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Vertical and horizontal distributions of dinoflagellate cysts in sediments[1]

Abstract—Studies of the distribution of dinoflagellate resting cysts have typically focused on the flocculent layer at the sediment–water interface. Simple coring methods now reveal a wide variety of vertical distributions of cysts in different estuarine and nearshore environments, often with significant subsurface concentrations of viable cysts. Both subsurface and surface maxima are found in both coarse and fine sediments. The results have implications with respect to maps of cyst distribution, to correlations between the observed patterns and hydrographic or sedimentary parameters, and to assessments of the role of this life cycle stage in "seeding" dinoflagellate blooms.

Many recent studies emphasize the potential importance of resting cysts in the initiation phase of dinoflagellate blooms (e.g. Steidinger 1975; Wall 1975). Cysts are also implicated in facilitating dispersal (Anderson and Wall 1978), and, for the toxic dinoflagellate *Gonyaulax tamarensis*, as a direct source of paralytic shellfish poison since the cysts may be more toxic than motile, vegetative cells (Dale et al. 1978). Fossilized dinoflagellate cysts have also been used extensively in stratigraphic palynology (Evitt 1970). However, little is known of the abundance of living cysts in different sedimentary environments, their vertical and horizontal distributions, or the factors affecting these spatial patterns.

Studies of cyst distributions have taken a variety of forms. Palynologists have mapped fossilized, acid-resistant cysts in terms of relative abundance (% of total assemblage) or number per gram dry weight of surface sediment (Davey 1971; Williams 1971; Reid 1972, 1974; Wall et al. 1977). Dale (1976) modified harsh palynological processing techniques to include less resistant forms in his analysis. Some workers attempted to correlate patterns of dinoflagellate cyst distribution with hydrographic and geological parameters, others examined the link between the species assemblage of cysts in sediments and the dinoflagellate populations in the overlying waters. Other efforts have been more qualitative, mapping the presence or absence of cysts of a particular species as a way of delineating its distribution pattern and the location of potential "seedbeds" for bloom initiation (Reid 1972; Anderson and Wall 1978; Lewis et al. 1979; Anderson et al. 1982).

In all of these efforts, an underlying assumption has been that the cysts are enriched in the flocculent layer above denser sediments (Dale 1979) because dinoflagellate cysts are less dense than sand and clay particles, and thus should accumulate above the heavier materials (Rhoads and Young 1970). Workers have thus consistently focused on surface sediments, with subsamples being scraped from the top of cores or Van Veen grabs, pumps used to "vacuum" the surface directly, or plankton nets dragged lightly across the bottom (e.g. Wall and Dale 1968; Davey 1971; Wall et al. 1977; Lewis et al. 1979).

We describe here preliminary studies of the vertical and horizontal distribution of dinoflagellate cysts in estuarine and nearshore sediments. The significant vertical structure seen in many of these samples suggests that previous efforts to correlate cysts in surface sediments with hydrographic features or motile, vegetative populations may be misleading due to the differential burial of deposited cysts. We suggest that for many purposes, cyst counts integrated over suitable

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depth intervals can provide the necessary resolution for meaningful correlations.

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Many devices have been used to collect undisturbed sediment samples for quantitative analysis of organisms, pollen grains, and chemical compounds (e.g. Henrici and McCoy 1938; Rhoads 1974; Onbe 1974; Turekian et al. 1978; Brush pers. comm.). Although the best way to collect samples is with SCUBA divers and handheld box cores (Aller 1980), this is not feasible for many field programs. For studies of dinoflagellate life cycle dynamics we needed a methodology suitable for the collection of many samples over a wide range of depths and sediment types from boats of small and medium size. We selected coring as the method satisfying these constraints while still providing realistic, reproducible data.

In shallow embayments we prefer hand coring, using either long sections of 5-cm-diameter tubing cut after withdrawal, or shorter sections of the same tubing held by a PVC sleeve and check valve. This assembly was attached to an adjustable handle that permitted sampling to 5 m. Cores thus obtained were visibly free of sediment distortions. The top few millimeters of the flocculent layer were resuspended somewhat during handling and transport, but settled within an hour, after which the overlying water was removed by siphon. No cysts were found in this discarded water. The core was then extruded cleanly with a rubber stopper piston driven from below. For vertical profiles, the first sample was a combination of the remaining surface water (<1 cm) and the first centimeter of sediment, all removed by pipette. As the core was extruded, 1 cm at a time, the outer perimeter of sediment was discarded to eliminate contamination of deeper layers due to wall friction and a known volume of sediment (3.8 cm^3) was taken from the center for processing. Measurements of distances between objects within the core before and after extrusion showed no compression for the sediments examined. Cores were extruded and processed as soon as possible after collection to minimize bioturbation effects and to ensure that cysts did not germinate. If we expected a delay in sample examination, we held the core subsamples at the ambient water temperature to maintain cyst dormancy.

Shallow water cores could be collected easily in this way, but gravity cores were necessary in deeper waters (Benthos, Inc., fitted with a 1.5-m-long, 7.5-cm-diameter core liner, with check valve). We did not use a core catcher at the end of the core liner because of possible mixing effects (Baxter et al. 1981). Although this meant that very sandy samples could not be collected, successful recovery was possible at all but a few locations. These gravity cores also maintained the existing sediment strata, but due to the large cross-sectional area, we sometimes added a subcoring step whereby a 2.2-cm-diameter tube was slowly pushed into a level area within the larger core, capped, and removed. Other processing steps are as described above, except that each centimeter extruded from the subcore was processed in its entirety.

We examined possible errors introduced by this subcoring method in a gravity core from the Potomac River injected with Rhodamine dye at selected intervals. Measurement of the equivalent intervals in the subcore indicated no change in the top 3 cm, but a uniform 20% compression over the rest of it. Data from the top few centimeters thus represent the actual profile, while counts at lower depths are probably biased slightly toward the surface. Nothing is known of compression during the initial gravity coring, although the subcoring data suggest some change in deeper layers.

We tested the methodology further by comparing cores from a 350-kg Soutar-type box corer to gravity cores from the same stations and to a subcore taken by hand from the box-core sample. The box core could be sectioned after the sequential removal of thin plates attached in horizontal strips across the frame.

Sediment subsamples were processed

by the methods of Wall and Dale (1968), with sonication for 1 min at 1.4 A to disaggregate the sediment followed by size fractionation of the slurry through Nitex sieves of 20–80- or 20–64-μm ranges, depending on the cysts being studied. The processed sediments were then examined microscopically in Sedgwick-Rafter slides; the volume examined typically represented 0.2–0.5 cm^3 of the original sediment. The volume of sediment efficiently examined per slide depends on the amount of material retained by the sieves and varies with sediment type. Where extraneous materials are abundant and cysts are not numerous more than one slide must be counted.

Only live cysts were tabulated, with the presence of microgranular cytoplasm in Brownian motion used most often as a sign of positive viability (Anderson and Wall 1978).

Sediments were oven-dried at 40°C and weighed, then wet-sieved (U.S. Standard 230 mesh). Particles retained were oven-dried and reweighed to give the percentage abundance of the coarse (sand) fraction.

One indication of the validity of this method is seen in the shape of the vertical distributions. Typical profiles of *G. tamarensis* cysts from different locations within a Cape Cod salt pond are relatively smooth, internally consistent (i.e. each describes a distinct distribution), and often show maximum concentrations well below the surface (Fig. 1A). Replicate cores taken at one station in the salt pond showed vertical distributions consistent in profile shape and total number of cysts (Fig. 2A).

Gravity cores from the more dynamic Potomac estuary also have smooth, consistent profiles for cysts of *Gyrodinium uncatenum,* with maximum concentrations in the top centimeter and virtually no cysts below 5 cm (Fig. 1B). Six months later there were maxima at 2-cm depths, with cysts as deep as 6 cm. Replicate profiles at one station are shown in Fig. 2B.

Figure 3 depicts the extensive vertical distribution of cysts of *Gonyaulax scrippsae* at 20-m depths of water in Buzzards Bay, Massachusetts. In this example (and in others not shown), the agreement between gravity coring and box coring is quite good; careful subcoring within the box-core sample also yielded a similar profile.

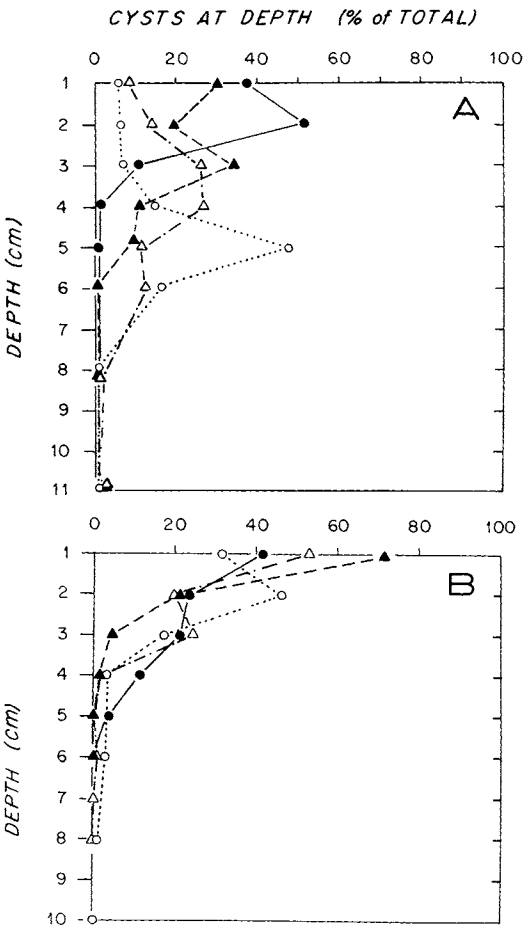

Fig. 1. Vertical distribution of two cyst types. A—Representative profiles of *Gonyaulax tamarensis* cysts from four different stations within Perch Pond—a shallow, estuarine embayment. Cores were taken 6–8 weeks after a dense bloom of this species. B—Representative profiles of *Gyrodinium uncatenum* cysts from four different stations in the Potomac River estuary, about 2 weeks after decline of *Gyrodinium* bloom.

Figures 1 and 3 demonstrate the variations possible in vertical profiles in different regions. It is also possible to find distinctly different vertical distributions of two types of cyst within the same core. For example, in one Perch Pond core, the highest concentration of *G. tamarensis*

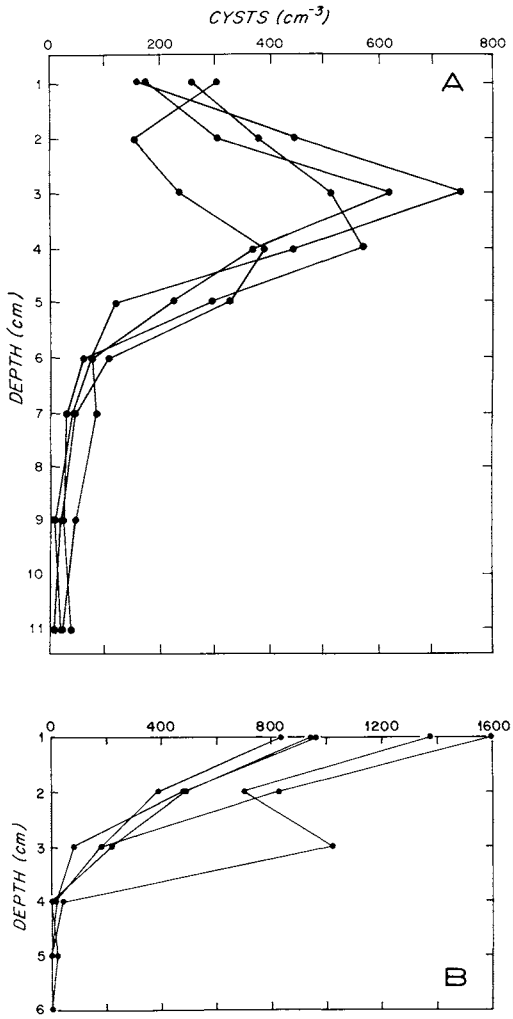

Fig. 2. Replicate vertical profiles. Each point represents a 1-cm interval above specified depth. A—Distribution of *Gonyaulax tamarensis* cysts in replicate cores from the same station in Perch Pond. B—Distribution of cysts of *Gyrodinium uncatenum* in Potomac River cores (sta. NP35).

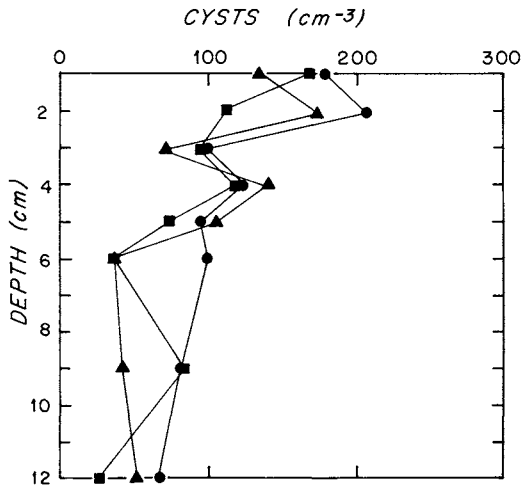

Fig. 3. Vertical profiles of cysts of *Gonyaulax scrippsae* at 20-m depth in Buzzards Bay: ●—gravity core; ▲—box core; ■—5-cm-diameter subcore from box-core sample. Each point represents a 1-cm interval above specified depth.

cysts was at 5 cm, whereas the cysts of *Heterocapsa triquetra* were numerous at the surface and decreased rapidly with depth (Fig. 4A). A dense bloom of *H. triquetra* ended 3 weeks before this core was taken; the most recent bloom of *G. tamarensis* was 11 months earlier. Although less dramatic than those in Perch Pond, differences in the vertical distributions of cyst types are also seen in Potomac cores (Fig. 4B). In these two examples, it seems possible that each profile represents the time of cyst deposition for that species, although such inferences about cyst age based on vertical position should be made with caution. Other possible explanations are differences in germination, predation, or settling characteristics, but this example does emphasize the dynamic nature of the deposition and sorting process and suggests that these methods could be useful in determining mixing rates.

It is evident that in the three areas studied (two estuarine, one nearshore), significant numbers of dinoflagellate cysts can be found below the sediment surface. In two of these environments, only relatively small fractions of the total cysts were found in the flocculent surface layer that has been the focus of previous sampling efforts. Even within a single embayment or estuarine system, significantly different vertical profiles were found from station to station, some with cysts enriched at the surface, others with maxima at depth (Fig. 1). No clear generalizations emerge from the sediment characteristics (Table 1). Subsurface cysts have been found in coarse and fine

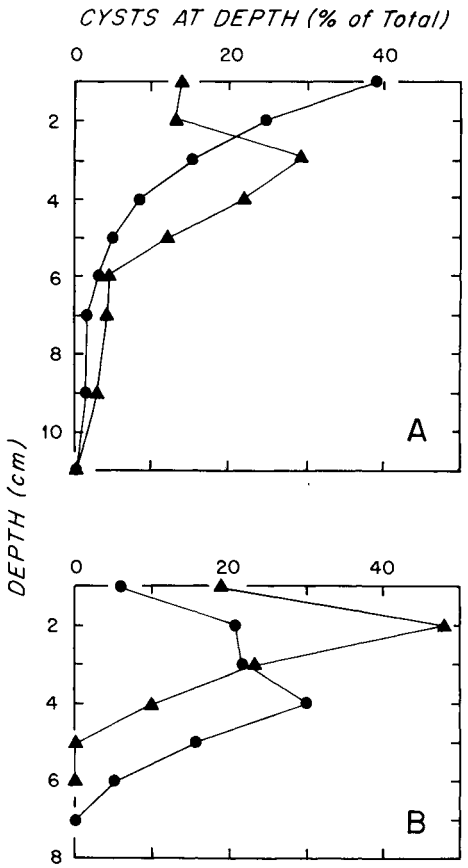

Fig. 4. Vertical distribution of different types of cyst in the same core. A—Cysts of *Gonyaulax tamarensis* (▲) and *Heterocapsa triquetra* (●) in Perch Pond. B—Cysts of *Gyrodinium uncatenum* (▲) and *Gymnodinium* sp. (tentative identification) (●) in Potomac River.

sediments (65 and 4% sand) as have surface maxima (55 and 1% sand). There is also no clear correlation with organic carbon content.

We must conclude that variations in time of cyst deposition, benthic animal activity, tidal scouring, and sediment characteristics will produce a wide range of vertical cyst distributions in bottom sediments. Where surface sediment samples might account for the majority of cysts at a given location, in other areas such a sampling focus would be misleading due to the differential burial of deposited cysts. The implications of this observation are important for maps of species distribution (Reid 1972, 1974) and efforts to correlate these patterns with hydrographic or sedimentary parameters (Davey 1971; Dale 1976; Wall et al. 1977). For example, Balch et al. (in press) recently conducted a survey of dinoflagellate cysts in surface sediments in an estuary near Plymouth, England. Their spatial data suggest that cysts accumulated in highest concentrations at the mouth of the estuary, whereas the upstream concentrations were very low. The investigators attempted to explain these low cyst concentrations as the result of reduced motile dinoflagellate abundance or heavy input of terrigenous debris to "dilute" the number of cysts per unit volume of sediment, but our results suggest a third possibility—that many cysts were buried in the muddy sediment of that section of the estuary and were never sampled.

Given these problems with correlations between cysts in the sediment and the biological and physical environment, we suggest a different approach to quantitative cyst analysis. The ideal data set would include cyst profiles throughout a

Table 1. Characteristics of selected sediment samples.

Location	Type of cyst	Cysts (% of total) top cm	Cysts (% of total) top 2 cm	Sand (%)	Org C (%)
Perch Pond	*Gonyaulax tamarensis*	6.4	12.8	4	6.0
Perch Pond	*Gonyaulax tamarensis*	30.1	48.5	29	6.5
Perch Pond	*Gonyaulax tamarensis*	33.7	50.2	55	2.5
Perch Pond	*Gonyaulax tamarensis*	7.9	22.3	92	0.92
Potomac River	*Gyrodinium uncatenum*	41.2	72.9	1	—
Potomac River	*Gyrodinium uncatenum*	62.3	80.6	27	—
Buzzards Bay	*Gonyaulax scrippsae*	18.3	40.2	65	—
Great Harbor	*Gonyaulax scrippsae*	37.6	56.7	29	—

study area, but the work involved is considerable and not always necessary. The top 6 cm of sediment from Perch Pond contained at least 97% of the total *G. tamarensis* cyst population at the time of sampling (Fig. 1A). It is possible to integrate the counts by subsampling from a well mixed slurry of the entire interval of interest to obtain an estimate of the total cysts per unit area and the average cysts per unit volume. A similar interval for the Potomac River would cover the top 4 cm (Fig. 1B).

When replicate cores are taken from one location and processed in this way, the variability encountered (Table 2) represents both the patchiness of the actual cyst distribution and the errors introduced in processing and counting. In the relatively quiescent environment of a shallow embayment, hand-coring from a small boat produced replicates with a coefficient of variation of about 14%, while gravity cores taken from a much larger vessel in the more dynamic current regime of the Potomac estuary yielded coefficients near 40%. Both boats were anchored, yet the cores in the Potomac reflect a larger sampling area for the replicates. Since cyst concentrations in cores from within an area often differ by amounts far greater than this, it appears feasible to map cyst accumulations on an areal basis and to correlate patterns with local hydrography.

Table 2. Variability in replicate core samples.

	Perch Pond*		Potomac R.†	
	PP 60	PP 80	SP 30	NP 30
Replicate cyst concn‡ (cysts·cm^{-3})	660	260	90	140
	830	240	100	380
	700	250	20	240
	790	300	120	240
	600	340	100	180
Mean	716	278	86	236
SD	94	42	38	91
C.V.	13	15	45	39

* Cysts of *Gonyaulax tamarensis*; shallow embayment, hand-cored with direct extrusion, top 6 cm combined.
† Cysts of *Gyrodinium uncatenum*, deeper estuary, gravity core; subcore taken and extruded, top 4 cm combined.
‡ Volume examined typically represented 0.2–0.5 cm^3 of original sediment.

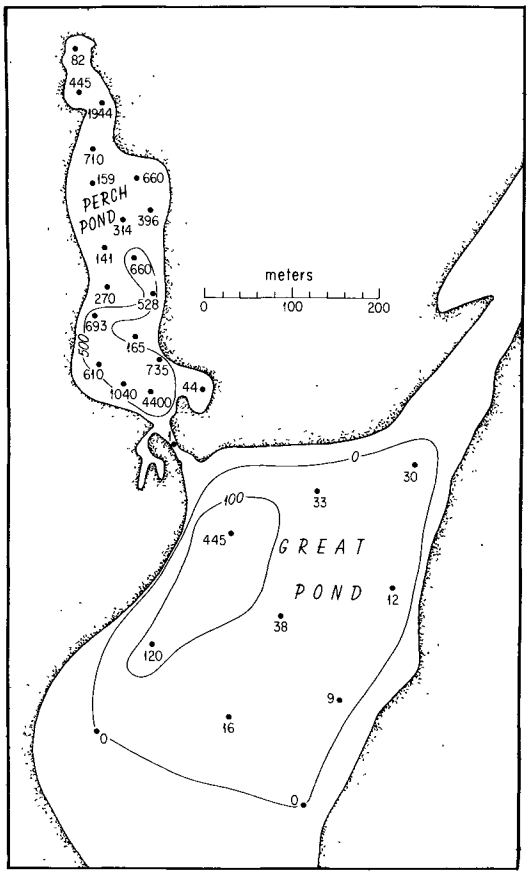

Fig. 5. Distribution of cysts of *Gonyaulax tamarensis* in Perch Pond and Great Pond. Values given are cysts·cm^{-3} in top 6 cm of sediment.

Figure 5 shows the results of such a survey in a Cape Cod embayment subject to recurrent blooms of the toxic red tide dinoflagellate *G. tamarensis*. Anderson and Wall (1978) and Anderson and Morel (1979) argued that the local estuarine population of this dinoflagellate originated from (and developed within) Perch Pond, seeded by germination of dormant cysts. This is further emphasized by the large concentrations of *G. tamarensis* cysts in Perch Pond, falling rapidly to zero in adjacent Great Pond. The average areal concentration of *G. tamarensis* in Perch Pond is 4.5×10^7 cysts·m^{-2}, representing a sizable inoculum in an embayment with an average depth of 1.5 m.

A similar study over a 65-km segment

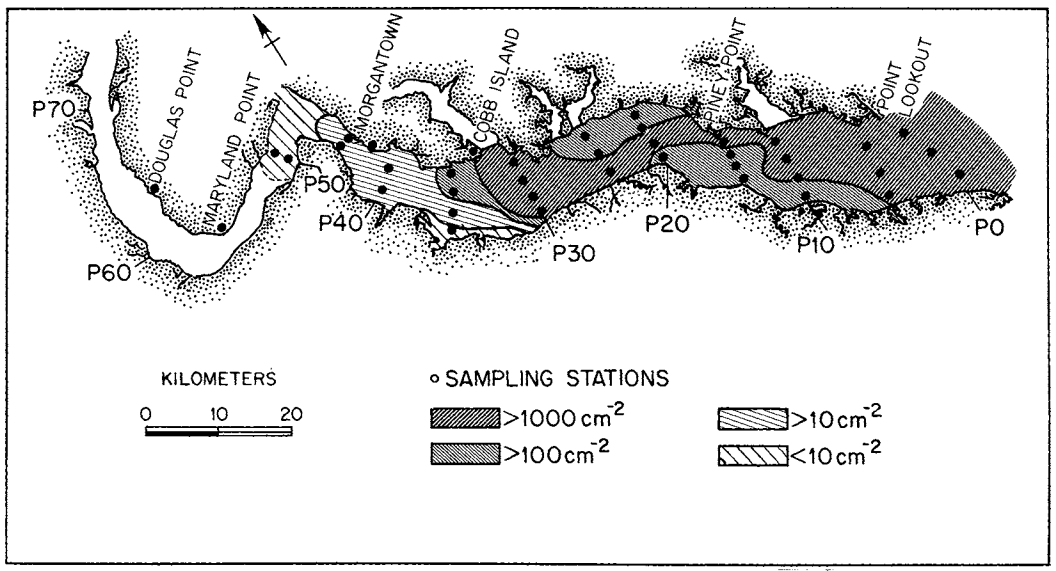

Fig. 6. Areal distribution of cysts of *Gymnodinium* sp. in Potomac River. Values are cysts·cm^{-2} based on top 4 cm of sediment.

of the Potomac River shows the distribution of another type of cyst (motile stage not yet positively identified, tentatively called *Gymnodinium* sp.) (Fig. 6). The pattern suggests a species with a preference for higher salinity Chesapeake Bay waters and with only limited distribution in the upstream, brackish waters of the Potomac.

One advantage of this counting method is that all cysts at a location are included, removing errors associated with differential burial and permitting patterns like those in Figs. 5 and 6 to be visualized. An associated disadvantage is that surface cysts and deeper cysts are treated equally. Since we do not yet understand the fate of subsurface cysts, this simply represents a convenient (and somewhat arbitrary) means of quantitatively mapping distributions over large areas. Once more is known about the actual depths from which cysts can germinate, such interval integration can be refined if the objective is only to study the bloom initiation process. At this time, however, given a sediment zone with significant bioturbation or physical mixing, subsurface cysts must be included in any quantitative analysis to account for the maximum potential inoculum or the total cysts actually deposited. Since the effects of germination, bioturbation, tidal scour, resuspension, and natural sedimentation processes are difficult to differentiate, interpretation of changes in cyst concentrations either between locations or through time should be approached with caution. Vertical profiles are interesting and provide useful insights, but they also should be used quantitatively only when the compression characteristics of the sediment are understood or held constant. Even the most gentle hand-coring within a box-core sample produced visible compression due to wall friction.

The biological and physical mechanisms underlying surface and subsurface cyst concentrations are not known, but we encountered many polychaetes, crustaceans, and bivalves during core processing. Biological reworking can occur to depths of 5 cm and greater (Rhoads and Young 1970; Rhoads 1974; Turekian et al. 1978; Aller 1980). This level of animal activity creates a mixed zone with a significant water content (up to 60% by weight in the upper 10 cm: Rhoads and

Young 1970). Given the vertical cycling of materials in this layer, the high water content, and our successful laboratory germination of *G. tamarensis* cysts isolated from 6-cm depths, it seems possible that subsurface cysts could participate in the bloom seeding process.

Thus far, our efforts have focused on the relatively shallow estuarine and nearshore environments. Although the depth of mixing and bioturbation in sediments of deeper coastal waters can be similar to that in estuaries, the rate of this mixing would be lower due to reduced physical and biological activity (Turekian et al. 1978). In such instances, the surface flocculent layer may indeed be enriched in dinoflagellate cysts, or subsurface peaks may take longer to develop. Along the continuum between shallow estuaries and deeper coastal waters, variations in the vertical distribution of cysts within the sediments may be of major importance with respect to the timing and magnitude of the seeding phenomenon.

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Decomposition of organic detritus: A selective role for microflagellate Protozoa[1]

Abstract—The decomposition of *Peridinium* cells was accelerated in the presence of bacterivorous microflagellates. The microflagellates enhanced the bacterial breakdown of the polysaccharide cell wall (theca) but did not increase the rate of degradation of the cell protoplasm. Hydrolytic bacteria which preferentially attacked the theca were stimulated by protozoan grazing and by the addition of inorganic phosphorus. An important role of microprotozoa in aquatic ecosystems may therefore be to selectively facilitate the breakdown of detritus with a high structural carbohydrate/low mineral content.

Although flagellated Protozoa (subphylum Mastigophora) are ubiquitous and frequently abundant in aquatic ecosystems (e.g. Pomeroy and Johannes 1968; Sorokin and Paveljeva 1972; Fenchel 1975), little is known about their specific ecological roles. One role seems to be enhancement of the decomposition rate of organic detritus (Barsdate et al. 1974; Harrison and Mann 1975; Fenchel and Harrison 1976). In Lake Kinneret (the Sea of Galilee) only a small portion (10–20%) of the intense spring bloom of the 20–30-μm dinoflagellate *Peridinium cinctum* fa *westii* is directly consumed by herbivores; most of the algal biomass, in the form of detritus, is degraded in the water and does not reach the sediment (Serruya et al. 1980). During the bloom season, 2–10-μm colorless microflagellates have been observed in the lake. In this report we present evidence that these microflagellates affect the decomposition of dead *Peridinium* by specifically accelerating the breakdown of the dinoflagellate theca, the carbohydrate cell wall which comprises up to 50% of the cell dry weight (Nevo and Sharon 1969). To our knowledge, this is the first case in which such a selective effect on the decomposition of an organic material has been demonstrated for Protozoa.

A culture of two microflagellate species was isolated from lake water enriched with dead *Peridinium* cells. The laboratory culture was composed of a 3–5-μm-diameter *Monas* sp. and 5-μm-long *Bodo* sp. (identified by B. S. C. Leadbeater).

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