Marine Micropaleontology, 20 (1992) 147–161
Elsevier Science Publishers B.V., Amsterdam

Burial of living dinoflagellate cysts in estuarine and nearshore sediments

Bruce A. Keafer[a], Ken O. Buesseler[b] and Donald M. Anderson[a]
[a]*Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*
[b]*Chemistry Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*

(Received March 5, 1992; revision accepted September 1, 1992)

ABSTRACT

Keafer, B.A., Buesseler, K.O. and Anderson, D.M., 1993. Burial of living dinoflagellate cysts in estuarine and nearshore sediments. *Mar. Micropaleontol.*, 20: 147–161.

The deposition and burial of living dinoflagellate cysts was studied in two different environments: the nearshore waters of the southern Gulf of Maine and a small shallow salt pond on Cape Cod, Massachusetts (Perch Pond). Vertical profiles of cysts and two naturally occurring radionuclides (^{210}Pb, ^{234}Th) differed significantly between the two environments. At 160 m depths in the Gulf of Maine, cyst profiles in the sediment often showed a subsurface peak in abundance 6–8 cm below the surface. The ^{210}Pb profiles were consistent with a rapidly mixed surface layer (2–6 cm thick) above another region (6 to at least 12 cm thick) where mixing was slower but still dominant over sediment deposition. The sediment mixing coefficient (D_b) ranged from 15 to 26 cm^2 y^{-1} in this lower region. The radiotracer profiles and modelling results both suggest that the subsurface peaks in cyst abundance are not the result of a pulse input in one year followed by burial (via bioturbation or sediment deposition). Instead, we hypothesize that they arise from a combination of germination from the surface mixed layer and mortality at depth. In contrast, the cyst and radiotracer profiles in the shallow Perch Pond embayment are consistent with a single thin (2 cm) mixed layer at the sediment surface. Burial of cysts below this level is due to a relatively high rate of sediment deposition (2.9 mm y^{-1}), with little or no biological mixing. This lack of mixing is consistent with reports of seasonal anoxia in Perch Pond, a recurrent process which kills benthic animals before they reach the size or community composition needed for deep bioturbation. Opportunistic, recolonizing species are only capable of mixing the top 1 or 2 cm. Resuspension and redeposition of cysts by wind and storms appears to be limited by the small size and somewhat protected location of the pond. The lack of deep mixing allows us to compare the survival of cysts of different species by modelling the decrease in cyst abundance below 2 cm. A simple exponential decay equation fits the data well, and indicates that the living cysts of some species (e.g., *Gyrodinium uncatenum, Gonyaulax polyedra*) are more susceptable to mortality in the deeper anoxic sediments than are *Gonyaulax verior* and *Alexandrium* (formerly *Protogonyaulax*) *tamarense*.

Introduction

Many of the dinoflagellates that inhabit coastal waters include a dormant, cyst stage in their life histories. The obvious importance of cysts in seeding or inoculating recurrent blooms, in species dispersal, in increasing genetic heterogeneity through sexuality, and for some species, in depositing fossilizable cell walls of value in stratigraphic palynology have resulted in numerous field and laboratory studies (reviewed in Dale, 1983; Anderson, 1984; Goodman, 1987). As field studies became more quantitative, it soon became apparent that cysts did not simply accumulate in the flocculent, oxidized layer at the sediment surface as had been presumed (e.g. Wall and Dale, 1968; Dale, 1979), but rather were rap-

Correspondence to: B.A. Keafer, Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA.

idly buried by bioturbation activity and sedimentation (Anderson et al., 1982). Under such conditions, the bulk of a benthic cyst population is deprived of light and oxygen, both of which affect germination. Some species require light for germination, while others can germinate in the dark, but at rates much slower than if light is supplied (Binder and Anderson, 1986; Anderson et al., 1987). Anaerobic conditions completely inhibit cyst germination of most, if not all, dinoflagellate species (Anderson et al., 1987).

A variety of cyst profile types have been observed in natural sediments, some with distinct subsurface abundance maxima (Anderson et al., 1982), and others with peak abundance at the surface and relatively few cysts at depth (Tyler et al., 1982). These differences presumably reflect the timing of cyst deposition and the subsequent effects of germination, bioturbation, mortality, sediment deposition and erosion. However, the relative importance of these factors has not been investigated in the context of dinoflagellate cyst profiles. We thus can only speculate that a maximum in cyst abundance at the sediment surface might result from a recent deposition event following a bloom (Anderson et al., 1982) or that subsurface peaks might reflect a pulse of deposition from a single, large bloom in the past, such as the massive 1972 New England red tide of *Alexandrium* (formerly *Protogonyaulax*) *tamarense* (Anderson and Keafer, 1985). As a result of this lack of knowledge of cyst burial dynamics, it has not been possible to estimate the age of buried cyst populations with any degree of certainty, nor has it been possible to quantify the inoculum size to the water column from benthic cyst populations.

If once the cysts are deposited to the sediments they undergo burial and mixing similar to the surrounding bulk sediments, then we should be able to use independent estimates of sediment accumulation and mixing rates to gain useful insights into the cyst distributions. Detailed models exist which use naturally occurring radionuclides, for example ^{210}Pb (half-life = 22.3 yrs) and ^{234}Th (half-life = 24.1 days), to estimate sedimentation and mixing rates (Turkekian and Cochran, 1978, and references therein). Comparisons of profiles between a tracer such as ^{210}Pb and the cysts can therefore provide an indication of processes other than physical mixing and sediment accumulation which affect the cysts, such as cyst germination, variability in the annual inoculum size, and the long term mortality rates of the buried cysts.

In this study, we provide the first concurrent measurements of dinoflagellate cysts and radioisotope tracers. We examined the sediments of two different marine environments; the deeper coastal waters of the Gulf of Maine and a shallow salt pond on Cape Cod, Massachusetts. Our objectives were to examine the relationship between cyst distributions and radiotracer distributions on short and long time scales, to quantify the relative importance of sedimentation versus bioturbation in cyst burial, and ultimately, to improve our understanding of the dominant processes that shape the vertical distribution and thus the "seeding" potential of deposited cysts.

Materials and methods

Study sites

The coastal site, designated Station 29, is located in the Gulf of Maine approximately 30 km off the coast of New Hampshire in Jeffreys Basin at a depth of approximately 160 m (latitude and longitude, 43°00'00.2"N and 70°18'56.6"W). The sediments consist almost entirely of fine-grained silts and clays (>99%) with very little organic matter (<1%). They have a brown color throughout with a very slight reddish tint near the surface.

The salt pond site is designated Station 1 in Perch Pond, a small, shallow, embayment (75,000 m^2) located in Falmouth, Massachusetts, with an average depth of 1.5 m. The sed-

iments here are also dominated by fine-grained silts and clays (~95%), but have a much larger component of organic material (~5%). The upper 1–2 cm contains an oxidized orange/brown layer, with black organic-rich and sulfide-laden sediments below.

Core collection and processing

Cores were collected in successive years (1985–1987) in the Gulf of Maine at Station 29 using a Craib Corer (Craib, 1968) which samples approximately the top 12 cm of the sediment column, leaving the sediment/water interface undisturbed. A gravity core was taken in 1986 to sample down below 12 cm to greater than 50 cm in order to establish the supported levels of ^{210}Pb from the decay of ^{226}Ra. Cores from Perch Pond Station 1 (depth = 2 m) were collected in 1987 using a hand-coring device with an extension that allows easy operation from an anchored rowboat. This device also allows one to retrieve a core with an undisturbed sediment/water interface.

Cores were immediately (within several hours) extruded and sectioned into intervals either on board ship or upon returning to the laboratory. To avoid artifacts from the coring and extrusion process, the outer edges of the sediment core were discarded, leaving the inner undisturbed sediments for sampling. The same depth intervals from approximately six cores were pooled in order to integrate the natural variability over a larger sample area and to allow enough sediment to be collected for accurate isotope analysis. The thickness of the sediment depth intervals ranged from 0.5 to 2.0 cm with the thinner intervals sampled near the top of the core to attempt to observe rapidly decaying ^{234}Th. Storage of all sediment samples was at 2–4°C.

Cyst and radiotracer analysis

The pooled sections for each depth interval in the core were diluted (1:5, sediment:seawater, v/v) and homogenized. A 5 ml subsample was taken for cyst counts, diluted to 50 ml, sonified for 45 seconds (setting 4, 4.0 A, Branson model S-75), then sieved once through 80 μm Nitex and again through 20 μm Nitex which retained the cysts of interest. This 20–80 μm fraction was resuspended in a known volume of seawater for microscopic examination of the cysts in a Sedgewick–Rafter counting slide at 160×.

The remaining sample was then processed non-destructively for isotopic analysis of ^{210}Pb and ^{234}Th. In order to remove the seawater without leaving significant quantities of salt and to decrease the drying time, the sample was initially centrifuged, then allowed to settle overnight or until there was no visible fine particulate material in the supernatant. The supernatant was discarded and the remaining sediment was dried at 60°C for 2–3 days. The dried sediment was then ground using a mortar and pestle and the powder was weighed (7.5 or 15.0 g) into plastic 4 ounce counting jars for analysis. Each sample was gamma counted on an intrinsic germanium planar detector (Canberra Industries, Inc.) for approximately 2 days resulting in counting errors of approximately 5–10% for ^{210}Pb (energy peak at 46.5 keV) and 10–20% for ^{234}Th (energy peak at 63.3 keV). Self-absorption corrections for the attenuation of low energy (< 100 keV) γ-radiation by the sample were made according to Cutshall et al. (1983). Efficiency calculations were made relative to a calibrated "standard pitchblend ore" (U.S. EPA Environmental Monitoring Systems Lab, Las Vegas) of known activity. All sediment activities are reported in units of disintegrations per minute per gram ($dpm\ g^{-1}$) calculated by the equation:

$$dpm\ g^{-1} = (cpm \times eff \times abs) / grams\ dry\ weight$$

where, *cpm* is the net count rate in the energy region of interest for a given sample geometry, *eff* is the detector efficiency for a given energy and sample geometry, and *abs* is the self-

absorption correction factor (Cutshall, 1983). Details of this procedure are provided in Buesseler (1986).

Cores were also collected to access the role of benthic populations in the movement of cysts by bioturbation. These cores were sieved through a 0.3 mm mesh screen. The organisms retained were preserved with formalin, stained with Rose Bengal, then microscopically sorted and enumerated.

Calculations and modelling

Sedimentation and mixing rates

The vertical distributions of naturally-occurring and man-made radionuclides in sediments have been used to estimate sediment mixing and accumulation rates in a variety of deep-sea (Guinasso and Schink, 1975; Carpenter et al., 1982; Cochran, 1985; DeMaster et al., 1985; Anderson et al., 1988) and coastal sites (Aller and Cochran, 1976; Nittrouer et al., 1979; Benninger et al., 1979; Krishnaswami et al., 1980). These rates are based upon modelling of tracer profiles in sediments. The basic assumption behind the models used most often is that the process of sediment mixing and accumulation is analogous to eddy diffusion over the time scale of interest provided by our tracer. In practice, this simplified diffusive formulation holds if the time and spatial scales over which a tracer profile integrates obscures discreet mixing or sedimentation events. In this case, the general equation for particle mixing, accumulation and radioactive decay can be written as:

$$\mathrm{d}/\mathrm{d}t(pA) = \mathrm{d}/\mathrm{d}z(D_\mathrm{b}\,\mathrm{d}A/\mathrm{d}z) - \mathrm{d}/\mathrm{d}z(pSA) - \lambda pA \qquad (1)$$

where, p=dry bulk density (g dry sediment/cm^3 wet sediment), A=activity of the radionuclide (dpm g^{-1} dry weight), z=depth in sediment profile (cm), D_b=sediment mixing rate (cm^2 y^{-1}), S=sedimentation rate (cm y^{-1}), and λ=decay constant of radionuclide ($=\ln 2/t_{1/2}$).

One of the most common tracers used in these models is ^{210}Pb. With a 22.3 year half-life, it can be used to follow sedimentation back 5–10 decades, and mixing events that occur regularly in many coastal and deep-sea environments. In using ^{210}Pb as a sediment tracer, we must distinguish between ^{210}Pb which is being deposited to the sediment surface (=excess ^{210}Pb, or ^{210}Pb^{ex}), from that which is found in the sediment matrix itself and is in equilibrium with the long-lived parent ^{226}Ra (=supported ^{210}Pb). We can estimate ^{210}Pb^{ex} from the difference between the total ^{210}Pb signal in the core, and the supported ^{210}Pb (i.e. ^{210}Pb^{ex}=^{210}Pb^{tot}−^{226}Ra). If the input of ^{210}Pb^{ex} is assumed to be in steady-state and the mixing and sedimentation rates are constant over the depths of interest, the solution to Eq. 1 becomes:

$$A = A_0 \exp(\{[S - (S^2 - 4D_\mathrm{b}\lambda)]/2D_\mathrm{b}\} \times z) \qquad (2)$$

where A_0 is the activity at z=0 and A is the activity at depth z. There are two unknowns in Eq. 2, D_b, the sediment mixing rate, and S, the sedimentation rate. In many coastal environments, sedimentation can be ignored. In this case, $S^2 << 4D_\mathrm{b}\lambda$, the reduced form of Eq. 2 becomes:

$$A = A_0 \exp[-(\lambda/D_\mathrm{b})^{1/2} \times z] \qquad (3)$$

This common form of the ^{210}Pb^{ex} mixing equation has been utilized in many studies of bioturbation in marine sediments (Krishnaswami et al., 1980; DeMaster et al., 1985; Anderson et al., 1988, and references therein). Using this formulation, it can be seen that on a log ^{210}Pb^{ex} vs. depth plot (Figs. 1 and 3) the slope of the straight line fit to the ^{210}Pb^{ex} profile ($=0.031/D_\mathrm{b}$) provides a direct estimate of the sediment mixing rate.

In the absence of sediment mixing, the steady state solution to Eq. 2 becomes:

$$A = A_0 \exp[-(\lambda/S) \times z] \qquad (4)$$

Both solutions (Eqs. 3 and 4) have been considered in this work. For a more complete treatment of the data including both sedimentation and mixing, numerical modelling of the data using more than one tracer is needed to lead to independent estimations of mixing and sedimentation rates (Anderson et al., 1988).

The assumption behind Eq. 1 of a constant sediment mixing rate over the depth of one's tracer profile is often approached by dividing the sediment column into more than one mixed-layer depths (such as in Benninger et al., 1979; Nittrouer et al., 1979). The most common case of this occurs in sediments where mixing rates in the upper centimeters of the core are sufficiently rapid to completely homogenize the ^{210}Pb signal (i.e. the vertical profile has infinite slope). The upper zone of rapid mixing is often underlain by a layer of decreased mixing activity, as seen by a break in slope in the log ^{210}Pb profile. Without a second tracer with a shorter half-life, such as ^{234}Th ($t_{1/2}$=24.1 days), the mixing rate in the upper box cannot be estimated.

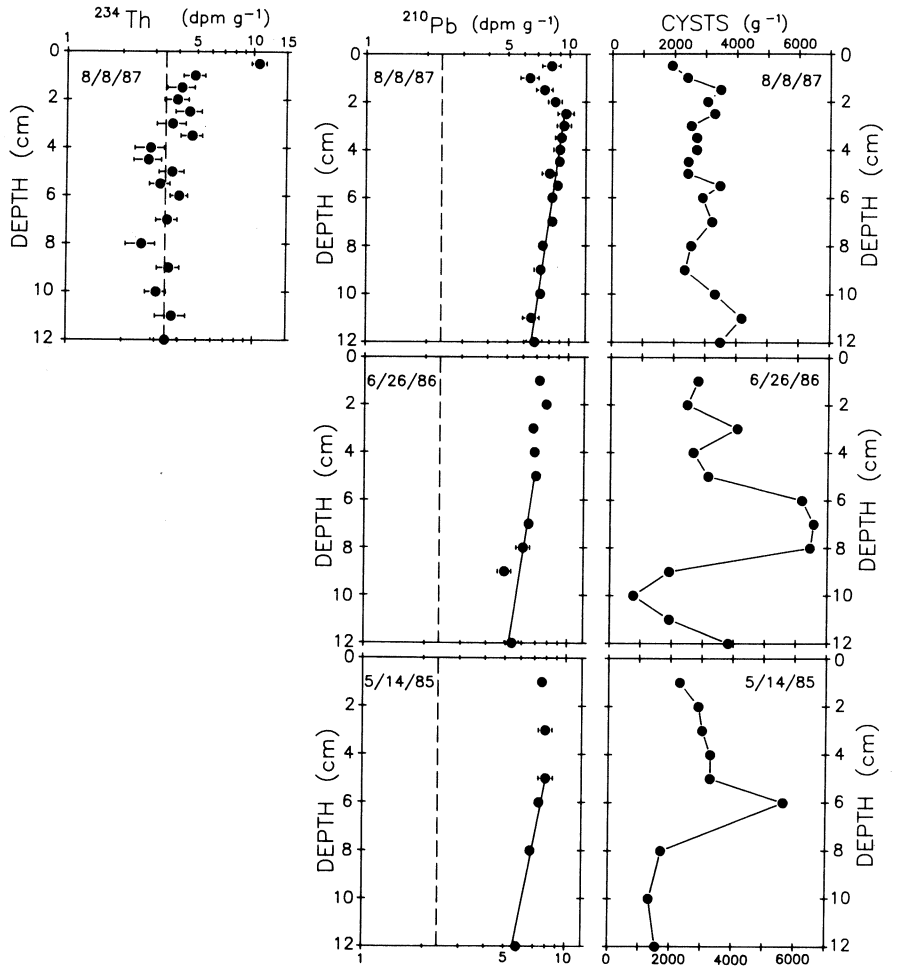

Fig. 1. Cyst (*Alexandrium tamarense*) and radiotracer profiles at Station 29 in the Gulf of Maine in 1985, 1986 and 1987 (bottom, middle and top panels, respectively). Supported ^{210}Pb and ^{234}Th levels are represented by the dashed vertical lines. The solid line through the data points represents those data points included in the regression analysis for the determination of the mixing coefficient (D_b).

Pulse input model

If the input of tracer is not in steady-state, but rather arrives at the sediment water interface as a pulse input of activity, then the solution to Eq. 1 becomes (Duursma and Hoede, 1967; Cochran, 1985):

$$A/A_0 = \exp(-z^2/4D_b t) \quad (5)$$

assuming constant porosity and negligible sedimentation and decay over the time interval (t) of interest. This pulse input solution will be used to model the fate of cysts deposited to the coastal site after an intense dinoflagellate bloom (Fig. 2).

Cyst decay vs. depth models

To characterize the exponential decrease of cysts with depth, we log-transformed cyst abundance data from 45 cores (1983–1987) for each species. Linear regression analysis was then performed on the points below the surface mixed layer (i.e. 2–12 cm determined from the ^{210}Pb data). The slope of the regression line represents the decay constant, k, as a function of depth for each species determined from Eq. 6:

$$N = N_0 \exp^{-kd} \quad (6)$$

where N=number of cysts at depth d below the surface mixed layer, N_0=number of cysts just below the surface mixed layer, k=decay constant (i.e. slope of the regression line), d=depth interval in centimeters between N_0 and N.

We can then determine parameter K for each species from Eq. 7 below, which represents the depth interval over which the number of cysts has been reduced by 50%, analogous to the determination of a half-life:

$$K = \ln 2/k \quad (7)$$

where K=the depth interval over which there is a 50% reduction in cyst number, k=decay constant derived from Eq. 6 above.

Results

Coastal site

Results of the concurrent ^{210}Pb and cyst profiles at Station 29 are shown in Fig. 1. ^{210}Pb profiles in all three years are similar, showing a surface mixed layer of approximately 2–6 cm, below which the isotope decays exponentially with depth (solid regression line). From the slope of the regression line, we have calculated both a mixing rate (D_b) from Eq. 3 of 15–26 cm^2 y^{-1} and a sedimentation rate (S) from Eq. 4 of approximately 8.0 mm y^{-1}. We measured supported levels of ^{210}Pb to be approximately 2.5 dpm g^{-1} (dashed line). Extrapolation to a depth where excess ^{210}Pb equals zero (i.e. ^{210}Pb tot.=2.5 dpm g^{-1}) yields the depth of the bottom of the mixed layer (20–30 cm). Thus, all depths which were sampled for cysts (12 cm maximum depth) contained excess ^{210}Pb.

Examination of the cyst profiles (Fig. 1) for *A. tamarense* show pronounced subsurface maxima in 1985 and 1986 at approximately 6–8 cm, while 1987 shows a more uniform distribution. All three years show lower cyst numbers in the surface.

The ^{234}Th profile (Fig. 1) shows no significant penetration of the short-lived isotope below 0.5 cm.

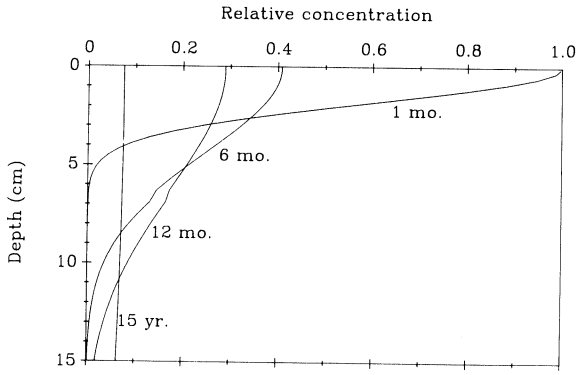

Fig. 2. Pulse input model using a mixing rate (D_b) of 20 cm^2 y^{-1} run for 1 month, 6 months, 12 months and 15 years (see Eq. 5 in text).

Salt pond site

The Perch Pond ^{210}Pb profile (Fig. 3) shows a surface mixed layer about 2 cm deep, with an exponential decrease of the isotope abundance down to 8 cm, below which the level appears constant between 8 and 12 cm at 5–6 dpm g^{-1}. Supported ^{210}Pb levels were somewhat lower at approximately 2.5 dpm g^{-1} (dashed line Fig. 3). The constant ^{210}Pb levels between 8 and 12 cm may represent a slumping event, or some other unknown physical deposition event. We chose the 2–8 cm depth interval to derive the slope for calculation of the mixing and sedimentation rates. The mixing rate (D_b) calculated from Eq. 3 was approximately 2.8 cm^2 y^{-1}, while the sedimentation rate (S) from Eq. 4 was 2.9 mm y^{-1} for the 2–8 cm sediment interval. The excess ^{234}Th (not shown) levels were not significantly above supported ^{234}Th levels, due in part to the reduced flux of excess ^{234}Th in this brackish environment where there is a relatively lower abundance of the parent isotope ^{238}U than in seawater.

Perch Pond has a much greater diversity of dinoflagellate cysts compared to the Gulf of Maine. Therefore, to gain a better understanding of the fate of these cysts, we evaluated six different cyst species rather than one. We observed basically two types of cyst distributions. Profiles of *Gyrodinium uncatenum* (Gu), *Gonyaulax rugosum* (Gr), and *Cochlodinium heterolobatum* (Ch), and *Gonyaulax polyedra* (not plotted) show a cyst maximum at the surface exponentially decreasing with depth (Fig. 3). *Alexandrium tamarense* (At), *Gonyaulax verior* (Gv) and an unknown *Scripsiella* species (Cp) represent species which typically show subsurface maxima in cyst abundance near 2 cm, below which the number also decreases exponentially. A closer examination of the exponential decay by regression analysis of log-transformed cyst abundances with depth (Fig. 4) from many cores (1983–1987) yielded a reasonably good fit for all species examined. In addition, the slopes of the regression line (i.e., the calculated decay constant k and parameter K from Eqs. 6 and 7) varied according to species (Table 1).

Evaluation of the benthic community structure over an annual cycle in Perch Pond revealed a low diversity of organisms and a significant die-off of all species present, due to

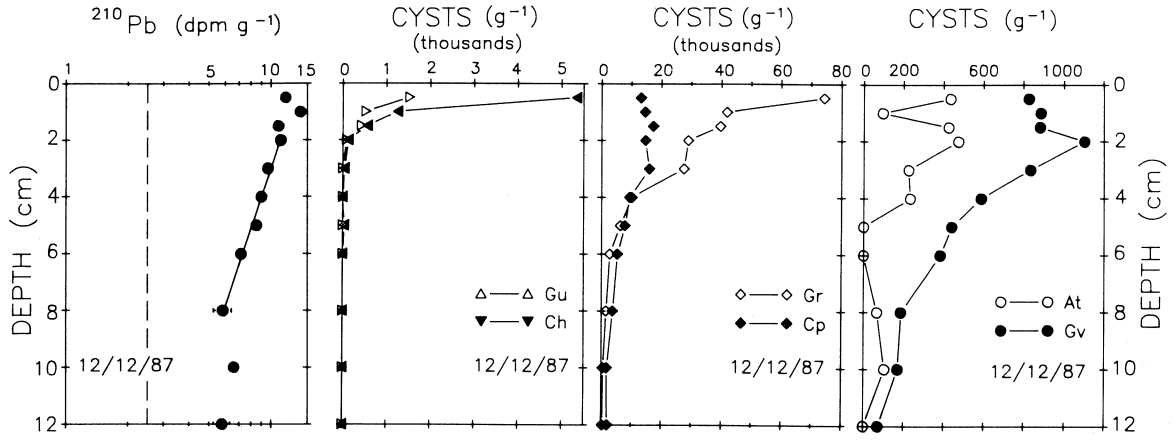

Fig. 3. Cyst and radiotracer profiles for Perch Pond, Station 1 in 1987. Species designations are: *Gyrodinium uncatenum* (*Gu*), *Cochlodinium heterolobatum* (*Ch*), *Gonyaulax rugosum* (*Gr*), an unknown *Scripsiella* sp. (*Cp*), *Alexandrium tamarense* (*At*) and *Gonyaulax verior* (*Gv*). Supported ^{210}Pb levels are represented by the dashed vertical line. The solid line through the data points represents those data points included in the regression analysis for the determination of the sedimentation rate (S).

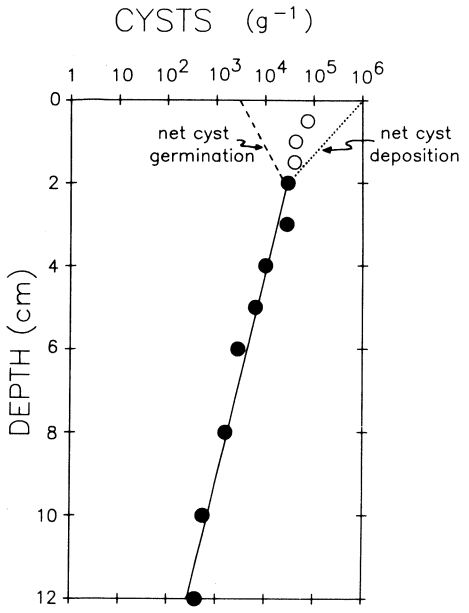

Fig. 4. Linear regression model of cyst mortality vs. depth for *Gonyaulax rugosum*. Closed circles (●) represent data points below the mixed layer and included in the model. Open circles (○) represent data points above the mixed layer not included in the model which are subject to germination, sediment resuspension and deposition of new cysts.

TABLE 1

Burial characteristics of selected cysts in Perch Pond

Species	K	r^2
Gyrodinium uncatenum	−1.52	0.85
Gonyaulax polyedra	−1.78	0.88
Gonyaulax rugosum	−2.43	0.91
Scripsiella sp.	−2.86	0.98
Gonyaulax verior	−3.79	0.94
Alexandrium tamarense	−4.67	0.82

oxygen stress that occurs during the summer (Fig. 5). In late July, we measured less than 1 ppm oxygen in the bottom waters. In addition, the surface sediments (<2 cm in depth) which were previously orangish-brown had turned completely black and were devoid of any worm tubes until later in the winter when recolonization by *Capitella* sp. and other shallow-burrowing polychaetes occurred.

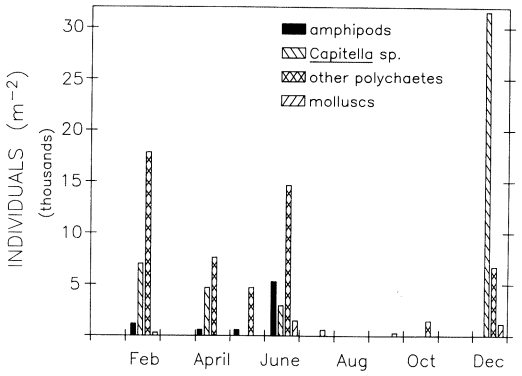

Fig. 5. Annual cycle of benthic community succession in Perch Pond in 1984.

Discussion

Vertical profiles of living dinoflagellate cyst abundance in surface sediments typically show considerable structure with depth (Anderson et al., 1982). Each profile represents the net result of biological processes unique to a species such as the rates of cyst deposition, germination, and mortality, all of which vary through time. The profiles are also shaped by physical processes such as mixing, sedimentation, and resuspension. The variability in these processes through time and between locations will have a significant impact on the rate at which cyst germination successfully inoculates the water column to initiate blooms, largely because of the need for oxygen and light for optimal germination (Anderson et al., 1987). As a first step in unravelling this complex but important issue of cyst dynamics in natural sediments, we examined the vertical profiles of living cysts and two naturally occurring radionuclides in two environments subject to recurrent dinoflagellate blooms.

Coastal site

The vertical profiles of *A. tamarense* cysts at Station 29 typically show peak abundances 4–8 cm below the sediment surface (Fig. 1; D.M. Anderson and B.A. Keafer, unpubl. data). One interpretation of such structure would be that

the peaks represent the remnants of a pulse input of cysts at one time that far exceeded the inputs at later dates. In the case of *A. tamarense*, the event would have been the 1972 New England red tide, which was the first and, relative to subsequent blooms, by far the most massive outbreak of that species to occur within the region in recent times (Mulligan, 1975; Anderson et al., 1982b). However, the isotope profiles obtained at Station 29 reveal at least two different mixing zones, neither of which, by itself, can explain the cyst profiles if the cysts are assumed to behave as passive particles. In those cores that had a subsurface peak in cyst abundance (1985, 1986), ^{210}Pb profiles were uniform over the top 6 cm (Fig. 1) and ^{234}Th was only detectable in the top 0.5 cm (Fig. 1). This is evidence for a surface layer that is well-mixed over intermediate time scales (i.e. decades), but not over shorter intervals (i.e. days to months). Below 6 cm, the exponential decrease in ^{210}Pb abundance would be due to either bioturbation or sedimentation.

If we assume the profile results from mixing alone, we calculate a particle mixing coefficient (D_b) of 15–26 cm^2 y^{-1} (Eq. 3). On the other hand, if we assume that the isotope profile is only a result of burial by sediment deposition, we obtain an apparent sedimentation rate of approximately 8.0 mm y^{-1} (Eq. 4). Brower (1984) studied several basins in this same region of the Gulf of Maine and calculated apparent sedimentation rates of 1.5–4.4 mm y^{-1} and particle mixing coefficients of 7.3–62.2 cm^2 y^{-1} using ^{210}Pb as a tracer. Using the longer lived isotope ^{14}C, Hulbert and Given (1975) calculated a sedimentation rate of 0.2–0.6 mm y^{-1} for Wilkinson Basin and Flight (1972) obtained a value of 0.2 mm y^{-1} for Jeffreys Basin near our Station 29. Both Brower's and our calculated apparent sedimentation rates are unrealistically high when compared to the rates derived from ^{14}C, while our mixing rates are within the range of Brower and other workers in shelf environments (Santchi et al., 1980; Carpenter et al., 1982).

Further proof of strong mixing in the Gulf of Maine is given by Livingston and Bowen (1979) who found fallout ^{239,240}Pu down to depths of 20 cm or more in 5 cores sampled in 1975 in the Wilkinson Basin. With the earliest global fallout ^{239,240}Pu inputs arriving only 20 years prior to their sampling, it is obvious that for this tracer to have reached this depth considerable downward mixing must be occurring (sedimentation alone would have buried the signal less than 2 cm, i.e. 20 yr$\times$1 mm/yr). Also, extrapolation of our ^{210}Pb regression line (Fig. 1) to background or supported levels determined from deep cores indicates that the depth of the lower mixing zone reaches 20–30 cm. This is consistent with the observations of Hines et al. (1991), who reported worm burrows several tens of centimeters in length in cores from this region. We thus concur with Brower's (1984) conclusion that biological mixing dominates over sediment accumulation in this coastal environment. Therefore, our estimated mixing coefficient of 15–26 cm^2 y^{-1} from the ^{210}Pb^{ex} profiles can be used to model sediment dynamics between the upper well mixed layer (0–6 cm) and the base of the mixed zone and sedimentation can be ignored ($S^2 << 4D_b\lambda$).

Using a mixing coefficient of 20 cm^2 y^{-1} estimated from the excess ^{210}Pb profiles and Eq. 5, a pulse input model was run to simulate the fate of cysts deposited from one major bloom followed by 15 years with no further input (i.e. 1972 bloom year). The results indicate that an initial layer of cysts deposited at the sediment surface will be dispersed relatively rapidly, such that within a year of the event, a significant fraction of the population would be mixed to depths 11 cm or greater (Fig. 2). We know that the mixing rates in the surface mixed layer (0–6 cm) are even greater than 20 cm^2 y^{-1}, so the actual depth of penetration would be even greater than shown in this figure. Peak abundances initially remain at the sediment surface, but become vertically homogeneous over time, while subsurface peaks are not generated

in any pulse input model runs. These results indicate that subsurface cyst peaks at the coastal station: (1) do not likely result from a single major bloom or series of bloom events of different magnitude; and (2) reflect processes other than passive particle mixing (i.e., germination and mortality, as discussed below). These conclusions are only valid for the coastal station benthic environment, since as will be shown for Perch Pond, there are conditions under which mixing is greatly reduced and sediment deposition dominates leading to possible correlations between total cyst wall profiles and specific bloom events.

The profile data and the modelling results provide other information about the fate of deposited cysts in Jeffreys Basin. Although the ^{210}Pb data indicate that a 6 cm thick surface layer is well-mixed over relatively long time scales, the ^{234}Th data (Fig. 1) and the model (Fig. 2) results show that on much shorter time scales (months), many cysts deposited after a summer or fall bloom would have a reasonable chance of remaining within a few centimeters of the oxygenated surface layer through the winter, such that many would be able to germinate the following year. Observations on chlorophyll *a* fluorescence of *Alexandrium tamarense* cysts from Station 29 implies that germination is confined to the top 1 cm (Anderson and Keafer, 1985). Concurrent geochemical measurements in replicate cores also from station 29 indicate that oxygen is probably depleted within the upper 0.5 cm (Hines et al., 1991). Since anoxia inhibits cyst germination (Anderson et al., 1987), deposited cysts buried below this level would remain in the sediment until continued mixing either brought them back to the oxygenated surface layer for germination or buried them deeper. Cysts would be uniformly distributed in this mixed layer (Fig. 1) but total abundance would decrease through time due to germination and to losses as some cells are mixed into the lower layer where bioturbation is less rapid (i.e. exponential decay portion of ^{210}Pb profiles).

The large difference between the half-lives of ^{210}Pb and ^{234}Th make it difficult to estimate the age of cysts at particular depths in the cores. Knowing that it takes approximately 4–5 half-lives for an isotope input to decay to background or supported levels and that this is achieved at 20–30 cm depths for ^{210}Pb within our cores, we estimate that cysts just below those depths would be about 100 years old (i.e. 4–5 half-lives$\times$22.3 years/half-life). However, virtually no living cysts of any species were observed at these depths. Above these depths, the mixing is too rapid (as is easily seen in the model results; Fig. 2), to permit estimates of cyst ages except to say that they are less than approximately 100 years old.

This result is not unexpected for *A. tamarense* because we know that inputs to this region are relatively new in recent times. However, other cosmopolitan species such as *Scripsiella trochoidea* may have been present in the Gulf of Maine for many millenia, yet we do not observe these living cysts at depths we know to be greater than 100 years old. Thus, living cysts have lifespans on the order of years to decades and are lost either by germination or mortality during their residence time in the sediments. Therefore, we hypothesize that the peak in living cyst abundance commonly seen at 6–8 cm depths results from the concurrent processes of germination from the well-mixed surface layer and the mortality of older cysts accumulating at depth in the slower mixed region of the profiles.

Salt pond site

A different distribution pattern of isotopes and cysts emerged from our examination of cores from Perch Pond. In this instance, we also gained information from comparisons among profiles of several different cyst types with ^{210}Pb. As seen in Fig. 3, cyst profiles had a variety of shapes, including a few with subsurface maxima. The ^{210}Pb profile shows a shallow mixed layer from the sediment surface to

2 cm, below which the isotope decreases exponentially.

The shallowness of the surface mixed layer is due in part to the death of all benthic animals during summer anoxia events in bottom waters (Fig. 5). The opportunistic community that recolonizes the sediments is not capable of mixing below depths of 1–2 cm (G. Hampson, pers. commun., 1989), and other deeper burrowing benthic organisms are unable to establish themselves given the stressed environment and the apparent recurrent cycles of anoxia (Pearson and Rosenberg, 1978; Rhoads and Boyer, 1982). Therefore, there is a definite lack of deep sediment mixing in Perch Pond that has occurred for an unknown number of years.

If we assume no biological mixing below 2 cm, we calculate a sedimentation rate of 2.9 mm y^{-1} from the ^{210}Pb data using Eq. 4. Our sedimentation rate estimate agrees well with published rates for salt marshes and estuaries along the east coast of North America, which range from 1.4 to 15.5 mm y^{-1} (compiled by Sharma et al., 1987). Perch Pond is well protected from both tidal scouring due to its small tidal prism and from the wind due to its small size (i.e. no fetch for waves to build) with trees and houses that totally surround the pond, thereby limiting resuspension of the bottom as a mechanism that mixes only the superficial sediments. Evidence for the lack of resuspension is seen in profiles at several stations before and after a hurricane in 1985 showing no major changes in vertical distributions (data not shown). If deep resuspension had occurred, we would have expected to see the ^{210}Pb and cyst distribution change to one that was either homogeneous over a deep mixed suface layer, or one with a surface maximum of cysts due to the slower settling rates of cysts versus sand and silt. We therefore conclude that the isotope distribution and cyst burial below the upper 2 cm are controlled largely by sedimentation in Perch Pond. This is in sharp contrast to our coastal site where mixing predominates.

The cyst profile shapes once again demonstrate the influence of the surface mixed layer in homogenizing the cysts and in facilitating the germination of those that are exposed to oxygen at the sediment surface. As was observed at the deep coastal station, subsurface maxima in cyst abundance lie at the base of that layer, although in Perch Pond it is at 2 rather than 6 cm. Some species are most abundant at the sediment surface (Fig. 3), a result we attribute to new deposition from recent blooms. This is especially evident for *C. heterolobatum*, which bloomed in Perch Pond 2 months before the cores were taken, reaching visible "red tide" cell concentrations.

Since burial below the thin mixed layer (2 cm depth) is due to sedimentation, it is possible to estimate the age of cysts at depth under the assumption that there has been no deep mixing. The sedimentation rate (S) of 2.9 mm y^{-1} calculated from the 2–8 cm interval in the core suggests that the living cysts at 3–4 cm depths are at least 3–6 years old (i.e., 1–2 cm below the bottom of the mixed layer X 1 cm deposition every 3 years). By the same argument, cysts at 8 cm would be about 18 years old. These estimates are minimum ages because we have not included the time necessary for the cysts to move through and "escape" the well-mixed surface layer. Unfortunately, our excess ^{234}Th data were not significantly above supported ^{234}Th levels to provide estimates of the rate of rapid mixing near the sediment surface. However, if we assume that the surface mixing rate in Perch Pond is at least 20 cm^2 y^{-1} (a rate which is almost fast enough to produce a nearly vertical slope in the ^{210}Pb profile, see Fig. 1), one can see from the pulse model results (Fig. 2) that a significant number of cysts could escape the surface mixed layer in 1 year or less. Therefore, the residence time in the surface mixed layer does not add significantly to our age estimates which range from 1 to 20 years in the interval from 2 to 8 cm. Below this 8 cm depth, the unexplained constant excess of ^{210}Pb at 8–12 cm prevents us from

estimating ages deeper in the core. Very few living cysts are observed below 8 cm anyway, thus, living cysts in Perch Pond, like the Gulf of Maine appear to have life spans on the order of years to decades.

The exponential manner in which cyst abundance decreases with depth below the mixed layer is similar to that shown in the ^{210}Pb profiles. Figure 4 shows how cyst abundance decreases logarithmically with depth for *G. rugosum*. A negative deviation from this pattern near the surface would result from net losses due to germination (dashed line) producing a subsurface peak in the profile, whereas a positive deviation from the excellent fit to the regression at the surface would suggest net gains due to new cyst deposition (dotted line). Below the mixed layer, the exponential decrease in cyst abundance is a reflection of mortality through time, analogous to the decay of radioactive isotopes. Thus, this simple schematic provides explanations for the two types of cyst distributions that we observe.

When the cyst abundance data for each species (averaged over 45 cores and starting at the base of the surface mixed layer) were modelled as a simple exponential decay with constant input (Eqs. 6 and 7), the fit (r^2) was quite good for most species (Table 1). These calculations yield a rate or decay constant k (units $= cm^{-1}$), which can be used to calculate the parameter K (Eq. 6) specifying the depth interval over which 50% of the cysts disappear. This parameter varies significantly between species, the relatively low values for *G. uncatenum* and *G. polyedra* indicating that the cysts of those species die more rapidly than other species with deeper distributions and higher K values (e.g. *A. tamarense* and *G. verior*). This rank ordering is consistent with our qualitative impressions of the viability of cysts of these different species under long-term laboratory storage. *G. uncatenum* and *G. polyedra* cysts tend to die with prolonged storage at 4°C, which approximates the bottom temperatures in Perch Pond during winter. Little is known about the longevity of buried cysts, but "half-lives" of 2–10 years might be expected (Huber and Nipkow, 1922, 1923; Anderson et al., 1987). We should emphasize that the above analysis refers to living cysts only. It says nothing about the resistance to decay of empty cyst walls.

Counting all cyst walls in varved sediments of the Santa Barbara Basin, Wall (1986) found that some blooms of *G. polyedra* could be related to a recorded peak in the deposition of its cyst. It is possible that Perch Pond may yield similar results due to the fact that sedimentation is dominant in that anoxic environment. However, we would not expect to find a comparable situation in the Gulf of Maine because mixing would smooth out the annual pulse inputs rapidly down to depths of greater than 12 cm.

One thought that emerges from the Perch Pond results is, that in other locations where anoxia is either constant or frequent in bottom waters, cyst profiles might well show considerable vertical structure that could reflect the magnitude of successive bloom events. In such a location, burial would be predominantly by sediment deposition which would cause cyst "pulses" from discrete blooms to remain relatively intact through time. This might for example, be the case in permanently anoxic basins such as those in Santa Barbara or the Black Sea.

Similarities between the two study sites suggest common explanations for features such as a subsurface cyst abundance maxima; differences accentuate not only the different benthic community dynamics but the extreme variability that probably characterizes the intensity and timing of cyst germination events as well. In this latter context, if the rates of bioturbation and physical mixing are similar in the surface layers of the two study sites, we would predict that the germination success of newly-deposited cysts would be higher in Perch Pond by virtue of the shallowness of its surface mixed layer and slow rate of burial by deposition. It

is commonly assumed that encystment is a more useful strategy in neritic waters than in pelagic regions (Wall and Dale, 1968; Dale, 1983), but our results refine this concept further and suggest that not all shallow environments might be equally favorable for germination. In particular, areas where the benthic community is stressed by high organic loadings or periodic anoxia events will be dominated by opportunistic animals that feed and burrow at or close to the sediment surface (e.g. the polychaete *Capitella*). This would reduce the depth of the well-mixed layer (Pearson and Rosenberg, 1978; Rhoads and Boyer, 1982) and keep cysts closer to the sediment surface for longer times. The impact of the excystment inoculum would be maximized under these conditions. This argues that eutrophic waters might be optimal habitats for certain cyst-forming dinoflagellate species—an intriguing possibility given the recent concern that red tides and other bloom events are increasing in areas where coastal development has increased pollution loading to coastal waters.

Overview

Concurrent measurements of cyst and naturally occurring radionuclide abundances have increased our understanding of the processes that affect cyst burial and thus their role in inoculating blooms. We conclude that the Gulf of Maine is a very dynamic sediment environment where cysts are rapidly buried to greater than 12 cm. The observed vertical cyst profiles are not only the result of bioturbation and passive physical particle mixing, but also other biological processes (i.e. germination and mortality) acting within this mixing-dominated environment. Some cysts may be mixed back to the surface for germination reducing the numbers in the surface mixed layer, while others will be buried still deeper where they may die, reducing the numbers of cysts at depth. The resultant distribution is seen as a subsurface maximum, near the base of the well-mixed surface layer.

In contrast, Perch Pond is a quiet, protected and sometimes stagnant environment where the surface mixed layer is shallow due to the lack of deep-burrowing organisms. Cyst burial is thus dominated by sedimentation. Observed distributions are again the result of biological processes (i.e. germination and mortality) acting within the sedimentary environment. Cysts may remain near the surface for relatively long time spans where they are subject to germination, resuspension or deeper burial by sedimentation. Once below 2 cm, the cysts cannot participate in seeding a bloom and will be buried over time. Eventually, the cysts will die where they may or may not be preserved in the fossil record (Dale, 1976). The resultant profile for the living cysts would be similar to those from the Gulf of Maine, where a subsurface maximum is observed near the base of the mixed layer. New depositions at the surface would only temporarily alter the distributions.

Living cysts in both environments appear to have "half-lives" on the order of years to decades. In addition, the rate at which cysts die varies with species suggesting that some cysts are more susceptable to mortality during burial than are others.

More detailed radiotracer profiles and cyst germination and mortality studies are needed if we are to completely understand the biological processes involved and the coupling of these processes with the physical environment. Only then will we be able to accurately estimate the ages of both live and dead cysts at various depths in the recent sediments or the rates at which cysts in the surface layer are exposed to oxygen and germinate under favorable conditions as that layer is homogenized. Further testing must also be done to show conclusively that sediment particles and cysts are physically mixed to the same extent and that selective feeding of cysts by benthic animals is not a mechanism that could produce the observed cyst distributions.

Acknowledgements

We thank D. Kulis for technical assistance and the captain and crew of the R/V *Jere Chase* for cruise support. We also thank G. Hampson for his technical expertise and invaluable discussions on bioturbation. Research supported in part by the NOAA National Sea Grant College Program Office, Department of Commerce, under Grant No. N86-AA-D-SGO90, WHOI project Nos. R/B-76 and R/B-92, by the Florence and John Schumann Foundation and by U.S. National Science Foundation grants to KOB (OCE-8700715 and OCE-8614545). Contribution No. 7184 from the Woods Hole Oceanographic Institution.

References

Aller, R.C. and Cochran, J.K., 1976. $^{234}Th/^{238}U$ disequilibrium in nearshore sediment: particle reworking and diagenetic time scales. Earth Planet. Sci. Lett., 29: 37–50.

Anderson, D.M., 1984. The roles of dormant cysts in toxic dinoflagellate blooms and shellfish toxicity. In: E. Ragelis (Editor), Seafood Toxins. Am. Chem. Soc. Symp. Ser., 262: 125–138.

Anderson, D.M. and Keafer, B.A., 1985. Dinoflagellate cyst dynamics in coastal and estuarine waters. In: D.M. Anderson, A.W. White and D.G. Baden (Editors), Toxic Dinoflagellates. Proc. 3rd Int. Conf. (June 8–12, 1985, St. Andrews, N.B., Canada.) Elsevier, Amsterdam, pp. 219–224.

Anderson, D.M., Aubrey, D.G., Tyler, M.A. and Coats, D.W., 1982a. Vertical and horizontal distributions of dinoflagellate cysts in sediments. Limnol. Oceanogr., 27: 757–765.

Anderson, D.M., Kulis, D.M., Orphanos, J.A. and Ceurvels, A.R., 1982b. Distribution of the toxic red tide dinoflagellate *Gonyaulax tamarensis* in the southern New England region. Estuarine Coastal Shelf Sci., 14: 447–458.

Anderson, D.M., Taylor, C.D. and Armbrust, E.V., 1987. The effects of darkness and anaerobiosis on dinoflagellate cyst germination. Limnol. Oceanogr., 32: 340–351.

Anderson, R.F., Bopp, R.F., Buesseler, K.O. and Biscaye, P.E., 1988. Mixing of particles and organic constituents in sediments from the continental shelf and slope off Cape Cod: SEEP-I results. Cont. Shelf Res., 8: 925–946.

Benninger, L.K., Aller, R.C., Cochran, J.K. and Turekian, K.K., 1979. Effects of biological sediment mixing on the ^{210}Pb chronology and trace metal distribution in a Long Island Sound sediment core. Earth Planet. Sci. Lett., 43: 241–259.

Binder, B.J. and Anderson, D.M., 1986. Green light-mediated photomorphogenesis in a dinoflagellate resting cyst. Nature, 322: 659–661.

Brower, C., 1984. Lead-210 in sediments of the Gulf of Maine. M.S. Thesis, Univ. Maine, Orono, 107 pp.

Buesseler, K.O., 1986. Plutonium Isotopes in the North Atlantic. Ph.D. Thesis, Massaschusetts Inst. Technol./Woods Hole Oceanogr. Inst., WHOI-86-32.

Carpenter, R., Peterson, M.L. and Bennett, J.T., 1982. ^{210}Pb-derived sediment accumulation and mixing rates for the Washington continental slope. Mar. Geol., 48: 135–164.

Cochran, J.K., 1985. Particle mixing rates in sediments of the eastern equatorial Pacific: Evidence from ^{210}Pb, $^{239,240}Pu$ and ^{137}Cs distributions at MANOP sites. Geochim. Cosmochim. Acta, 49: 1195–1210.

Craib, J.S., 1965. A sampler for taking short undisturbed marine cores. J. Cons. Cons. Int. Explor. Mer, 30: 34–39.

Cutshall, N.H., Larsen, I.L. and Olsen, C.R., 1983. Direct analysis of ^{210}Pb in sediment samples: self-absorption corrections. Nucl. Instrum. Methods, 206: 309–312.

Dale, B., 1976. Cyst formation, sedimentation, and preservation: factors affecting dinoflagellate assemblages in recent sediments from Trondheimsfjord, Norway. Rev. Paleobot. Palynol., 22: 39–60.

Dale, B., 1979. Collection, preparation, and identification of dinoflagellate resting cysts. In: D.L. Taylor and H.H. Seliger (Editors), Toxic Dinoflagellate Blooms. Proc. 2nd Int. Conf. Elsevier/North Holland, Amsterdam, pp. 443–452.

Dale, B., 1983. Dinoflagellate resting cysts: "benthic plankton." In: G.A. Fryxell (Editor), Survival Strategies of the Algae. Cambridge Univ. Press, pp. 69–136.

DeMaster, D.J., McKee, B.A., Nittrouer, C.A., Brewster, D.C. and Biscaye, P.E., 1985. Rates of sediment reworking at the HEBBLE site based on measurements of ^{234}Th, ^{137}Cs and ^{210}Pb. Mar. Geol., 66: 133–148.

Duursma, E.K. and Hoede, C., 1967. Theoretical, experimental and field studies concerning molecular diffusion of radio isotopes in sediments and suspended solid particles of the sea. Part A: Theories and mathmetical calculations. Neth. J. Sea Res., 3: 423–457.

Flight, W.R., 1972. The Holocene sedimentary history of Jeffreys Basin. M.S. Thesis, Univ. New Hampshire, 173 pp.

Goodman, D.K., 1987. Dinoflagellate cysts in ancient and modern sediments. In: F.J.R.Taylor (Editor), The Biology of Dinoflagellates. Blackwell, Oxford, pp. 649–722.

Guinasso, N.L. and Schink, D.L., 1975. Quantitative estimate of biological mixing rates in abyssal sediments. J. Geophys. Res., 80: 3032–3043.

Hines, M.E., Bazylinski, D.A., Tugel, J.B. and Lyons, W.B., 1991. Anaerobic microbial biogeochemistry in sediments from two basins in the Gulf of Maine. Estuarine Coastal Shelf Sci., 32: 313–324.

Huber, G. and Nipkow, F., 1922. Experimentelle Untersuchungen über die Entwicklung von *Ceratium hirundinella*. O.F.M. Z. Bot., 14(5): 337–371.

Huber, G. and Nipkow, F., 1923. Experimentelle Untersuchungen über Entwicklung und Formbildung von *Ceratium hirundinella*. O. Fr. Müller. Flora Allg. Bot. Ztg., 116: 114–215.

Hulbert, M.H. and Given, D.N., 1975. Geotechnical and chemical property relationships for Wilkinson Basin, Gulf of Maine sediments. J. Sediment. Petrol., 45: 504–512.

Krishnaswami, S., Benninger, L.K., Aller, R.C. and Von Damm, K.L., 1980. Atmospherically-derived radionuclides as tracers of sediment mixing and accumulation in nearshore marine and lake sediments: evidence from ^{7}Be, ^{210}Pb, and $^{239,240}Pu$. Earth Planet. Sci. Lett., 47: 307–318.

Livingston, H.D. and Bowen, V.T., 1979. Pu and ^{137}Cs in coastal sediments. Earth Planet. Sci. Lett., 43: 29–45.

Mulligan, H.F., 1975. Oceanographic factors associated with New England red-tide blooms. In: V.R. LoCicero (Editor), Toxic Dinoflagellate Blooms. Proc. 1st Int. Conf. Mass. Sci. Technol. Fdn., Wakefield, MA, pp. 23–40.

Nittrouer, C.A., Sternberg, R.W., Carpenter, R. and Bennett, J.T., 1979. The use of ^{210}Pb geochronology as a sedimentological tool: application to the Washington Continental Shelf. Mar. Geol., 31: 297–316.

Pearson, T.H. and Rosenberg, R., 1978. Macro benthic succession in relation to organic enrichment and pollution in the marine environment. Oceanogr. Mar. Biol. Ann. Rev., 16: 229–311.

Rhoads, D.C. and Boyer, L.F., 1982. The effects of marine benthos on physical properties of sediments: A successional perspective. In: P.L. McCall and M.J.S. Tevesz (Editors), Animal–Sediment Relations. Plenum, New York, pp. 3–52.

Santchi, P.H., Li, Y.H., Bell, J.J., Trier, R.M. and Kawtaluk, K., 1980. Pu in coastal marine environments. Earth Planet. Sci. Lett., 51: 248–265.

Sharma, P., Gardner, L.R., Moore, W.S. and Bollinger, M.S., 1987. Sedimentation and bioturbation in a salt marsh as revealed by ^{210}Pb, ^{137}Cs, and ^{7}Be studies. Limnol. Oceanogr., 32: 313–326.

Turkekian, K.K. and Cochran, J.K., 1978. Determination of marine chronologies using natural radionuclides. In: J.P. Riley and R. Chester (Editors), Chemical Oceanography. Academic Press, New York, 2nd ed., 7, pp. 313–360.

Tyler, M.A., Coats, D.W. and Anderson, D.M., 1982. Encystment in a dynamicenvironment: deposition of dinoflagellate cysts by a frontal convergence. Mar. Ecol. Progr. Ser., 7: 163–178.

Wall, D., 1986. Dinoflagellate cysts and acritarchs from California Current surface sediments. Ph.D. Thesis, Univ. Saskatchewan, Canada.

Wall, D. and Dale, B., 1968. Modern dinoflagellate cysts and evolution of the Peridiniales. Micropaleontology, 14: 265–304.