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# What controls the mixed-layer depth in deep-sea sediments? The importance of POC flux

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*Abstract*

The depth of biogenic particle mixing, i.e., the mixed-layer depth ($L$), is fundamental in models of organic-matter recycling and paleoreconstructions for deep-sea sediments. Factors postulated to control $L$ in the oxygenated deep sea include particulate organic carbon (POC) flux, oxygen penetration into the sediment, and a balance between the downward mixing and decay of labile POC. We explore the dependence of $L$ on biogeochemical characteristics by compiling, from 36 sites in three oceans, an internally consistent set of deep-sea estimates of $L$, POC flux, biogenic mixing intensity ($D_b$), and POC reactivity. We use excess $^{210}$Pb as a tracer for $L$ and $D_b$ to avoid the confounding effects of tracer-dependent mixing. We find that $L$, estimated from the penetration depth of excess $^{210}$Pb, varies systematically with POC flux, with an asymptotic function explaining 88% of the variance in $L$. Stepwise multiple regression suggests that the penetration depth of excess $^{210}$Pb (and estimated $L$) is much more likely to be controlled by POC flux than by (1) the sediment inventory of excess $^{210}$Pb or (2) biogenic mixing intensity ($D_b$). In addition, $L$ is negatively related to oxygen penetration into the sediment ($r = -0.629$) and not significantly related to predictions of $L$ from a recent mixing/POC-decay model. We conclude that in the food-poor deep sea, POC flux substantially controls the size and activities of the sediment-mixing benthos and, in turn, the thickness of the biogenic mixed layer. Thus, in contrast to previous suggestions, average mixed-layer depth is not environmentally invariant but rather responds predictably to ecologically important parameters such as POC flux.

The mixing of sediment grains by animal activity (i.e., biogenic particle mixing) profoundly influences the structure and geochemistry of marine sediments. In particular, the recycling and burial of organic carbon, nutrients, and pollutants, as well as the resolution of the stratigraphic record, depend substantially on the rates and depths of biogenic sediment mixing (e.g., Aller 1982; Wheatcroft et al. 1990; Smith et al. 1993).

In deep-sea regions characterized by low current velocities, low sedimentation rates, and well-oxygenated bottom water, biogenic mixing is thought to control the movement of particles in near-surface sediments. Under these conditions, biogenic mixing is usually parameterized as eddy diffusion, described by an intensity coefficient $D_b$ (units of length$^2$ time$^{-1}$) that operates over a sediment depth interval, $L$, called the mixed-layer depth (e.g., Guinasso and Schink 1975; Boudreau 1998). Based on this formulation, at steady state, the depth distribution of a particle-bound chemical species with first-order decay (e.g., a particle-associated radionuclide) in sediment of constant porosity is described by the following equation:

$$D_b \frac{d^2C}{dz^2} - kC = 0 \quad \text{for } 0 < z < L \tag{1}$$

where $C$ is the concentration of the particle-bound chemical species, $z$ is depth, $L$ is the mixed-layer depth, and $k$ is a first-order decay constant (time$^{-1}$). For radioisotopes, $k = \lambda$, the radioactive decay constant. As pointed out by Boudreau (1994, 1998), this equation is easy to use and generally produces good fits to sediment concentration profiles. Thus, it is widely applied in models of sediment geochemistry, despite the fact that numerous more complicated (and seemingly more biologically realistic) functionalities for biogenic mixing have been developed, including advective transport and nonlocal exchange (Boudreau 1997).

The depth of the surface mixed layer in sediments ($L$), as measured from profiles of particle-associated radionuclides, varies by more than an order of magnitude over the world ocean, ranging from 0 to 30 cm (e.g., Boudreau 1998). A similarly broad range in $L$, i.e., 2 to 20 cm, is observed in the deep sea below 1,000 m (Boudreau 1998; this study). A variety of factors are postulated to influence the magnitude of $L$, including the increase in sediment compaction with depth into the sediment (Jumars and Wheatcroft 1989), particulate organic carbon (POC) flux to the sediment surface (Smith 1992; Trauth et al. 1997), the penetration depth of

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oxygen into the sediment (Dhakar and Burdige 1996), and a balance between the downward mixing and decay of labile POC (i.e., food for deposit feeders; Boudreau 1998). Across the full range of marine environments (intertidal to abyssal depths, fully oxic to fully anoxic), some of these variables are expected to have complex influences on $L$, and the relative importance of these factors will clearly vary. For example, it is well documented that at extremely high rates of POC flux (e.g., near sewage outfalls, in eutrophic estuaries and beneath coastal upwelling zones), organic loading and oxygen stress cause a reduction in the abundance, body size, and burrowing depths of the macrobenthos and megabenthos, yielding low $L$ (e.g., Pearson and Rosenberg 1978; Diaz and Rosenberg 1995; Smith et al. 2000). At very low rates of POC flux (e.g., at abyssal depths below oligotrophic central gyres) the abundance and body size of macrobenthos and megabenthos are also greatly reduced, in this case due to food limitation (Hessler 1974; Gage and Tyler 1991), again yielding an expected reduction in $L$ (Smith 1992). Such varying relationships clearly have frustrated attempts to derive simple correlations between $L$ and environmental variables over the entire world ocean (e.g., Boudreau 1994, 1998).

In this paper, we compile an internally consistent data set to explore the functionality of $L$ in deep-sea environments with well-oxygenated bottom waters, where we expect the relationship between mixing depth and POC flux to be monotonic. In particular, we test the prediction that $L$ will vary positively with annual POC flux (Smith 1992), falling to a minimum in oligotrophic regions and approaching an asymptotic value in relatively eutrophic settings. The sequence of reasoning behind this prediction is as follows: (1) based on dimensional analyses, the rates and depths of biogenic mixing in the deep sea appear to be controlled by the larger deposit-feeding benthos (i.e., the macrofauna and megafauna), with body size controlling the length scales of particle displacement (Wheatcroft et al. 1990; Smith 1992); (2) in the food-poor deep sea, the abundance and mean body size of macrobenthos and megabenthos, including important sediment mixers, appear to be strongly correlated with annual POC flux to the seafloor (Thiel 1979; Smith 1992; Smith et al. 1997); (3) above a certain POC-flux threshold, i.e., under relatively eutrophic conditions, infaunal body size is likely to be released from food limitation and become controlled by other factors, such as body-plan constraints or the costs of burrowing through compacted sediments (Jumars and Wheatcroft 1989), ultimately causing $L$ to plateau in relation to POC flux.

We also test the prediction that, in the deep sea, $L$ will show little relationship to oxygen penetration into the sediment as long as bottom waters remain well oxygenated. We make this prediction because the larger benthos apparently responsible for most biogenic mixing (Wheatcroft et al. 1990) should be able to maintain contact with oxygenated bottom water, even if they live $>$10 cm deep in anoxic sediments. In addition, we use the newly compiled deep-sea data set to test the generality of the Boudreau (1998) model, which explicitly relates the magnitude of $L$ to $D_b$ and the decay constant ($k$) for organic carbon. Boudreau's model predicts a balance between downward mixing and decay, leading essentially to environmental invariance in mean $L$. Finally, we evaluate the relationship between mixed-layer depth and water depth because a variety of potentially important (but difficult to measure) environmental parameters (e.g., POC flux) co-vary with the depth of the water column (Smith 1992; Boudreau 1994).

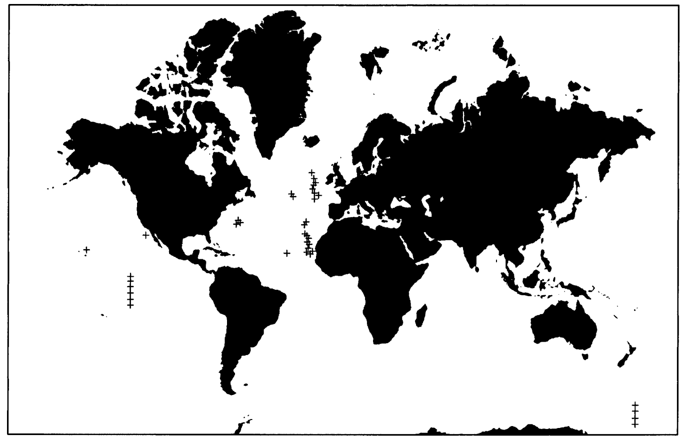

Fig. 1. The 36 seafloor stations (crosses) from which data were compiled for this study. The coordinates and depths of stations, and scientific sources, are given in Table 1.

## The data set and methods

To address the dependence of $L$ on biogeochemical characteristics in the deep sea, we have compiled an internally consistent set of deep-sea estimates of $L$, POC flux, $D_b$, and $k$. These variables are derived from measurements and models using $^{210}$Pb as a tracer, avoiding the inclusion of potentially large errors resulting from tracer-dependent mixing (e.g., Smith et al. 1993). We have compiled data from a total of 36 stations in the North Atlantic, the North and Equatorial Pacific, and the Southern Ocean (Fig. 1). Our data set is derived from a broad array of deep-sea habitats, ranging from high latitudes with seasonal phytodetritus deposition to equatorial settings, from oligotrophic to eutrophic production regimes, from water depths of 1,240 to 5,000 m, and from terrigenous to fully pelagic sediments (both carbonate rich and poor). For all sites, we have estimates of mean mixed-layer depth evaluated from profiles of excess $^{210}$Pb. In addition, for many sites our data include mixing depth estimated from profiles of $^{14}$C, penetration depth of oxygen into the sediments, biogenic mixing-rate constants ($D_b$) estimated using excess $^{210}$Pb, kinetic constants of organic-carbon mineralization (based on models using $D_b$ for $^{210}$Pb), and deep-sea POC flux derived from sediment traps or (in one case) benthic-flux measurements.

The Atlantic data originate from four programs: BOFS, EUMELI, SEEP I, and BENGAL. BOFS cruises occurred in 1989 and 1990 along a transect from 60°N to 19°N around 20°W (Table 1) with water depths ranging from 1,750 to 4,800 m (Brand and Shimmield 1991; Thomson et al. 1993, 1995). EUMELI cruises took place between 1991 and 1993 at sites located on an east–west transect (31°W to 18°W) around 20°N and covered water depths from 2,000 to 4,600

Table 1. The locations and sources of data for the stations used in this study.

| Site and station No. | Latitude | Longitude | Water depth (m) | Reference(s) |
|---|---|---|---|---|
| BOFS | | | | Brand and Shimmield 1991; Thomson et al. 1993, 1995; Newton et al. 1994 |
| 11878 | 47.15°N | 22.49°W | 3,945 | |
| 11880 | 47.80°N | 19.68°W | 4,540 | |
| 11881 | 49.85°N | 21.29°W | 4,220 | |
| 11882 | 50.68°N | 21.86°W | 3,560 | |
| 11886 | 52.52°N | 22.09°W | 4,025 | |
| 11889 | 53.70°N | 21.33°W | 3,275 | |
| 11891 | 55.19°N | 20.35°W | 2,080 | |
| 11896 | 58.65°N | 19.42°W | 1,756 | |
| 11898 | 59.10°N | 20.12°W | 2,790 | |
| 23 | 32.54°N | 20.39°W | 4,650 | |
| 25 | 28.06°N | 22.06°W | 4,830 | |
| 26 | 24.48°N | 19.89°W | 3,660 | |
| 27 | 24.48°N | 20.39°W | 4,010 | |
| 28 | 24.56°N | 22.82°W | 4,855 | |
| 29 | 20.53°N | 21.12°W | 4,000 | |
| 30 | 19.67°N | 20.67°W | 3,565 | |
| 31 | 19.00°N | 20.16°W | 3,295 | |
| EUMELI | | | | Legeleux et al. 1994, 1996; Bory et al. 2001 |
| Oligo | 21.03°N | 31.10°W | 4,550 | |
| Meso | 18.30°N | 21.05°W | 3,150 | |
| Eutro | 20.33°N | 18.35°W | 2,050 | |
| SEEP-I | | | | Anderson et al. 1988; Biscaye et al. 1988 |
| Sta. 5 | 39.8°N | 70.92°W | 1,305 | |
| Sta. 6 | 39.58°N | 70.95°W | 2,362 | |
| Sta. 7 | 39.16°N | 70.72°W | 2,700 | |
| BENGAL | 48.38°N | 16.50°W | 4,800 | Lampitt et al. 2001; Reyss unpubl. data |
| EQPAC | | | | Pope 1996; Hammond et al. 1996; Smith et al. 1997 |
| 5°S | 4.74°S | 139.73°W | 4,250 | |
| 2°S | 1.86°S | 139.72°W | 4,380 | |
| 0° | 0.12°N | 139.73°W | 4,310 | |
| 2°N | 2.58°N | 140.14°W | 4,410 | |
| 5°N | 5.08°N | 139.65°W | 4,400 | |
| 9°N | 8.93°N | 139.86°W | 4,990 | |
| HOT | 22.92°N | 159.83°W | 4,600 | |
| SCB | 33.20°N | 118.50°W | 1,240 | Pope 1996; Archer et al. 1989; Fornes 1999 |
| AESOPS | | | | Sayles et al. 2001 |
| Sta. 2 | 56.88°S | 170.17°W | 4,970 | |
| Sta. 3 | 60.24°S | 170.19°W | 3,950 | |
| Sta. 4 | 63.11°S | 169.74°W | 2,900 | |
| Sta. 5 | 66.14°S | 169.63°W | 3,150 | |

m (Table 1; Rabouille et al. 1993; Legeleux et al. 1994; Rabouille et al. pers. comm.). The SEEP I data come from the continental slope of the northwest Atlantic, studied during 1983–1984 by Anderson et al. (1988) and Biscaye et al. (1988). The Bengal data come from J.-L. Reyss (pers. comm.) and Lampitt et al. (2001), with seafloor samples collected at 4,800 m in July 1997 and POC fluxes measured from 1996 to 1998. The Equatorial Pacific data come from the EQPAC Program's benthic cruise in November–December 1992, with stations on an abyssal, cross-equatorial transect at approximately 140°W (Table 1; Smith et al. 1997). In addition, North Pacific data from 1,240 m in Santa Catalina Basin (SCB) are included, which was sampled in 1987–1988 during multiple cruises (Archer et al. 1989; Smith et al. 1993; Pope 1996) and in 1995–1998 during multiple cruises (Fornes 1999). Data from the Southern Ocean come from the AESOPS program conducted in 1998 at depths ranging from 2,740 to 5,440 m (Sayles et al. 2001).

Analytical methods are described in detail in the original papers (*see references in Table 1*). Excess $^{210}$Pb ($^{210}Pb_{xs}$) profiles were evaluated in all sediment cores considered here. Mixed-layer depth was defined as the depth below which $^{210}$Pb activity in excess of its parent ($^{226}$Ra) dropped to $<1$ dpm $g^{-1}$. When $^{226}$Ra was not measured directly (four profiles from Brand and Shimmield 1991), its activity was assumed to equal the $^{210}$Pb activity at the base of the core (i.e., at a depth of 10–16 cm). For all cores, the decrease in $^{210}Pb_{xs}$ downcore was substantial since surface activities ranged from 10 to 80 dpm $g^{-1}$. At the oceanic sites we considered, sedimentation rates are roughly 0.05–2 cm per hundred years (Anderson et al. 1988; Auffret et al. 1992; Thomson et al. 1993; Pope 1996; Fornes 1999), so the penetration depth of $^{210}Pb_{xs}$ (half-life = 22 yr) should be controlled by the depth of biogenic mixing over a 100-yr time scale. Since $^{210}Pb_{xs}$ has a radioactive half-life similar to much of the inventory of sediment organic carbon (e.g., Rabouille et al. 1993; Hammond et al. 1996), we consider $^{210}Pb_{xs}$ to be a tracer for moderately reactive organic carbon ($k = 10^{-1}$ to $10^{-2}$ yr$^{-1}$).

Twenty of the 36 sites we consider were also subjected to radiocarbon dating (Table 2), allowing us to compare $L$ derived from $^{210}$Pb and $^{14}$C. In these cores, the $^{14}$C mixed-layer depth was defined as the intercept between a line through the top points in the profile (demarking a mixed layer of constant age) and the straight line defining the sedimentation rate below the mixed layer (for examples, see Thomson et al. 1995).

At nine of the stations we consider (the EUMELI and EQPAC stations, Tables 1 and 2), first-order degradation-rate constants ($k$) were calculated for sedimentary organic matter using $^{210}$Pb mixing coefficients in diagenetic models (see Rabouille et al. 1993 and Hammond et al. 1996 for calculations). The $k$'s we use in the present analyses were all calculated using similar modeling approaches and are those for organic carbon of intermediate reactivity ($0.01 < k < 0.1$ yr$^{-1}$). The $k$'s from our nine stations are equivalent to the $k$'s used in Boudreau (1998), which were based on the relationship published by Tromp et al. (1995).

Oxygen profiles were measured at the various stations using either oxygen electrodes or pore-water extractions (Brand and Shimmield 1991; Hammond et al. 1996; Relexans et al. 1996; Rabouille et al. pers. comm.). BOFS oxygen profiles were extracted from the BODC data base (Shimmield 1990).

POC fluxes were compiled from the literature. Except for the eutrophic site of EUMELI, they are all derived from sediment traps moored at depths of roughly 1,100–3,000 m (Honjo and Manganini 1993; Newton et al. 1994; Honjo et al. 1995; Smith et al. 1997; Khripounoff et al. 1998). Trap deployment times were $\geq$1 yr at all sites except for Santa Catalina Basin, where traps were deployed for a total of 172

Table 2. Mixed-layer depth determined from profiles of $^{210}Pb_{xs}$ and $^{14}C$, penetration depth of oxygen into sediment porewaters, seabed $^{210}Pb_{xs}$ inventories, annual POC flux from sediment traps, kinetic constant for the mineralization of organic carbon of intermediate reactivity, and bioturbation coefficients for the stations considered in this study. Except for the EQPAC stations, bioturbation coefficients were taken directly from the sources cited in Table 1. For the EQPAC data, we recalculated bioturbation coefficients using all data points from Pope (1996) exceeding 1 dpm g$^{-1}$ within the sediment mixed layer, as was done in the other studies. The estimates of mixed-layer depth from the model of Boudreau (1998) (Eq. 3) are also given.

| Station | Mixed-layer depth $^{210}Pb_{xs}$ (cm) | Mixed-layer depth $^{14}C$ (cm) | $^{210}Pb_{xs}$ inventory (dpm cm$^{-2}$) | Penetration depth $O_2$ (cm) | POC flux (mol C m$^{-2}$ yr$^{-1}$) | Kinetic constant $k$ (yr$^{-1}$) | Bioturbation coefficient $D_b$ (m$^2$ yr$^{-1}$) | Boudreau mixed-layer depth (cm) |
|---|---|---|---|---|---|---|---|---|
| BOFS 11878 | 7.5 | | | 6 | | | | |
| BOFS 11880 | 9.5 | 8.7 | 17.6 | 6.5 | 0.17 | | | |
| BOFS 11881 | 8 | 8.9 | | 5.5 | | | | |
| BOFS 11882 | 9.5 | 9.3 | | 4 | | | | |
| BOFS 11886 | >10 | 9.3 | | 6 | | | | |
| BOFS 11889 | >10 | 9.4 | | 5 | | | | |
| BOFS 11891 | 8 | | | 4.5 | | | | |
| BOFS 11896 | 6 | 13.5 | | 4 | | | | |
| BOFS 11898 | 8 | | | 9 | | | | |
| BOFS 29 | 8.5 | 10 | | 8 | | | | |
| BOFS 30 | 8.5 | 8 | | 2 | | | | |
| BOFS 31 | 10.5 | 10.5 | | 1.5 | | | | |
| BOFS 23 | 4.5 | 8.5 | | 10 | 0.09 | | | |
| BOFS 25 | 3.5 | 4.5 | | | | | | |
| BOFS 26 | 6 | 5.5 | | | | | | |
| BOFS 27 | 5 | 6 | | | | | | |
| BOFS 28 | 3.5 | | | | | | | |
| Eumeli Oligo | 3 | | | | 0.03 | 0.023 | 0.1 | 8.8 |
| Eumeli Meso | 7.5 | | | 6 | 0.15 | 0.04 | 0.2 | 9.5 |
| Eumeli Eutro | 14 | | | 2 | 0.5 | 0.085 | 0.8 | 13.0 |
| SEEP Sta. 5 | 12 | | | | 0.42 | | | |
| SEEP Sta. 6 | 9 | | | | 0.18 | | | |
| SEEP Sta. 7 | 9 | | | | 0.18 | | | |
| Bengal | 11 | | | | 0.34 | | | |
| EQPAC 5°S | 3.5 | | 19.3 | | 0.077 | 0.013 | 0.089 | 11.1 |
| EQPAC 2°S | 5.5 | | 20.7 | | 0.11 | 0.013 | 0.21 | 17.0 |
| EQPAC 0° | 8 | 7.5 | 34 | | 0.135 | 0.013 | 0.27 | 19.3 |
| EQPAC 2°N | 7.5 | 5.5 | 41 | | 0.124 | 0.013 | 0.34 | 21.6 |
| EQPAC 5°N | 7 | 7.5 | 34.5 | | 0.117 | 0.075 | 0.22 | 7.3 |
| EQPAC 9°N | 2 | | 7.7 | | 0.029 | 0.075 | 0.019 | 2.1 |
| HOT | 1.8 | | 23.8 | | 0.04 | | | |
| SCB | 11.2 | | | 0.5 | 0.57 | | | |
| AESOPS Sta. 2 | 7 | | 27.5 | | 0.06 | | 0.16 | |
| AESOPS Sta. 3 | 5.5 | | 10.6 | | 0.06 | | 0.709 | |
| AESOPS Sta. 4 | 6 | | 18.1 | | 0.14 | | 0.094 | |
| AESOPS Sta. 5 | 7 | | 33.6 | | 0.11 | | 0.109 | |

d (Fornes 1999). An annual flux is calculated for each of the sediment-trap sites. For the EUMELI-Eutro site, the POC flux was estimated using the oxidant flux at the sediment-water interface (Rabouille et al. 1993). At those stations where both sediment-trap and seafloor oxidant-flux data exist (e.g., the BOFS stations at ~33° and 48°N, and the EQPAC transect), they agree to within 30% (Shimmield et al. 1995; Smith et al. 1997).

Regression analyses were conducted with SigmaStat (1994) and the significance of product-moment correlation coefficients ($r$) was determined from Rohlf and Sokal (1969). A $p$ level of 0.05 was used as the criterion for statistical significance.

## Results

The mixed-layer depth, $L$, estimated for our deep-sea sites using $^{210}Pb_{xs}$ or $^{14}C$ ranged from 2 to 14 cm (Table 2). At 14 out of the 16 stations (88%) for which both $^{210}Pb_{xs}$ and $^{14}C$ profiles were available, there was excellent correspondence between the two isotopes in mixing depth, with $L$ differing by $\leq$2 cm (Table 2). At the two sites where the isotopes disagreed on $L$ (BOFS 11,896, 1,756 m depth; BOFS 23, 4,650 m), the $^{210}Pb_{xs}$ mixing depth was about half that for $^{14}C$. This occasional difference in mixing depths probably results from the different characteristic time scales of the two isotopes (thousands of years for $^{14}C$ versus ~100 yr for

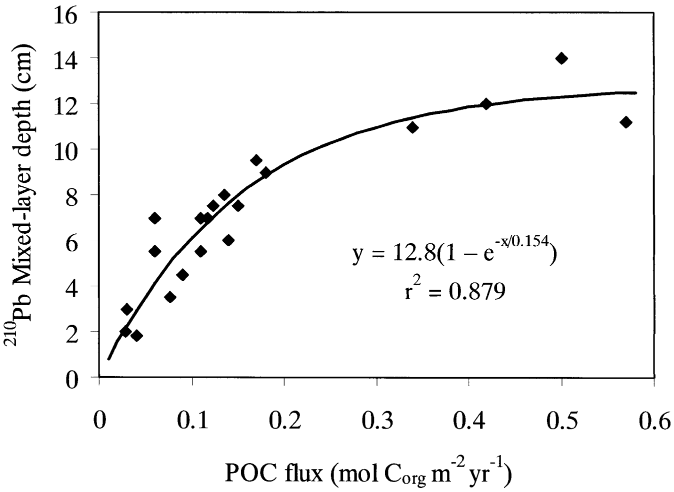


Fig. 2. $^{210}$Pb mixing depth, $L$, as a function of annual POC flux for all deep-sea stations >1,200 m depth for which POC flux and $^{210}Pb_{xs}$ profiles are available. The equation for the statistically significant ($p < 0.0001$) asymptotic regression curve is shown.

$^{210}Pb_{xs}$); $^{14}$C is more likely to record rare, deep mixing events. We conclude that, in general, the mixing depths of $^{210}Pb_{xs}$ and $^{14}$C are quite similar, and that $^{210}Pb_{xs}$ reliably records the depth to which active biogenic mixing occurs over 100-yr time scales.

POC fluxes at our sites varied by more than an order of magnitude, from 0.03 to 0.5 mol $C_{org}$ m$^{-2}$ yr$^{-1}$ (i.e., 0.4–6 g $C_{org}$ m$^{-2}$ yr$^{-1}$). Stations with the lowest POC flux came from the subtropical oligotrophic gyres (Atlantic and Pacific) and the Southern Ocean; those with moderate POC fluxes came from the equatorial upwelling zone, the Southern Ocean, and the mesotrophic region off west Africa; and those with the highest fluxes were from the temperate North Atlantic and the Mauritanian upwelling zone (Tables 1 and 2). In terms of POC flux, our stations range from oligotrophic to quite eutrophic by deep-sea standards (Smith and Hinga 1983; Smith et al. 1997).

At the 21 stations for which we have POC-flux data, the $^{210}$Pb mixed-layer depth, $L$, showed a very strong relationship to annual POC flux (Fig. 2). In particular, under oligotrophic conditions (i.e., where POC flux <0.2 mol C m$^{-2}$ yr$^{-1}$), $L$ increased essentially linearly with the rain rate of POC (Fig. 2). Above a flux rate of 0.2 mol $C_{org}$ m$^{-2}$ yr$^{-1}$, i.e., under more eutrophic conditions, $L$ gradually leveled off as POC flux increased. Thus, across all our stations, the relationship between $L$ and POC flux is well described by an asymptotic function (fitted with SigmaStat) of the form:

$$L = L_{\min} + (L_{\max} - L_{\min})(1 - \exp[-F_c/F_c^*]) \qquad (2)$$

where $L$ is the mixed-layer depth, $F_c$ is the POC flux, $L_{min}$ is a minimum mixed-layer depth (set equal to 0), $L_{max}$ is the maximum (or asymptotic) mixed-layer depth (12.80 cm), and $F_c^*$ is a fit constant equal to 0.154. This equation explains 88% of the variance in $L$ ($r^2 = 0.879$; Fig. 2).

Is the relationship in oligotrophic settings between POC flux and $L$ spurious, i.e., is this linearity actually driven by other parameters that covary with POC flux? In oligotrophic settings, where the rain of sinking particles is very small, the seabed flux and inventory of $^{210}Pb_{xs}$ could be so low that $^{210}Pb_{xs}$ becomes diluted to undetectable levels before reaching the bottom of the sediment mixed layer. If this were the case, we would expect a tighter relationship between $^{210}Pb_{xs}$ inventory and $L$ than between POC flux and $L$. Alternatively, mixing intensity ($D_b$) could control the apparent mixing depth ($L$) if mixing occurred so slowly that $^{210}Pb_{xs}$ decayed to undetectable levels before reaching the bottom of the mixed layer. In this case, we would expect a stronger relationship between $D_b$ and $L$ than between POC flux and $L$. In fact, for the 13 oligotrophic stations for which we have POC flux, $^{210}$Pb inventory, and $D_b$ data, we find that $L$ is substantially more strongly correlated with POC flux ($r = 0.847$) than with either excess $^{210}$Pb inventory ($r = 0.547$) or $D_b$ ($r = 0.077$) (Fig. 3). (Omission of the outlying data point for $D_b$ in Fig. 3C raises the $r$ only to 0.349.) In a stepwise multiple linear regression using POC flux, $^{210}Pb_{xs}$ inventory, and $D_b$ as independent variables, and $L$ as the dependent variable, POC flux is added first and explains 72% of the variance ($p < 0.003$); the addition of $^{210}Pb_{xs}$ inventory and $D_b$ does not significantly increase the percentage of variance explained ($p > 0.30$ and $p > 0.49$, respectively). We thus conclude that POC flux is very likely to be the master variable controlling $L$.

The measured penetration depth of oxygen at our deep-sea sites varied from 2 cm to 10 cm (Table 2). There was a significant negative correlation between oxygen penetration and the depth of the mixed layer, $L$, based on $^{210}Pb_{xs}$ profiles ($r = -0.629$, $p < 0.01$, $n = 16$; Rohlf and Sokal 1969) (Table 2; Fig. 4). The relationship between oxygen penetration and $^{14}$C mixed-layer depth was very weak and not statistically significant ($r = -0.230$, $p \gg 0.05$, $n = 10$; Rohlf and Sokal 1969).

At the nine sites for which degradation-rate constants for organic carbon ($k$) and biogenic mixing rates ($D_b$) were available, we computed the mixed-layer depth ($L$) using the equation of Boudreau (1998):

$$L = 4(9D_b/8k)^{1/2} \qquad (3)$$

where $D_b$ is the $^{210}$Pb biogenic mixing-rate constant throughout the mixed layer ($L$) and $k$ is a first-order reaction-rate constant for organic carbon in this layer. Values of $L$ estimated from the model of Boudreau (1998) ranged from 2.1 to 41 cm (Table 2) and were not significantly correlated with mixed-layer depths measured directly with $^{210}Pb_{xs}$ ($r = -0.05$, $p \gg 0.05$). The model of Boudreau (1998) explained about 2.5% of the variance in $^{210}$Pb mixing depth among these nine sites (Fig. 5), while the POC-flux relationship derived above explained 95% of the variance for these stations.

The mixed-layer depth for $^{210}Pb_{xs}$ exhibited a weak, but statistically significant, negative dependence on water depth across all our stations ($r = -0.573$, $p < 0.01$, $n = 36$). When restricted to the 21 stations for which we have POC-flux estimates, the relationship was similar ($r = -0.565$, $p < 0.01$, $n = 21$), with water depth explaining about 32% of the variance in $L$. If the water-depth axis is reversed by converting depth to elevation above 5,000 m, we find a statistically significant ($p < 0.0004$) asymptotic relationship between seafloor elevation and $^{210}Pb_{xs}$ mixed-layer depth (Fig. 6).

## Discussion

Our results demonstrate that sediment mixed-layer depth, *L*, in the well-oxygenated deep sea varies systematically with several environmental parameters, including annual POC flux and oxygen penetration into the sediment. As predicted, POC flux to the deep-sea floor exhibits a strong, positive, asymptotic relationship to *L* over the full range of oxygenated deep-sea habitats (Fig. 2). The positive relationship between *L* and POC flux is likely driven by the influence of food availability on both infaunal body sizes and feeding strategies. In the quiescent deep sea, POC flux appears to be positively correlated with body size of those animals thought to control mixing, i.e., the deposit feeders (e.g., Hessler 1974; Thiel 1979; Jumars and Gallagher 1982; Wheatcroft et al. 1990; Smith 1992); larger body sizes in turn should increase the particle step lengths and mixing depths of biogenic reworking (Wheatcroft et al. 1990; Smith 1992). Higher POC fluxes may also cause a shift in deposit-feeding strategies by enhancing the food availability, abundances, and feeding rates of subsurface deposit feeders at given depths within the sediment (Rice and Rhoads 1989). Such enhanced subsurface feeding should also deepen the mixed layer as POC flux rises from low to moderate levels (Rice and Rhoads 1989; Smith 1992). We suspect that the leveling of the *L* curve at higher POC fluxes reflects a release of food limitation on body sizes and burrowing depths in eutrophic deep-sea environments (e.g., in the upper bathyal zone). Here, mixed-layer depths may ultimately be limited by the costs of displacing compacted sediments (Jumars and Wheatcroft 1989) or due to other ecological or evolutionary constraints on the body sizes of dominant sediment mixers.

The strength of the relationship between POC flux and *L* highlights the importance of organic-carbon availability in controlling community-level processes in much of the deep sea (e.g., Hessler 1974; Smith et al. 1997). Apparently, mixed-layer depth, along with community respiration, benthic community biomass, and biogenic mixing intensity (Smith and Hinga 1983; Smith et al. 1997), become food limited as one moves into the oligotrophic abyss. The POC flux versus *L* relationship is strong enough ($r^2 = 0.88$) to be of some predictive value, for example, in estimating mixed-layer depths in well-oxygenated abyssal regions for which only POC-flux data (either from sediment traps or benthic-flux chambers) are available. Estimates of *L* in the fossil record might also be used to help reconstruct the POC-flux regime for paleocommunities from the deep sea and other relatively oligotrophic settings (e.g., beneath permanent sea ice).

It is important to note that the asymptotic portion of our POC flux versus *L* curve (Fig. 2) clearly represents the left side of a peaked (or hump-shaped) curve in the broader relationship between POC flux and mixed-layer depth. At very high levels of organic loading, bottom waters become depleted in oxygen and infaunal communities become stressed by low oxygen and the buildup of toxic metabolites (e.g., sulfide), yielding small body size, surface-oriented life styles, and reductions in sediment mixed-layer depths (e.g., Pearson and Rosenberg 1978; Diaz and Rosenberg 1995; Levin et al. 2000; Smith et al. 2000). Such a peaked pattern

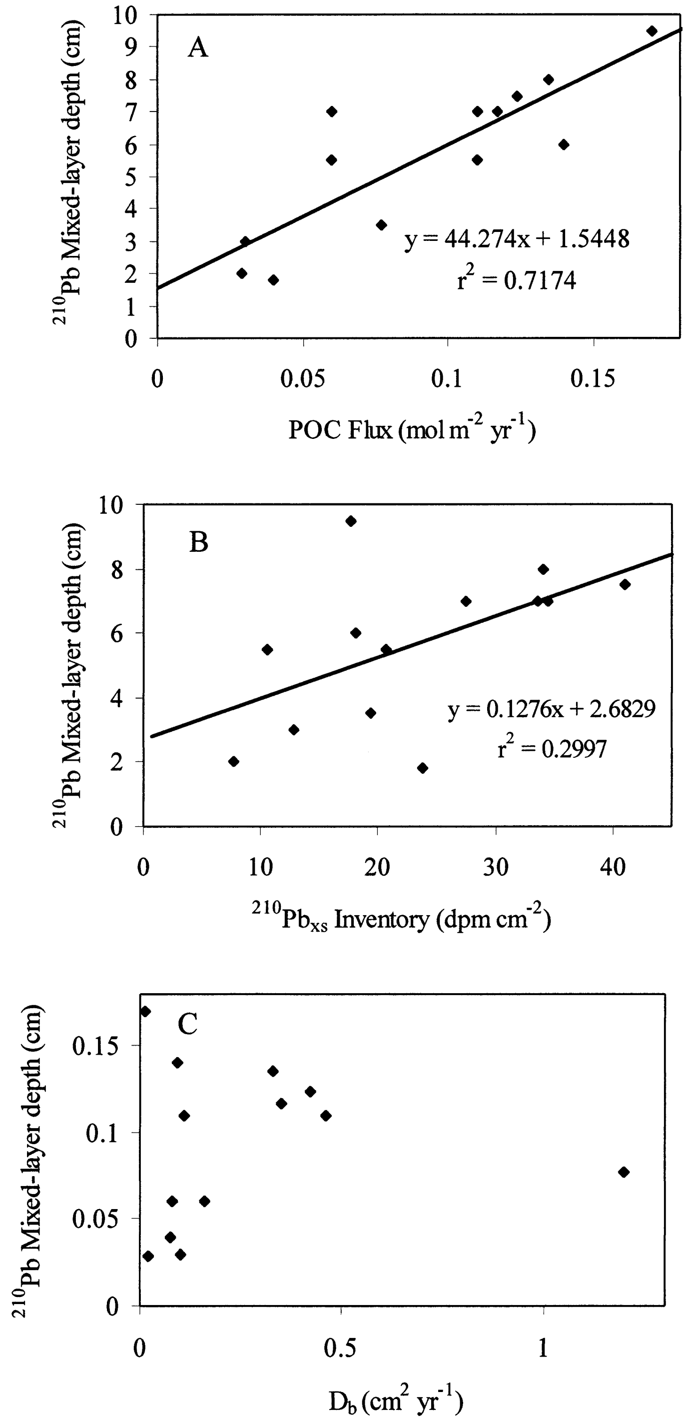


Fig. 3. The relationship between $^{210}$Pb mixed-layer depth (*L*) and (A) annual POC flux, (B) $^{210}Pb_{xs}$ inventory, and (C) $^{210}$Pb bioturbation coefficient ($D_b$) at the 13 oligotrophic stations. Oligotrophic sites are defined as those at which annual POC flux is less than 0.20 mol m$^{-2}$ yr$^{-1}$. The point considered to be an outlier in Fig. 3C is at $D_b = 1.2$.

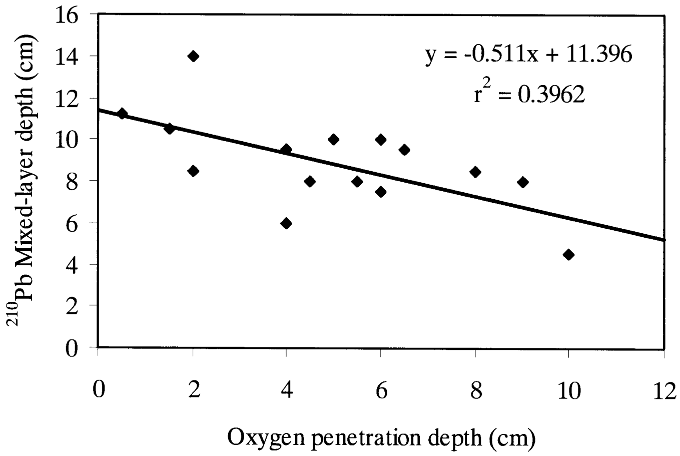


Fig. 4. Mixed-layer depth for $^{210}Pb_{xs}$ as a function of the penetration depth of porewater oxygen into deep-sea sediments.

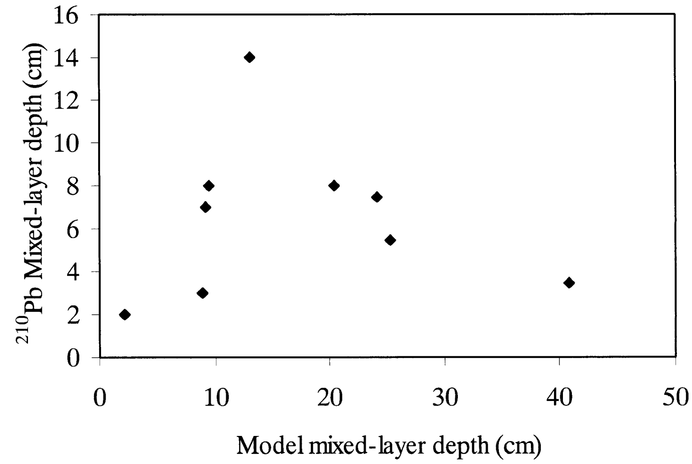


Fig. 5. Mixed-layer depth calculated with the model of Boudreau (1998) ($L = 4[9D_b/8k]^{1/2}$) versus $L$ measured with $^{210}Pb_{xs}$ profiles in the nine deep-sea sites for which the appropriate parameters ($D_b$ and $k$) have also been measured. A linear regression for these data yields an $r^2 = 0.025$.

in $L$ is evident, for example, on the Arabian Sea slope at depths from 400 to 3,400 m, where low bottom-water oxygen reduces $L$ at 400 m and declining POC flux apparently limits $L$ at 3,400 m (Smith et al. 2000).

Our positive $L$ versus POC-flux relationship agrees qualitatively with the findings of Trauth et al. (1997), who compared $^{14}C$ mixed-layer depth to the calculated flux of POC to the seafloor below 2,500 m. The $L$ versus POC-flux relationship ($r^2 = 0.65$) of Trauth et al. was weaker than ours and did not exhibit an asymptotic functionality, most likely because their estimates of annual seafloor POC flux (calculated from a general equation deriving seafloor flux from surface-water productivity and water-column depth) were subject to large errors.

We found a weak negative relationship (rather than no relationship) between penetration depth of oxygen into the sediment and sediment mixed-layer depth ($L$). This result contradicts the model formulation of Dhakar and Burdige (1996), who proposed that sediment-mixing benthos in the deep sea would be excluded from sediments with anoxic porewaters. We postulate that the negative relationship between oxygen penetration and $L$ occurs because POC flux, rather than porewater oxygen, controls the size and feeding depths of benthos in deep-sea habitats with oxygenated bottom waters. Thus, an increase in POC flux enhances $L$ (due to increases in body size and deeper deposit feeding by benthos) at the same time that $O_2$ penetration declines due to enhanced sediment oxygen demand (Rabouille and Gaillard 1991). Under this scenario, the larger infauna that control mixing depths (e.g., sipunculids, molpadiid holothurians, echiurans, irregular urchins) are able to survive in anoxic porewaters because they maintain respiratory contact with the sediment-water interface. This scenario is highly consistent with the observation that sediments in many marine habitats with oxygenated bottom water are heavily bioturbated to depths well below the mean penetration depth of oxygen in porewaters (e.g., Bromley 1990; Wheatcroft et al. 1990; Smith et al. 1993).

Our findings differ from those of Boudreau (1998), who concluded that mean $L$ does not change with water depth and is likely to be environmentally invariant across all marine habitats. Within the deep sea (i.e., from 1,200 to 5,000 m depth), we find a weak dependence of $L$ on water depth and a very strong dependence of $L$ on POC flux. We suspect that the water depth versus $L$ relationship is actually controlled by the well-known decline in POC flux with increasing water-column depth (e.g., Suess 1980; Martin et al. 1987). Boudreau (1998) postulated that relative constancy in mean $L$ over the world ocean results from a feedback between the food dependence of biogenic mixing and the decay of organic matter within the sediment column. However, the model of Boudreau (1998) relating organic-matter concentration, organic-matter reactivity, and biogenic mixing rate (Eq. 3 above) explained little of the variance in mixed-layer depth among our deep-sea sites (Fig. 5), while our asymp-

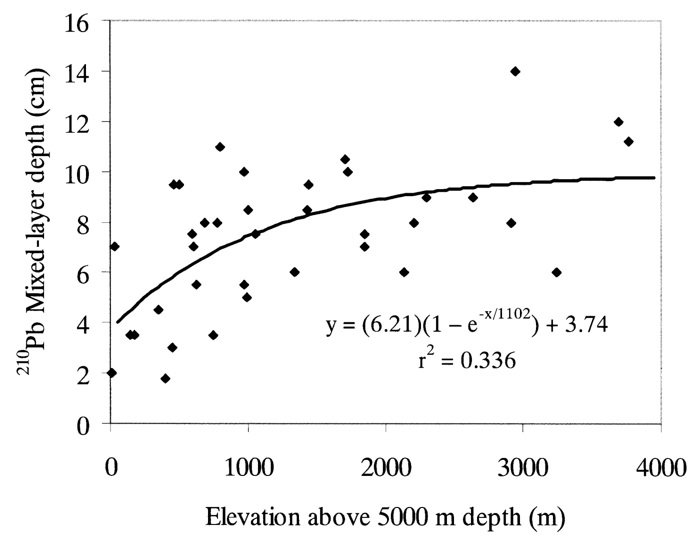


Fig. 6. Inverse depth (or elevation) versus $^{210}Pb$ mixed-layer depth at our 36 deep-sea sites. The selection of 5,000 m depth as the zero elevation point is arbitrary. The equation for the statistically significant ($p < 0.0004$) asymptotic regression curve is shown.

totic POC-flux model explained 88% (Fig. 2). Furthermore, calculation of $L$ using the model of Boudreau (1998) requires knowledge of the average $D_b$ within the mixed layer, which in turn depends on prior knowledge of $L$; the Boudreau formulation is thus not useful for predicting $L$ from field data. We conclude that mixed-layer depth does in fact vary systematically as a function of POC flux to the oxygenated deep-sea floor. Because mixed-layer depth is an important independent variable in models of sediment diagenesis and paleotracer profiles (Bard et al. 1987; Boudreau 1997; Charbit et al. pers. comm.), our findings may significantly improve understanding of geochemical processes and the paleooceanographic record in deep-sea sediments.

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