these relationships, we hypothesize that a long-term change in community structure involving the replacement of a Stage III sere with a pioneering stage may result in a decrease in bioturbational nutrient cycling from bottom sediments to primary producers in the water column.

Bottom-water Hypoxia: Eutrophication of coastal areas often results in the sedimentation of labile planktic detritus at a rate which exceeds the ability of the benthic system to metabolize this detritus by aerobic pathways. Excess labile organic matter therefore accumulates, producing a high demand for oxygen which (depending on oxygen supply rates) may result in bottom water hypoxia. This phenomenon is particularly acute in the summer period when the combined potential for high water temperatures, low oxygen solubility, little wind mixing, and water column stratification exists (Officer *et al.*, 1984). Although hydrographic factors are of first-order importance for the supply of oxygen, Stage III seres may play an important role in preventing the build-up of labile organic matter in sediments. Deep biogenic irrigation of the sediment column increases pore-water oxygen and maintains positive Eh conditions up to several centimeters below the surface (Lee & Swartz, 1980). Figure 6 shows that under subcritical input rates of labile detritus, Stage III macrofauna may be able to balance the potential deleterious effects of inputs of labile organic matter by stimulating microbial processes. According to Aller (1981), this is done by: 1) increasing particle surface areas, 2) grazing, which keeps microbial populations in log-phase growth, 3) flushing metabolites from pore waters, thereby keeping electron acceptors continually supplied by irrigation, particle reworking, and multi-dimensional diffusion, 4) secreting mucus to provide new reactive substrates, and 5) subducting labile surface organic matter to be metabolized at

depth. A major research issue in benthic ecology that needs to be addressed is the determination of the critical organic loading rate for Stage III seres, i.e., the rate which causes their local extinction. Once this is known, the datum may prove valuable for managing anthropogenic inputs of nutrients and labile organics.

Once the critical organic loading rate is exceeded, Stage III taxa are locally eliminated, and organic enrichment species (*sensu* Pearson & Rosenberg, 1978) dominate (Fig. 7). This may be related to the accumulation of antibiotic decomposition products (Bader, 1954), low dissolved oxygen (Rhoads & Morse, 1971), sulphides, or a combination of these factors. As described earlier, the influence of Stage I seres on nutrient cycling and aeration of the sediment column may be very limited. Hence, sulphate reduction and methanogenesis predominate over oxidative metabolism. These metabolites, sulphides, ammonium, and methane contribute further to bottom water oxygen demand as they diffuse into the water column. The loss of a Stage III sere from an area and its replacement by a Stage I sere may be expected to be accompanied by a major change in both the depth and rate of biogenic processing of bottom sediments. Evidence of such a retrograde succession is an early warning sign of the potential for developing hypoxic or anoxic conditions in the near future. An important attribute of Stage III seres is that they apparently serve to prevent the accumulation of labile organic matter; Stage I seres, in contrast, tend to be associated with storage areas of high BOD organic matter. Dense tube mats associated with some pioneering seres may in themselves promote the sedimentation of fine organic particulates by changing flow conditions near the bottom (Lee & Swartz, 1980; Nowell *et al.*, 1981; Rhoads & Boyer, 1982). Spatial gradients between Stage I and Stage III seres can be very sharp, suggesting that once a critical organic loading rate is exceeded, Stage III taxa are completely eliminated (eg. Fig. 9C).

Methods of *in situ* successional mapping

In order to obtain *in situ* data about organism-sediment relationships, we have developed a new method of obtaining information about the seafloor. This has been accomplished with sediment-profile imaging. The instrument consists of an op-

tical prism operated like an inverted periscope which cuts a vertical profile of up to 20 cm of the sediment column. This optical corer transects the bottom at a fall rate of about 6 cm sec⁻¹ in order to minimize physical disturbance. The prism is filled with distilled or filtered water so that ambient bottom turbidity does not compromise image quality. Optical resolution is approximately 0.06 mm. The instrument is deployed from a vessel, and once lowered to the bottom, an image can be taken every 40 seconds. An example of a sediment-profile camera is shown in Fig. 8. A survey taken with such a sediment-profile camera can generate up to 200 images in one survey day. Efficient data analysis and recording is accomplished with computer digital image analysis, permitting systematic measurement of up to 22 variables per image in about 4–6 minutes. For mapping purposes, several of these parameters are considered together, expressed as an Organism-Sediment Index (Table 2). In some cases, tentative taxonomic identifications can be made from imaged epifaunal species or from diagnostic structures produced by infauna. More detailed descriptions of the instruments and the theory of image interpretation are given in Rhoads & Germano (1982) and Germano (1983a).

An example of how reconnaissance maps can be generated by a sediment-profile camera survey and

Table 2: Method of calculating the Organism-Sediment Index. This index reflects the apparent mean redox potential discontinuity depth in the sediment, the presence or absence of sedimentary methane, dissolved oxygen over the bottom, and successional stage.

Chemical parameters		Biological parameters	
Mean apparent RPD depth, (cm)	Index value	Successional stage (Primary succession)	Index value
0	0		
>0	-0.75	1 Azoic	-4
	0.76–1.50	2 Stage 1	1
	1.51–2.25	3 Stage 1–2	2
	2.26–3.00	4 Stage 2	3
	3.01–3.75	5 Stage 2–3	4
	>3.75	6 Stage 3	5
Methane present	2	(Secondary succession)	
No/low O ₂	4	Stage 1 on Stage 3	5
		Stage 2 on Stage 3	

Benthic index = Sum of chemical and biological index values.
Potential index range: -10 to +11.

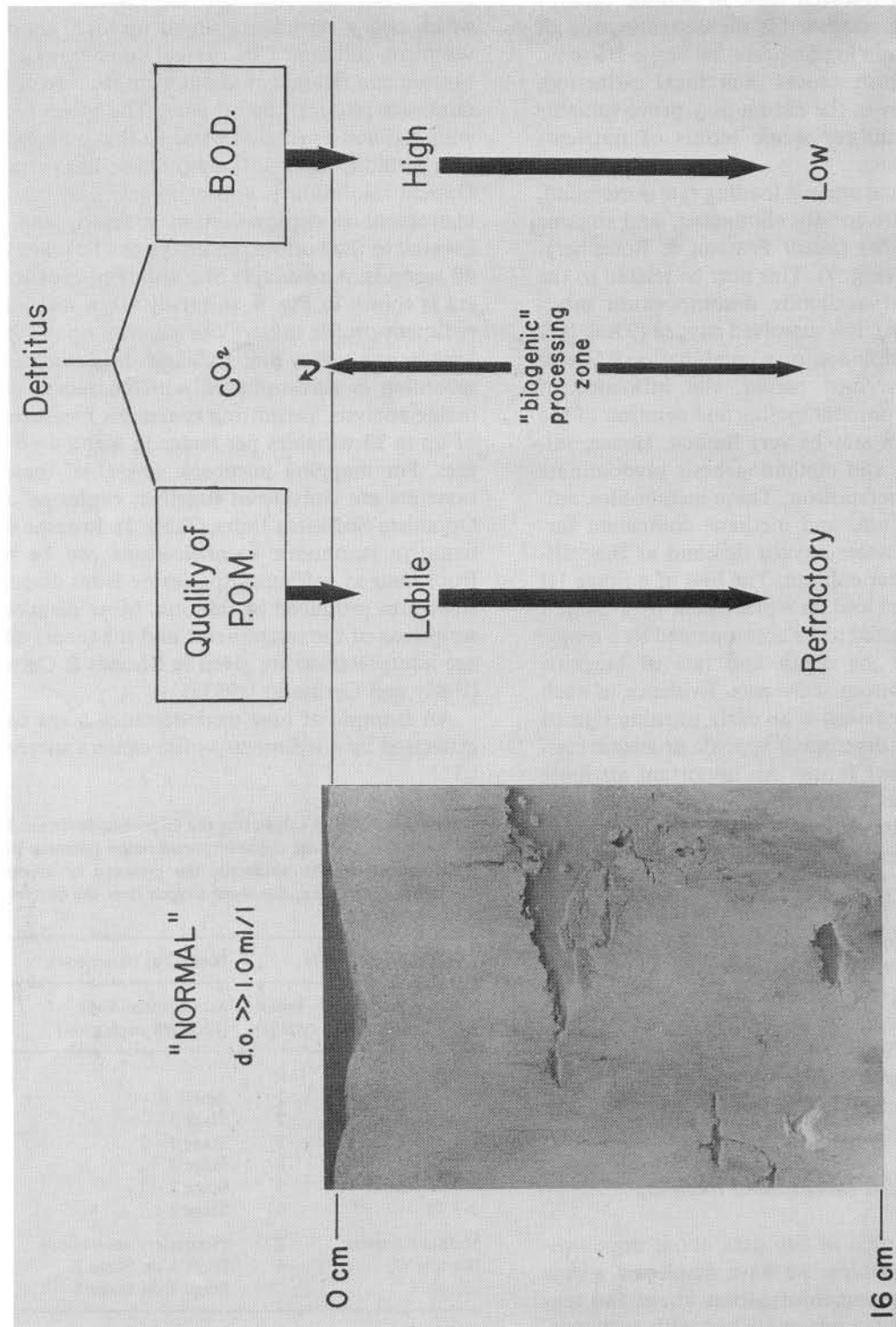


Fig. 6. Stage III seres appear to be able to prevent the build-up of pore-water nutrients and labile organic matter by their deep bioturbation and head-down feeding habit. This apparently can only take place below a critical organic loading rate, where the overlying water is maintained in an aerobic condition. This critical loading rate has not been documented for stage III systems. We infer these relationships from mapping enrichment gradients in the Chesapeake Bay and western Long Island Sound.

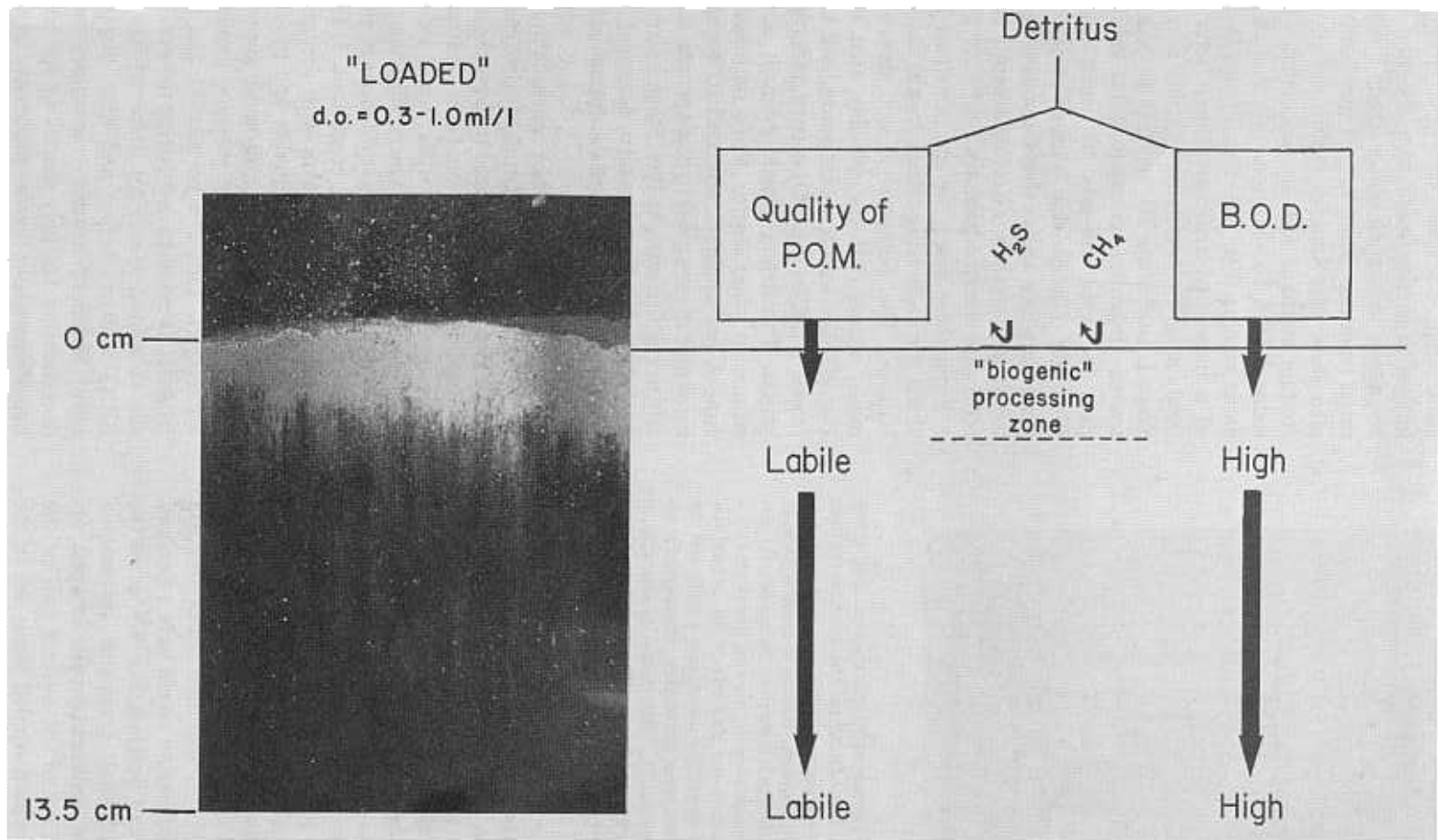


Fig. 7. Stage I seres are characterized by a shallow biogenic processing zone. This type of association is commonly well-developed in a partially aerated (dysaerobic) zone. Such bottom types may be periodically productive but the long-term storage of labile organic matter may result in anoxia and total loss of macrofaunal productivity.

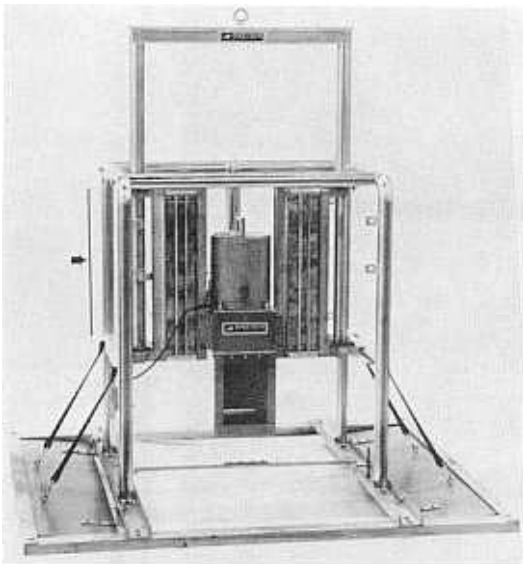


Fig. 8. An example of a Sediment-Profile Camera. The arrow identifies a scale bar which equals 50 cm. The doors on the base are only used to deploy the instrument on very soft substrata. The optical prism is held above the bottom to avoid a pressure wave disturbance as the camera is lowered to the bottom. As tension is released on the winch wire, the inverted periscope cuts a vertical profile of the bottom at a slow rate of fall. Several station replicates are taken by pulling the camera a meter off the bottom and setting it back onto the bottom. Photographic sequencing is done automatically. This system is operable to 4000 meters. Photograph provided by Benthos, Inc., North Falmouth, Massachusetts.

used to make management decisions is shown in Fig. 9 for an 3.2 sq. km area in the lower Chesapeake Bay off the mouth of the Rappahannock River. This survey involved occupying 30 stations (3 replicates each) on a 6×5 orthogonal sampling grid. The survey was completed in one day and the maps were available to managers within 30 days. The purpose of the survey was to evaluate this area (as well as three others of similar size) as potential sites for dredged material disposal. The goals of the project were to find site(s) where disposed sediment would be contained (no sediment transport) and where the disposal operation would have a minimal impact on the ambient benthos. Fig. 9A shows the distribution of sediment grain-size determined through analysis of sediment-profile images; organic-rich silt-clays are in the western half of the area and fine to medium rippled sands are in the

eastern half. The sands were observed in the profile images to overlay muds near the sand-mud facies boundary, indicating that a strong kinetic gradient exists from east (high) to west (low). Profile images also show that stations within the silt-clay facies contain methane and are associated with shallow redox depths. This is apparently an area of high organic loading (Fig. 9B). The silt-clay facies consists of a mosaic of azoic or Stage I seres, while the sandy areas are populated by either Stage I or both Stage I and Stage III seres (Fig. 9C). The contoured Organism-Sediment Index values indicate that the area consists of three major zones (Fig. 9D). This division is based on past survey experience which shows that Organism-Sediment Index values less than +6 reflect recently disturbed or otherwise stressed habitats.

From these maps, we can construct hypotheses about the underlying causes for the mapped distributions. The bathymetry, not shown on these maps, shows that the silt-clay area (zone A of Fig. 9D) lies within a depression, and sandy areas (zones B & C of Fig. 9D) occupy a topographic elevation. The strong kinetic gradient is apparently related to water depth. Azoic or Stage I seres in zone A are apparently related to organic enrichment and the seasonal hypoxia which occurs annually in the Chesapeake Bay. Stage I seres in zone C may be related to massive sediment movement which precludes the establishment of Stage III taxa.

From these maps we can conclude the following: 1) Containment of disposed dredged material would probably be assured in Zone A; it is a natural, low-kinetic, depositional area. 2) Impacts to the ambient benthic population would be minimized by disposal in Zone A. The existing benthic ecosystem is already stressed, as evidenced by the presence of Stage I seres or azoic conditions. 3) Filling-in of this low kinetic depression with dredged material may improve both the quality and productivity of zone A by bringing the bottom up above the depth of stratification for the seasonal hypoxic bottom water layer. This can be verified and impacts to fisheries assessed by comparing the potential of the site as a food source for demersal fish through a BRAT analysis before and after disposal operations. Standard benthic community analyses for documenting key prey species or for testing other hypotheses about bottom processes can also be per-

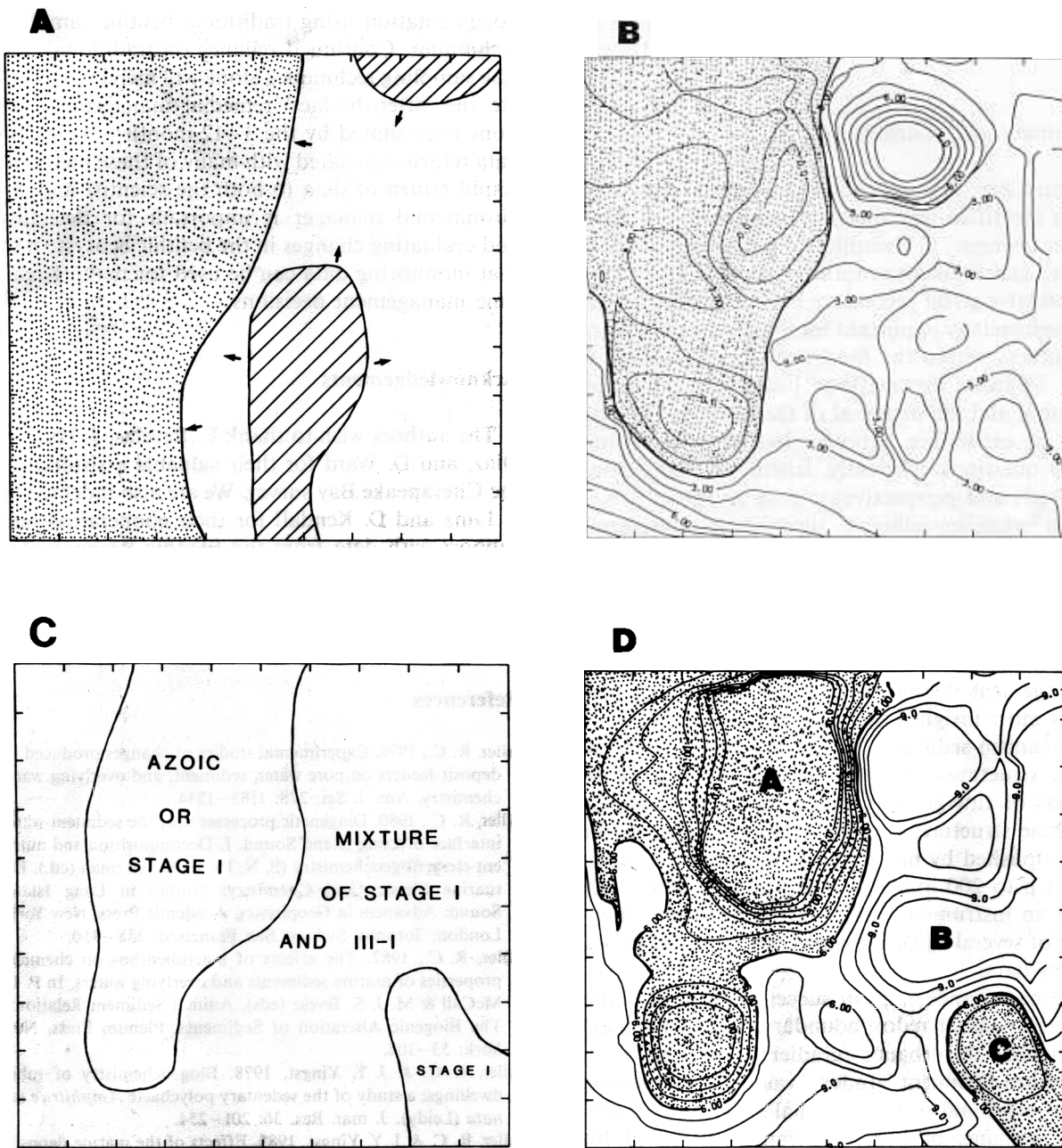


Fig. 9. An example of remotely acquired benthic data from a one-day reconnaissance mapping exercise using a sediment-profile camera. The four maps (A-D) are of the same 3.2 sq. km area in the lower part of the Chesapeake Bay, south of the Rappahannock River. Sampling was done in August, 1983 on a 6 × 5 station matrix. The mapped data are from three station replicates. (A) Modal grain-size shows the western half consists of silt-clay (> 4 phi is stippled) and the eastern half consists of fine-sand (3–2 phi is white) or medium sand (2–1 phi is cross-hatched). Arrows show the direction of movement of the sand as deduced from profile images showing ripples and the superposition of sand-over-mud. (B) Contoured values of the mean apparent redox depth as measured from density-sliced images. Images showing the presence of thin (or no) apparent redox boundary or methanogenic sediment were obtained from the stippled area. (C) The distribution of successional seres as inferred from sediment-profile images. (D) The contoured values of Organism-Sediment Indices (see Table II). Values less than 6 are contained within stippled areas. For purposes of ground-truth sampling, this part of the seafloor consists of three major benthic facies (A, B, and C). See text for further explanation.

formed with the box core samples taken as part of the BRAT investigation.

Summary and conclusions

Four key major management questions have been identified regarding the significance of long-term changes in benthic community structure. These questions focus on how such change might potentially affect secondary production leading to a commercially important food web, the transfer of pollutants within the food web, the flux of N, P, and Si from the seafloor back into the water column, and the potential of the changed community to experience hypoxia. In order to address these questions efficiently, traditional monitoring methods and perspectives require revision.

An organism-sediment successional conceptual model has been used to predict the relative importance of pioneering (Stage I) seres relative to high-order (Stage III) seres on these management issues. Although these relationships are imperfectly known, existing data are sufficient to guide management decisions until future research provides more insight into these problems.

Organism-sediment dynamics may be inferred from structures observed in the upper 20 centimeters of fine-grained sediments. *In situ* imaging of these structures through remote sensing can be accomplished by utilizing a sediment-profile camera. Up to 200 images per day can be taken with such an instrument, allowing reconnaissance mapping of several square kilometers of seafloor in one survey data.

Reconnaissance maps of successional seres, depth of the apparent redox boundary, sediment modal grain-size, disturbance gradients inferred from Organism-Sediment Index values, information about erosional or depositional regimes, sedimentary methane, or bedforms can be prepared for large data sets within a few weeks after a survey. The effect of the documented changes in benthic community structure on higher food webs may be evaluated through a Benthic Resource Assessment Technique (BRAT) which relates benthic prey availability to commercially-important foraging predators. If extraordinary change is detected in organism-sediment relations, these reconnaissance maps may be used to locate stations for further

documentation using traditional benthic sampling techniques. Continued reliance on traditional marine sampling techniques alone will merely perpetuate the 'after-the-fact' remedial management actions necessitated by the 3–12 month time lag on data return associated with many of these methods. Rapid return of data to both the scientist and environmental manager is important for detecting and evaluating changes in the benthic ecosystem so that monitoring data can be used for making real-time management decisions.

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