frontiers in Earth Science

ORIGINAL RESEARCH
published: 25 June 2019
doi: 10.3389/feart.2019.00157

The Critical Role of Bioturbation for Particle Dynamics, Priming Potential, and Organic C Remineralization in Marine Sediments: Local and Basin Scales

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Specialty section:
This article was submitted to Marine Biogeochemistry, a section of the journal Frontiers in Earth Science

Received: *13 March 2019*
Accepted: *05 June 2019*
Published: *25 June 2019*

Citation:
Aller RC and Cochran JK (2019) The Critical Role of Bioturbation for Particle Dynamics, Priming Potential, and Organic C Remineralization in Marine Sediments: Local and Basin Scales. Front. Earth Sci. 7:157. doi: 10.3389/feart.2019.00157

Bioturbation promotes priming and total remineralization of sedimentary organic matter (C_{org}) in multiple ways. A primary local mode is the injection of reactive C_{org} from the water column, surface sediment, and mucus secretions into deposits. During feeding, burrowing, and construction activities by benthic fauna, labile substrates are brought into close association with more refractory material over a wide range of time scales, geometries, and depths, enhancing decomposition of the less reactive components (priming). One measure of these local interactions is the particle mixing coefficient, D_B, which can be estimated from the averaged penetration of particle-reactive radionuclides into deposits. Patterns of D_B in Long Island Sound, an estuarine system with well-defined sources of naturally occurring radionuclides, show consistent positive correlations between D_B and total inventories of excess ^{234}Th ($t_{1/2}$ = 24 days) and ^{210}Pb ($t_{1/2}$ = 22 years) at local and basin scales. These correlations, maintained seasonally in the case of ^{234}Th, demonstrate not only the penetration of plankton-derived, reactive C_{org} into deeper regions of deposits during bioturbation over monthly (~5–10 cm) to decadal timescales (~20–100 cm) but also the enhanced capture of labile substrates from the water column across basin scales into bioturbated patches as the intensity of reworking increases. In Long Island Sound, sedimentary Chl-*a* distributions and benthic nutrient regeneration (e.g., NH_4^+ fluxes) reflect these particle exchange processes. Basin and regional scale capture of labile substrates into bioturbated deposits can be generally demonstrated, for example, along the highly productive Cape Hatteras continental margin. Thus, total and net remineralization necessarily increase with the biogenic enhancement of the quantity of labile particulate substrate in deposits. This capture, intermixing, and close association of reactive and refractory substrates (reductant blending), and thus the optimization of priming potential, represent important, often overlooked, pathways by which bioturbation generates biogeochemical conditions conducive to maximum efficiency of remineralization.

Keywords: bioturbation, priming, sediment diagenesis, carbon remineralization, reductant mixing, particle mixing, natural radionuclides

INTRODUCTION

Benthic fauna influence the cycling of sedimentary organic matter in multiple ways, generally stimulating conditional remineralization rates through modification of transport – reaction conditions in deposits, direct respiration, and the formation of new labile biomass, but sometimes inhibiting decomposition through the production of refractory material or toxic compounds (Aller et al., 2001; Kristensen and Kostka, 2005). One major consequence of macro- and meiofaunal activity is the constant redistribution, packaging or fragmentation, and re-exposure of reactive and refractory sedimentary C_{org} within deposits. During feeding, burrowing, and construction activities by benthic fauna, relatively labile substrates are brought into close association with more refractory material over a wide range of time scales, depth scales, and geometries. For example, particles of different reactivity and origin can be intermixed randomly in a diffusion-like manner (Gerino et al., 1998; Meysman et al., 2003). In other cases, surface-derived, labile C_{org} can be injected into excavated subsurface pockets as highly reactive fill surrounded by relatively refractory material (Aller and Aller, 1986; Wanless et al., 1988; Smith et al., 1996). Particles of varied size and reactivity can be also be specifically segregated, coated with mucus secretions, and organized into distinct structures, for example, burrow, tube walls, or tracks and trails (Pillay and Branch, 2011; Hannides and Aller, 2016). These types of effects and their relative importance depend on population density, size distributions, and species-specific behaviors (Rhoads, 1974; François et al., 2002; Solan et al., 2008). In general, the bringing together of relatively labile and more refractory organic matter within bioturbated deposits: reductant mixing, must promote the phenomenon referred to as priming. Priming is defined by the enhanced remineralization (typically ∼10–30%) of otherwise low-reactivity organics (refractory) in association with the decomposition of relatively labile organic material in terrestrial soils, aquatic sediments, and natural waters (Löhnis, 1926; Stevenson, 1986; Graf, 1992; Hee et al., 2001; van Nugteren et al., 2009; Bianchi et al., 2015).

In addition to modification of particle interactions and reactivity distributions within deposits, benthic fauna can affect sediment mass properties by enhancing or reducing susceptibility of deposits to erosion, or by promoting accumulation of sediment through particle capture and biodeposition (Eckman et al., 1981; Rhoads and Boyer, 1982). Thus, depending on their functional group composition (e.g., feeding type, mobility, life habit) and population density, benthic communities can affect sediment resuspension, lateral transport and water column particle dynamics over basin scales for a given physical boundary layer and circulation regime. The coupling of vertical transport of particles within deposits with the horizontal exchange of particles between sedimentary facies, results in continuous interactions of organic matter having wide variations in reactivity. These interactions can vary temporally and spatially in intensity. Benthic communities and associated bioturbation are thus intimately involved in promoting the conditions necessary for extensive priming interactions at local, facies, and basin scales.

Here, we examine interactions between reactive particle pools and particle dynamics as they relate to sedimentary facies and benthic communities both locally and across basinal scales using as a primary example Long Island Sound, an estuarine lagoonal system on the Northeast coast of N. America (**Figure 1**). We summarize and utilize the distributions of the natural radionuclides ^{234}Th, ^{210}Pb, and ^{14}C, and correlations with sedimentary reactive Chl-*a* and benthic nutrient fluxes, to track and reveal particle exchange behavior and age distributions, the latter correlating directly with organic C (C_{org}) reactivity (Middelburg, 1989). These patterns illustrate coupled biological and physical processes governing interactions between particle pools associated with organic matter having widely varying reactivity and thus priming potential. The LIS data are historical (1974–1993) and, in addition to illustrating fundamental processes, represent a reference to which subsequent studies of possible progressive changes can be compared. Examples from the Peconic Bay estuary system (Long Island) and from the Cape Hatteras continental margin off North Carolina are also used to further elucidate controls and to generalize the role of bioturbation in promoting particle dynamics and priming at local and depositional system scales.

We do not address in this contribution, the multiple additional impacts bioturbation has on remineralization processes (e.g., Aller et al., 2001; Kristensen and Kostka, 2005). For example, C_{org} decomposition in bioturbated deposits is enhanced by injection of metal oxides during particle reworking, provision of O_2, SO_4^{2-} and local generation of additional metal oxides during irrigation, and overall increased metabolite exchange. The episodic exposure to O_2, a virtually unlimited supply of additional high order oxidants, and the minimized build-up of metabolites, result in oscillating redox conditions over multiple frequencies and durations, and increased remineralization. Thus, bioturbation not only promotes intermixing and association of reactive and refractory substrates (reductant mixing) and thus priming potential, but typically generates a range of biogeochemical conditions conducive to maximum efficiency of remineralization within sedimentary deposits.

BACKGROUND

Long Island Sound is an W-E trending estuarine basin along NE North America, with dimensions approximately ∼150 km long, ∼30 km maximum width, and ∼18 m average depth, the latter estimate ranging to ∼24 m depending on exactly where boundaries are drawn (e.g., Bokuniewicz and Gordon, 1980). Morphologically it is characterized by four primary regions referred to as the Narrows, Western, Central, and Eastern basins, the latter separated by relict coastal plain and glacial deposits that form ∼ N-S trending shoals (**Figure 2A**). The physical oceanography and hydrography have been recently summarized by O'Donnell et al. (2014): The primary source of fresh water to the Sound is the Connecticut River, located near the eastern end of the system. Thus, the Sound is an atypical estuary from the perspective of primary river input location. Tidal exchange occurs at the western end with the Hudson River through the

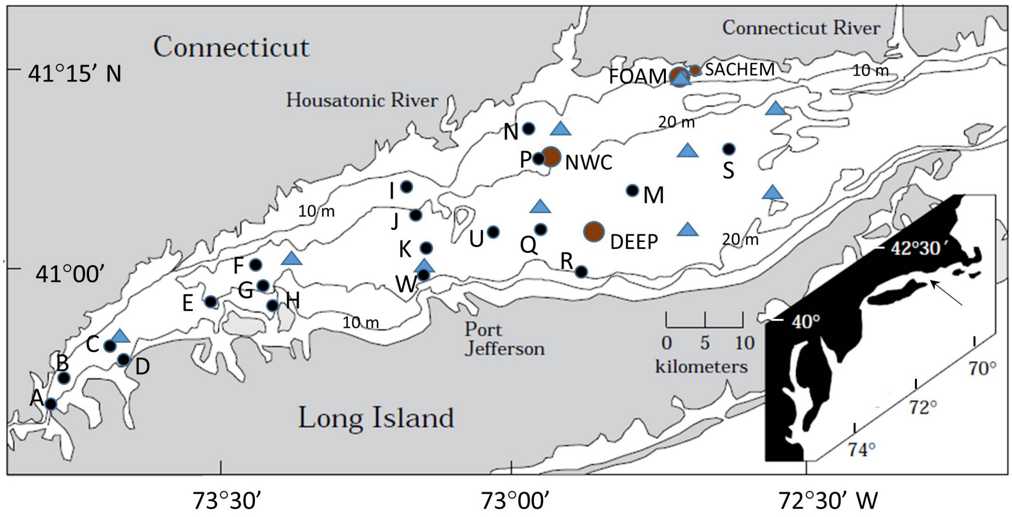

FIGURE 1 | Map of Long Island Sound (LIS) showing locations of bottom sampling stations. Long-term study sites in the central basin: SACHEM, FOAM, NWC, and DEEP are indicated with circles (brown). August 1977 survey sites are marked by triangles (blue). The 19 Long Island Sound Study (LISS) sites are indicated by small solid circles (black) sampled seasonally for 1 year, or in the case of reference sites (A, B, G, P, R, S) over a 2 year period. The PULSE site is located near P (Gerino et al., 1998).

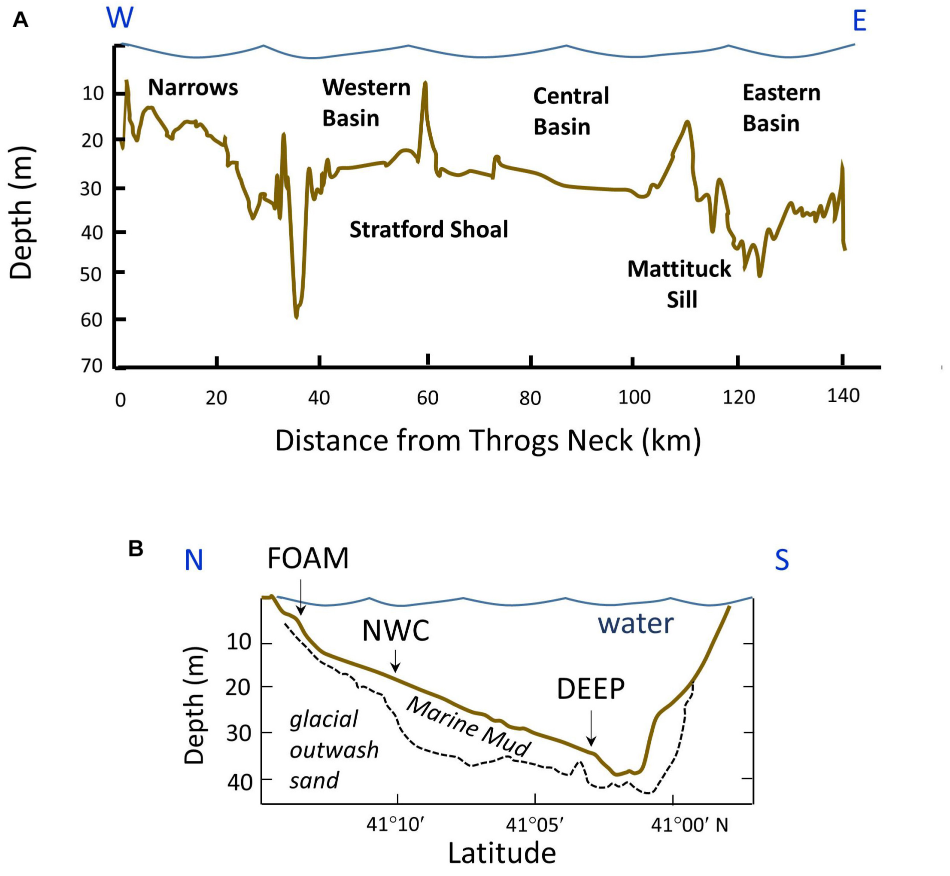

FIGURE 2 | (A) W-E bathymetric profile along the axis of LIS indicating major shoal and basin features (modified after Auster et al., 2009). **(B)** N-S cross section of central basin through approximately 72° 53′ W with seismically determined thickness of marine mud outlined (post ~13 kyr; modified after Bokuniewicz et al., 1976). The long-term sampling stations in the central basin are projected onto this plane to illustrate relative bathymetry and deposition rates (~0.03–0.08 mm year^{-1}).

East River channel, and at the eastern end with Block Island Sound and the Atlantic Ocean through the Race (**Figure 1**). Mean tidal range (semi-diurnal) increases east to west, varying from ∼0.84 to 2.2 m. Cyclonic gyres are present in the three primary basins, and there is a tendency for residual westward flow along the shallow north coast (Connecticut) and deeper water, and eastward flow along the south coast (Long Island). Water exchange is greatest in the east and decreases to the west. As a result of these circulation patterns and enhanced primary production related to anthropogenic nutrient inputs, the Western Narrows is typically hypoxic in late summer. Seasonal surface temperature ranges from ∼0 to 24°C, and salinity from ∼25 to 27 in the west and ∼29 to 31 in the east, with spatial and temporal gradients depending on vicinity to rivers and season.

The sediments in the Sound generally fine westward, with sands, gravel, migrating bedforms, and erosive regions characterizing the eastern boundary, and muds characterizing much of the more western basin regions (Bokuniewicz and Gordon, 1980; Knebel and Poppe, 2000; Poppe et al., 2000). There is considerable heterogeneity, however; and areas of erosion, redistribution, and deposition can be in close proximity (Knebel and Poppe, 2000). The long term sediment accumulation rates measured seismically or estimated from ^{14}C range from ∼0.03 to 0.08 mm year^{-1} (Bokuniewicz and Gordon, 1980; Lewis and DiGiacomo-Cohen, 2000; Cuomo et al., 2014; **Figure 2B**). The modern ^{210}Pb and long-term sediment budgets indicate that there is only minor net import of sediment from adjacent shelf regions, and that particle sources are largely from the Connecticut coastline rivers, primarily from the Connecticut River, and internally redistributed debris (Benninger, 1978; Lewis and DiGiacomo-Cohen, 2000). Although net accumulation rates of sediment are generally low, particles are continuously resuspended and refluxed by currents, waves, and episodic storm events, and small particles can move throughout the Sound. The muddy basin regions of the Sound are emphasized here.

Benthic faunal distributions and activity track the sedimentary depositional environments, intensity of physical disturbance, and, particularly in the Western Narrows, seasonal hypoxia (Sanders, 1956; McCall, 1977, 1978; Zajac et al., 2000, 2013; Cuomo et al., 2014). In general, sediments in Long Island Sound are intensely bioturbated, although nearshore shallow regions (<10 m) and eastern sands are often physically reworked by tidal currents, waves, and episodic storms (McCall, 1977, 1978; Aller et al., 1980; Bokuniewicz and Gordon, 1980; Lewis and DiGiacomo-Cohen, 2000). Muddy deposits are commonly characterized by the deposit-feeding protobranch bivalves *Nucula annulata* and *Yoldia limatula*, the opportunistic suspension feeding bivalve *Mulina lateralis*, and the polychaete *Nephtys incisa* (Sanders, 1956; Reid et al., 1979; Zajac et al., 2000, 2013), with protobranchs in particular intensively reworking the upper 0–5 cm of deposits (Rhoads and Young, 1970). Although the abundance of individual species varied, the protobranch bivalve – *Nephtys* community was stably present from the 1950s to at least the mid-1985s, the time of the last synoptic benthic survey (Zajac et al., 2000). In central basin sandy silts, deeper burrowing infauna such as the polychaetes *Sabaco elongata*, *Clymenella torquata*, *Melinna cristata*, and *Pherusa affinis* are also common. The mantis shrimp *Squilla empusa*, which burrows 1–3 m into the seabed (Myers, 1979), can be readily observed by direct observation of the seabed (e.g., diving) and its activities evidenced by sedimentary structures (Benninger et al., 1979; Aller, 1980) but it, and other deeply burrowing species (>20 cm), are unreliably reported in standard benthic surveys. Qualitative depictions of a subset of these fauna and their typical life habits at central basin sites are illustrated in **Figure 3**. Except in regions of migrating bedforms, immediately following current scour or storm events (<15 m water depth), or during periods of hypoxia (Narrows; methane bubbles are present during hypoxic periods), surface deposits throughout most of Long Island Sound are dominated by bioturbation activity and biogenic sedimentary structures (**Figure 4**).

SAMPLING AND ANALYTICAL METHODS

The data in this synthesis come from multiple studies and were acquired primarily from sites throughout Long Island Sound but with an emphasis on the Central Basin and stations along the W-E axis (**Figures 1**, **2**). Sediment box cores or pipe cores were retrieved by divers (1974–1979; 1992–1993; Aller and Cochran, 1976; Aller et al., 1980; Gerino et al., 1998), or obtained remotely using either a Soutar box corer for surface sediment sampling or a gravity corer for deeper radiochemical measurements [1989–1991 previously unpublished; Long Island Sound Study (LISS)]. These techniques ensured retention of an undisturbed sediment surface, confirmed by inspection. Many locations were sampled seasonally (**Figure 1**: NWC, P, LISS sites). Surface water samples discussed here in order to illustrate benthic inputs of organic matter during the spring bloom period, are from a single site in the central basin (P; **Figure 1**) and were obtained during 1992–1993 (Gerino et al., 1998).

Sediment analyses summarized here include the radionuclides ^{234}Th ($t_{1/2}$ = 24.1 days), ^{210}Pb ($t_{1/2}$ = 22 years), ^{14}C ($t_{1/2}$ = 5730 years), Chl-*a*, and x-radiography. ^{234}Th and ^{238}U measurements on samples taken in 1974–1979 and 1989–1991 were done in the same manner, namely leaching dried ground sediment in hot 8N HCl and then separating the leachate from the residual sediment by centrifugation. An aliquot (∼80% of the leach solution) was spiked with a ^{232}U/^{228}Th yield tracer. The remaining solution was left unspiked for determination of the natural ^{228}Th/^{232}Th activity ratio in the sample. The leachates were processed by ion exchange chromatography to separate the U and Th fractions, which were then electroplated onto stainless steel disks. The Th planchet was immediately counted on a gas flow proportional counter to determine the beta activity (^{234}Th) and subsequently counted on silicon surface barrier detectors to assay the alpha activities of ^{232}Th and ^{228}Th. All excess ^{234}Th (^{234}Th$_{xs}$) activities (= measured ^{234}Th – measured ^{238}U) were corrected to the time of collection. Uncertainties are based on 1σ counting errors. For the 1992–1993 samples, cores were sectioned and ^{234}Th was determined on most samples by gamma spectrometry, using the 63 keV ^{234}Th peak. Similarly, ^{210}Pb and ^{226}Ra measurements were made by gamma spectrometry

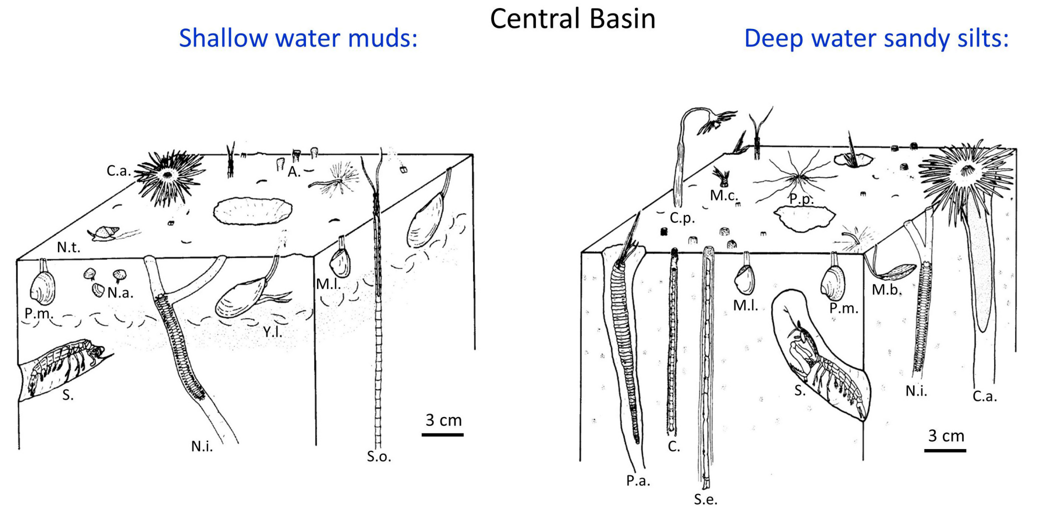

FIGURE 3 | Schematic illustrations of major faunal components and life habits of benthic communities typically found in shallow water (<20 m) and deep water (>20 m) regions of the central basin of LIS (adapted from Aller, 1980). The deeper water regions of the central basin are often characterized by deeper feeding and deeper burrowing species. Abbreviations: Y. l., *Yoldia limatula*; N.a., *Nucula annulata*; N.i., *Nephtys incisa*; M.l., *Mulinia lateralis*; P.m., *Pitar morrhuana*; C.a., *Ceriantheopsis americanus*; N.t., *Nassarius trivitatus*; S.o., *Spiochaetopterus oculatus*; P.a., *Pherusa affinis*; C.p., *Corymorpha pendula*; M.c., *Melinna cristata*; C., *Clymenella* sp.; S.e., *Sabaco elongata* (drawn with some segments missing because of length); P.p., *Pista palmata*; S., *Squilla empusa*; A., *Ampelisca*; M.t., *Macoma tenta*. Biogenic structures formed by several of these species are illustrated in x-radiographs (**Figure 4**). A biogenic shell layer (illustrated example) or heavy mineral layer often forms as a feeding lag deposit in the presence of *Yoldia* (Rhoads and Young, 1970).

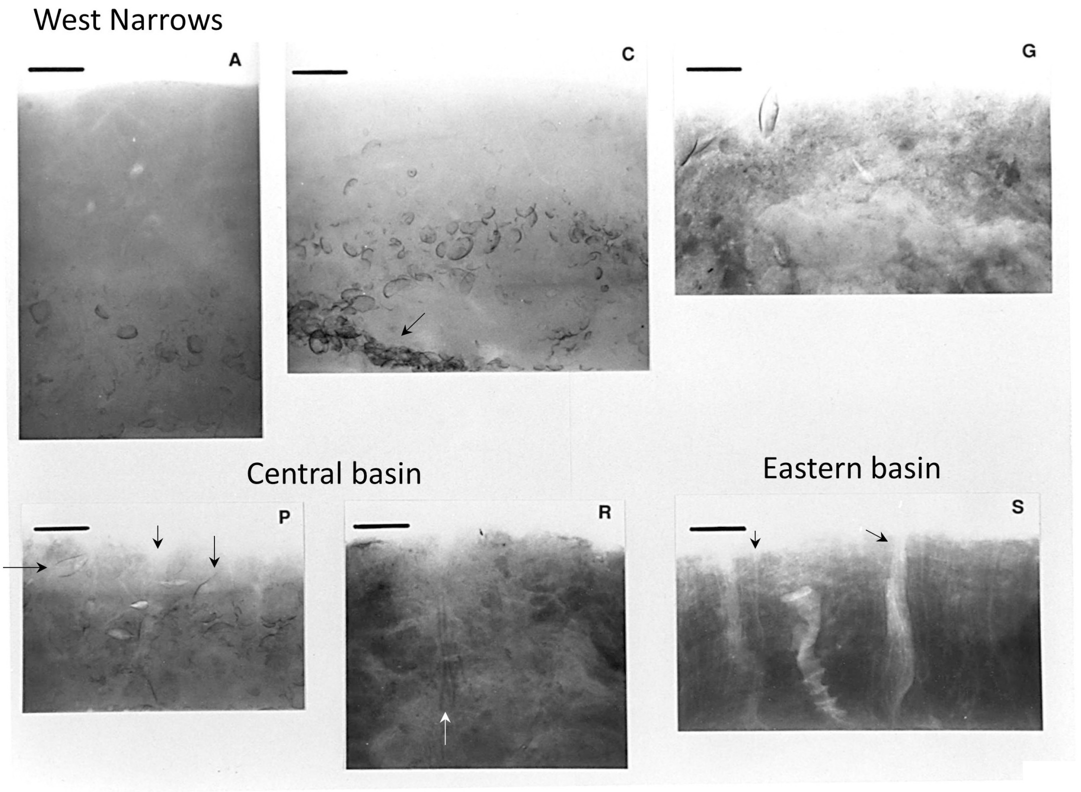

FIGURE 4 | X-radiographs of upper 10–15 cm of sediment at LISS reference stations (**Figure 1**; May–June 1988). Bioturbate structure dominates at all stations. Shell layers and aggregations (stations C, G; dominantly shells of *Mulinia lateralis*; black arrow station C) reflect both biogenic and physical sorting processes. Tubes of the parchment worm *Chaetopterus* (not shown in **Figure 3**) and dense aggregations of *Clymenella* tubes are evident at station S (black arrows); *Yoldia* in life position and a *Ceriantheopsis* tube are shown at station P (black arrows); a section of a *Sabaco* tube is indicated at station R (white arrow). Scale bars = 3 cm.

at all sampling times. The 46.3 keV ^{210}Pb and 352 keV ^{214}Pb gamma peaks were used. Self-absorption corrections were made for ^{210}Pb and ^{234}Th using a calibration that relates the cpm/dpm of a standard to effective sample "density," as determined by the attenuation of a gamma source counted through the sample vs. an empty sample container. Additional analytical techniques and details of sediment processing are given in the references cited in association with each data set.

RESULTS AND DISCUSSION

Average Age of Sedimentary C_{org}

^{14}C ages of bulk sedimentary C_{org} in the central basin of LIS demonstrate a typical surface sediment value of ~2900 years, with a range from ~2000 to 4000 and excursions to >6000 years, the latter presumably representing episodic deposition of more deeply eroded material (**Figure 5**; Benoit et al., 1979; Krishnaswami et al., 1984; Krom and Bennett, 1985). These bulk ages represent mixtures of modern planktonic and sewage inputs, moderately aged soil debris, and recycled fossil carbon (e.g., Trumbore et al., 1989; Plante et al., 2013). In 1975, the Δ^{14}C value of LIS plankton was ~281 (corrected for sediment contribution by Krom and Bennett, 1985) and of sewage sludge ~429 (Benoit et al., 1979). Age of C_{org} is a direct indicator of lability, and in this case an apparent bulk C_{org} decomposition rate constant can be estimated as $\sim 0.8 \times 10^{-4}$ year^{-1} (pseudo-first order coefficient) (Middelburg, 1989; Middelburg et al., 1993). Thus, LIS deposits represent a bulk C_{org} reservoir containing a spectrum of relatively refractory C_{org} fractions with average ^{14}C age ~3000 years into which younger and more labile material is constantly introduced by sedimentation and bioturbation processes. The vertical gradients in ^{14}C activity are likely minimized by deep bioturbation (1–3 m; e.g., *Squilla*) but are nevertheless consistent with sediment accumulation rates in the range of the long-term seismically determined values (Benninger et al., 1979; Benoit et al., 1979; Krishnaswami et al., 1984).

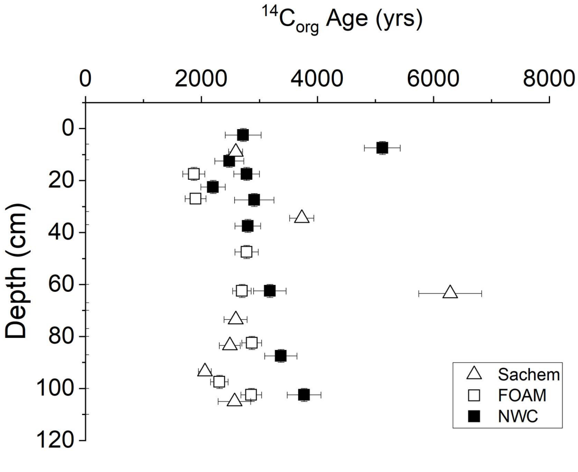

FIGURE 5 | ^{14}C age distributions in cores from Sachem, FOAM, and NWC sites in central basin (Benoit et al., 1979; Krishnaswami et al., 1984; Krom and Bennett, 1985).

Local Input of Reactive Organic Matter

The rapid penetration of labile, planktonically derived C_{org} into the background of more refractory sedimentary substrates in LIS deposits can be demonstrated by tracking the fate of Chl-*a* supplied to the seabed during the spring bloom period. Sedimentary Chl-*a* decomposition follows pseudo-first order kinetics with rate coefficients ~0.02–0.04 days^{-1}, similar to the decay constant of the natural radionuclide ^{234}Th (λ = 0.0287 days^{-1}) (Sun et al., 1991). The exact timing of the spring bloom in LIS can vary substantially from year to year, ranging from February to April. In 1993, the bloom occurred in late March–early April in central LIS (**Figure 6**). Chl-*a* derived from the bloom was deposited on the seabed (Station P; 15 m depth) and rapidly penetrated to depths >10 cm by diffusive, advective, and nonlocal biogenic transport modes (Gerino et al., 1998). In the absence of bioturbation, bloom inputs would otherwise be restricted to the upper ~1 mm based on sediment accumulation rates, resuspension depths, and lack of deep reworking by storms during the study period. Prior to spring bloom deposition, sedimentary Chl-*a* was at near background levels for the preceding late fall and winter months, consistent with degradation timescales and lowered primary production. The Chl-*a* profiles illustrate the dynamic response of the seabed to production of labile C_{org} in the water column and the role of bioturbation in promoting interactions between C_{org} reductants of varied reactivity. Although the scaling of these examples documents interactions over ~10 cm, infilling of burrow structures (e.g., *Squilla*) with surface material can take place to depths >1 m in LIS (Benninger et al., 1979).

An alternative example of the rapid penetration, utilization, and dissipation of spring bloom inputs of labile substrates in a background of more refractory C_{org} is provided by exoenzyme activity seasonally at a mud site in central Great Peconic Bay (**Figure 7**). This site (8 m depth) has very similar sediment and environmental properties to the central LIS station P (Waugh and Aller, 2017). The average ^{14}C age of C_{org} in the Peconics is ~1800 ± 290 years (upper ~50 cm; Cochran et al., 2000). In this case, the seasonal activity of the exoenzyme leucine aminopeptidase shows the presence of disseminated, low activity in the upper ~8 cm during July, minor activity during Nov, deposition of labile spring bloom debris at the surface in March (with physical disturbance from a storm), and penetration of reactive substrate throughout the upper 6–7 cm by May (Cao et al., 2013). This exoenzyme activity is not dependent on oxygen availability, and thus reflects a range of sediment redox conditions. The bottom water temperature in May is comparable to that in November (~12–13°C), illustrating the critical importance of labile substrate availability and inputs rather than temperature *per se* in determining remineralization rates (priming). The rapid dissemination of bloom debris into the upper ~10 cm, results from intense bioturbation largely by maldanid polychaetes (e.g., *Sabaco*, *Clymenella*) and infaunal ophiuroids (*Amphioplus*), as reflected in profiles of the

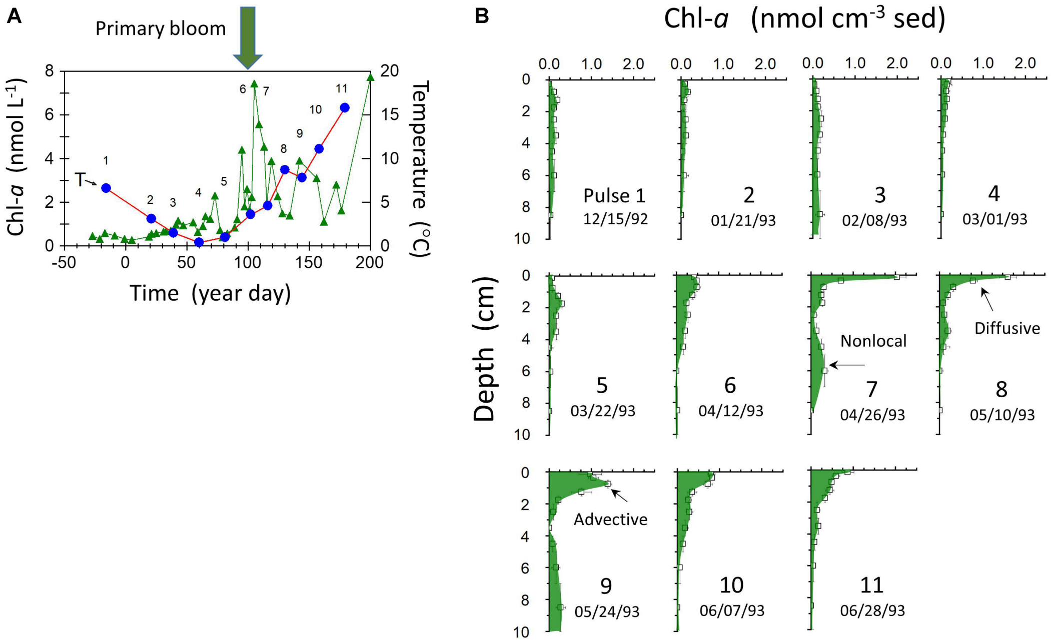

FIGURE 6 | (A) Water column Chl-*a* (triangles) and temperature (circles) at station P (**Figure 1**) from 12/15/1992 to 6/28 1993 (year day indicated relative to January 1, 1993). **(B)** Sediment profiles of total Chl-*a* at successive sampling dates [sampling number labels also indicated in panel **(A)**]. Distribution features indicative of diffusive, advective, and nonlocal transport mechanisms on the time scale of Chl-*a* decay are indicated.

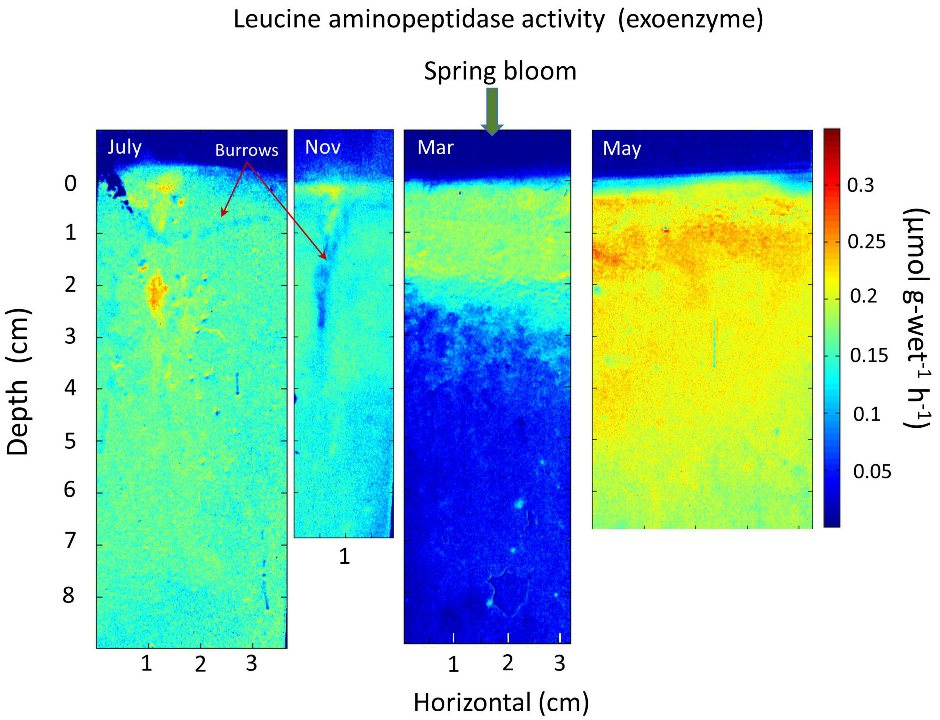

FIGURE 7 | Seasonal exoenzyme leucine aminopeptidase activity in central Great Peconic Bay muds (Station 1; 8 m depth; Cao et al., 2013). The spring bloom input is evident during March (layer resuspended and emplaced during a storm event). Labile, reactive substrate is mixed into the deposit by intense deposit-feeding activity, penetrating at least 7 cm by May. May and November have similar temperatures (~12–13°C), so that comparison of May, July, and November patterns (assuming periodic behavior) demonstrates the progressive remineralization and depletion of reactive substrates during spring–summer to fall periods, and the critical role of substrate availability introduced during particle reworking. Priming processes are presumably maximized during April–May in this system and in Long Island Sound.

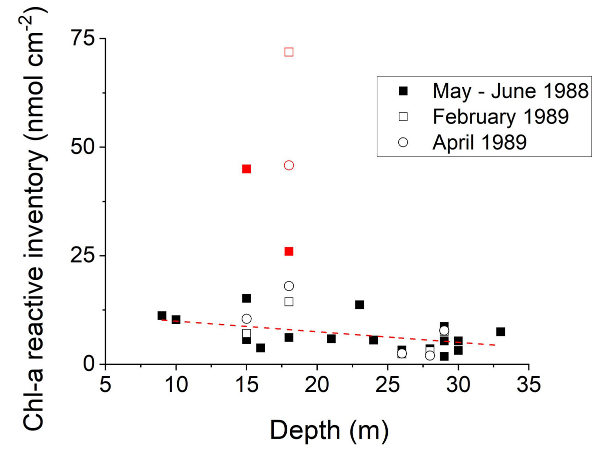

FIGURE 8 | The inventory of Chl-*a* in the upper 10 cm at LISS stations during bloom or post-bloom periods in 1988 and 1989. Ignoring the four samples from the western Narrows (red; inserted graph), the regression (dotted line; $y = -0.24x + 12.4$) is statistically significant ($r^2 = 0.23$; $p < 0.05$). There is a tendency to focus labile planktonic C_{org} into the shallower regions (Sun et al., 1994).

cosmogenic nuclide ^{7}Be ($t_{1/2}$ = 53 days) that show penetration to >12 cm (Aller et al., 2019).

Basin Wide Patterns of Labile C_{org} Supply

Profiles of sedimentary Chl-*a* in LIS sediments were determined seasonally at the 19 LISS sites (**Figure 1**; Sun et al., 1994). Late winter–spring period Chl-*a* inventories in the upper 10 cm of deposits show a regular pattern versus bathymetric depth, with higher inventories in shallower regions of LIS (**Figure 8**). The western Narrows sites show extremely high deposition of Chl-*a* during late winter–spring consistent with the elevated input of sewage derived nutrients and relatively low water exchange in that region. Although the water column in the Narrows is well-oxygenated during the winter, spring and early summer, it typically becomes hypoxic during late August (Cuomo et al., 2014). During the hypoxic period, bottom deposits in this region show greatly reduced infaunal activity, and, as revealed by x-radiographs, methane bubbles are present in deposits a few centimeters below the sediment surface (data not shown). At other times of the year, these deposits are colonized by macrobenthos and bioturbated (e.g., **Figure 4**). The sediment Chl-*a* inventory patterns are consistent with satellite image estimates of water column Chl-*a* showing relatively enhanced concentrations in the western Sound and Narrows at all times of the year (seasonal images[1]). Although elevated surface water Chl-*a* is also evident along the shorelines, in general there are minor N-S gradients compared to W-E gradients. Direct measurements of primary production in Long Island Sound are relatively limited, with estimates ranging from ∼400 to 1000 gC m^{-2} $years^{-1}$ (90–230 mmol m^{-2} $days^{-1}$), declining moderately from west to east, and averages in the central and western areas of ∼400 ± 80 gC m^{-2} $years^{-1}$ (Riley, 1941, 1956; Goebel et al., 2006).

Radionuclide Tracers of Reactive C_{org} and Particle Dynamics

Monthly and Seasonal Timescales

Particle-reactive ^{234}Th is produced continually in the water column by the decay of dissolved ^{238}U, and provides a natural tracer of particle dynamics and the fate of labile C_{org} in LIS (Aller and Cochran, 1976; Aller et al., 1980). The production of ^{234}Th varies with ^{238}U activity, and thus directly with salinity (^{238}U = 2.45 × (S/35) dpm L^{-1}; where S = salinity). Once formed by decay, ^{234}Th is scavenged from solution within <1 day onto abundant suspended particles in LIS, resulting in excess activity of ^{234}Th above the particulate ^{238}U background ($^{234}Th_{xs}$). This excess activity decays with a half-life of 24.1 days (decay constant λ = 0.0288 day^{-1}). As in the case of Chl-*a* produced in the water column, the $^{234}Th_{xs}$ can be deposited on the seabed and reworked into deposits by bioturbation or physical reworking. Fine, organic rich particles are particularly efficient at scavenging ^{234}Th, as illustrated by the direct correlation of $^{234}Th_{xs}$ in surface sediment with indicators of particle size or C_{org} (**Figure 9A** and **Supplementary Tables 1–5**). This association and its further correspondence with labile C_{org} are confirmed by the direct correlation between summer period $^{234}Th_{xs}$ inventories and measurements of fluxes of remineralized NH_4^+ from bottom sediments (**Figure 9B**).

Vertical gradients of $^{234}Th_{xs}$ in deposits can be used to derive particle mixing coefficients, D_B, and to estimate other modes of particle transport (e.g., nonlocal; **Figure 6**) (Aller and Cochran, 1976). In the present cases, D_B was estimated assuming exponential decreases of $^{234}Th_{xs}$ with depth, and optimal fits to the integrated activities measured over finite sampling intervals (*per* Aller et al., 1980). Because the quantity of $^{234}Th_{xs}$ is fixed by ^{238}U concentrations in the water column at secular equilibrium, the inventory of $^{234}Th_{xs}$ activity in LIS sediments must equal the source ^{238}U activity. If, for example, particles simply settled out of the water column vertically to the bottom, the inventory of $^{234}Th_{xs}$, I_{Th}, would equal the integrated ^{238}U activity in the immediate overlying water column: $I_{Thxs} = z \times (2.45 \times S/35)/10$ dpm cm^{-2}; where z = water depth in meters. In LIS, salinity varies from 24 to 29, averaging ∼27, and average depth is 18–20 m, suggesting that $^{234}Th_{xs}$ inventories should vary directly with depth and salinity but average 3.4–3.8 dpm cm^{-2}.

A summary of sedimentary $^{234}Th_{xs}$ inventories in LIS shows values scattered around the expected overall mean, implying that all $^{234}Th_{xs}$ produced in the LIS water column is found in bottom deposits (**Figure 10A** and **Supplementary Tables 1–5**). The lack of direct correlation between inventories and depth demonstrates that distributions do not result from simple 1-D vertical settling and that fine particles are cycled laterally through much of LIS on ^{234}Th decay time scales (∼1 month). When annual average inventories are normalized to the theoretical inventory expected from production in the immediately overlying water column, it is

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[1] https://coastwatch.chesapeakebay.noaa.gov

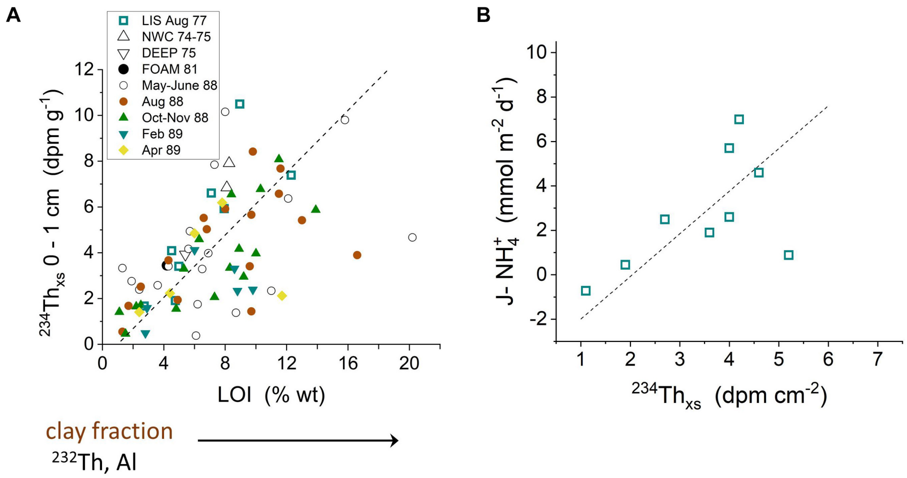

FIGURE 9 | (A) ^{234}Th$_{xs}$ activities in the upper 0–1 cm correlate directly with % weight loss on ignition (LOI), indicative of organic matter content (Aller et al., 1980; Krishnaswami et al., 1984). ^{234}Th$_{xs}$ activities also correlate directly with ^{232}Th (not shown), an indicator of small, clay mineral-rich particles. A geometric mean regression for all data is plotted (dashed line: $y = 0.68x - 0.67$; correlation coefficient $r^2 = 0.31$; $p < 0.001$). Correlations can vary between seasonal data sets. **(B)** ^{234}Th$_{xs}$ inventories (0–5 cm) correlate directly with the benthic flux of NH$_4^+$ from sediment at the same sampling location and time, demonstrating the coherence between ^{234}Th$_{xs}$ and labile organic matter inventories during at least the summer periods when planktonic production is relatively high (August) (Aller and Benninger, 1981).

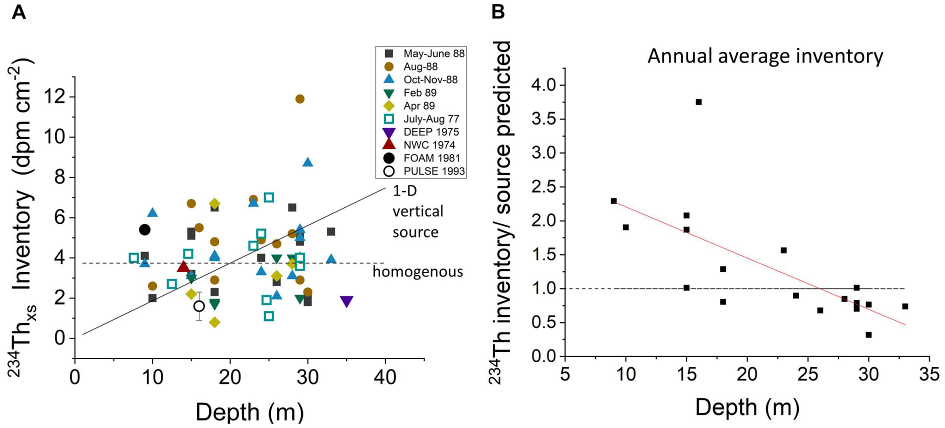

FIGURE 10 | (A) The relationship between ^{234}Th$_{xs}$ inventories in sediments and water depth. Inventories do not show the increase with depth expected for simple vertical settling of particles (solid line) but tend to be homogenized by lateral transport, scattering about the mean value expected for ^{234}Th$_{xs}$ at the average depth of LIS (horizontal dotted line). **(B)** The average annual inventories at LISS sites normalized to the theoretical value at the same sites (^{238}U source in immediate overlying water). The trend shows the tendency to focus ^{234}Th$_{xs}$ into shallow regions (<20 m) at the expense of deeper ones on ^{234}Th decay timescales (~month), consistent with Chl-*a* inventory patterns (**Figure 8**).

clear that activity is differentially focused into relatively shallow water regions <25 m (**Figure 10B**). The coherence between the Chl-*a* inventory and ^{234}Th$_{xs}$ inventory spatial patterns shows that water-column derived labile C$_{org}$ behaves similarly, at least during periods when Chl-*a* is generated (**Figures 8**, **10B**).

The critical role of bioturbation in mediating the capture of labile C$_{org}$ in this sedimentary system is demonstrated quantitatively by the relationship between biological reworking rates, D$_B$, estimated from ^{234}Th$_{xs}$ profiles at each site and the corresponding ^{234}Th$_{xs}$ inventory (**Figure 11**; D$_B$ calculated *per* Aller et al., 1980). A positive correlation exists between D$_B$ and ^{234}Th$_{xs}$ inventory throughout LIS (except during February 1989, see below), with regions of more rapidly mixed sediment having higher ^{234}Th$_{xs}$, and by inference, labile C$_{org}$.

Annual and Decadal Timescales

The distributions of the particle reactive radionuclide ^{210}Pb ($t_{1/2} = 22$ years; $\lambda = 0.0315$ year^{-1}) in LIS reveal similarities and differences with the ^{234}Th$_{xs}$ patterns. The sources of ^{210}Pb$_{xs}$ to LIS are dominated by atmospheric deposition and detrital inputs from the Connecticut River with relatively minor contributions from the open shelf (Benninger, 1978). Thus, as in the case of ^{234}Th$_{xs}$, LIS behaves as a largely closed system with respect to ^{210}Pb$_{xs}$, and its distribution reflects particle cycling, reworking,

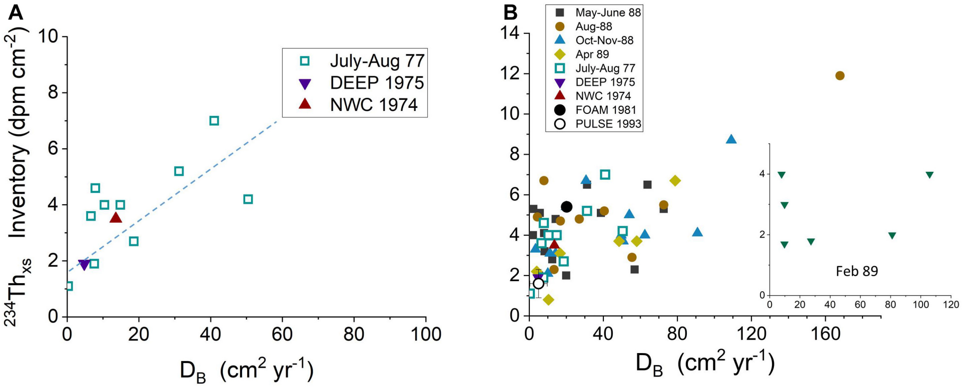

FIGURE 11 | (A) Relationship of ^{234}Th$_{xs}$ inventories with bioturbation rates measured as D$_B$, diffusive mixing coefficients, in diver-collected cores during summer periods (1974–1977) (Aller et al., 1980). **(B)** Relationship of ^{234}Th$_{xs}$ inventories with bioturbation rates estimated as D$_B$, diffusive mixing coefficients, in diver-collected and remotely collected cores (LISS) during all seasons (1974–1991). Except during February 1989 (insert), there is a direct correlation between ^{234}Th$_{xs}$ inventories and bioturbation rates (data from Aller et al., 1980; Cochran et al., 1991).

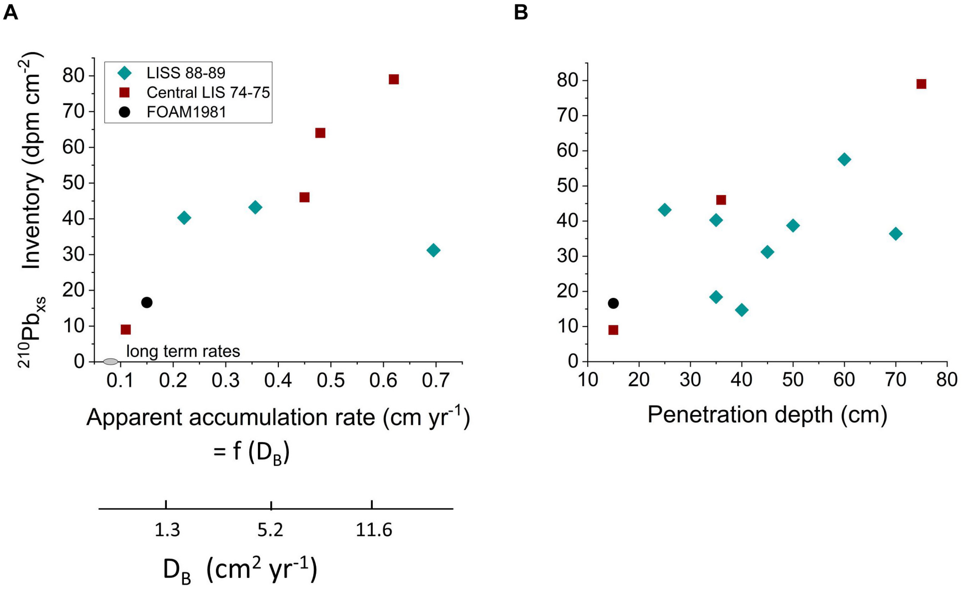

FIGURE 12 | (A) ^{210}Pb$_{xs}$ inventories in the central basin of LIS correlate with biogenic transport of particles estimated as either apparent accumulation rate (advection) or equivalent transport by diffusive mixing (D$_B$). ^{234}Th$_{xs}$ advection rates greatly exceed the long term accumulation rate estimated in the basin either from ^{14}C gradients or seismically (range plotted as gray ellipse on *x*-axis). **(B)** ^{210}Pb$_{xs}$ inventories correlate with ^{210}Pb$_{xs}$ penetration depth throughout LIS. Deep mixing results in greater exchange of nonreactive for reactive particles over ^{210}Pb$_{xs}$ decay timescales (decades).

and net deposition processes internal to LIS but over longer timescales than ^{234}Th$_{xs}$. By analogy, ^{210}Pb$_{xs}$ should track the behavior of particulate C$_{org}$ of moderate lability that is commonly present in sedimentary deposits (Westrich and Berner, 1984; Middelburg et al., 1993; Sayles et al., 2001). ^{210}Pb$_{xs}$ inventories in LIS deposits show a direct correlation with biogenic vertical transport (**Figure 12A** and **Supplementary Table 6**), as calculated from either apparent sediment accumulation rates (biogenic advection model) or equivalent magnitudes of D$_B$ (biogenic diffusion model) (end-member transport calculations *per* Benninger et al., 1979; Gerino et al., 1998). Regardless of the exact transport mechanisms, the penetration rates of ^{210}Pb$_{xs}$ into LIS deposits far exceed those predicted from net accumulation of sediment (0.03–0.08 cm year^{-1}). These relationships show that surface-derived sedimentary material of moderate lability is, like the more labile fraction tracked by ^{234}Th$_{xs}$, captured and subducted into deposits during biogenic reworking. The additional correlation between ^{210}Pb$_{xs}$ penetration depth and inventory shows that locations that are more deeply mixed accumulate greater quantities of moderately reactive material (**Figure 12B** and **Supplementary Table 6**). Thus, the more physically stable, often deeper regions of LIS, such as at stations DEEP and R in the central basin which are inhabited by abundant deep burrowing species of macrobenthos (**Figure 3**), tend to accumulate more $^{210}Pb_{xs}$, and by inference, moderately reactive C_{org} into the bulk refractory C_{org} background.

Coupling of Physical and Biological Sediment Reworking

The supplies of labile planktonic material (Chl-*a*), $^{234}Th_{xs}$, and $^{210}Pb_{xs}$ in LIS are fixed by primary production, ^{238}U concentrations, and atmospheric/river inputs, respectively. The radiochemical sources are relatively constant, so that the differential accumulation of reactive material in deposits of one region is at the expense of another, that is, overall quantities cannot be changed only redistributed. Primary production is more episodic or periodic (seasonal) than are radiochemical supplies but organic particles are subject to the same redistribution processes. The mechanism by which reactive particle capture occurs into specific regions reflects the exchange of nonreactive for reactive material vertically in deposits during bioturbation (excavation), resuspension at the sediment-water interface (injection into water column), and lateral mixing – homogenization by physical transport and particle diffusion through the basin (Aller et al., 1980; Aller, 1982). Even in the absence of net accumulation of sediment, the exchange of reactive material by the coupling of vertical (biological) and horizontal (physical) transport will result in the capture and accumulation of reactive material into biologically mixed patches (**Figure 13**).

The time and spatial scales of biological reworking are controlled by benthic community compositions, which in turn are strongly influenced by physical conditions and interact with them, for example, by altering sediment mass properties and susceptibility to resuspension – erosion (Rhoads and Boyer, 1982). As mentioned earlier, in LIS, the shallow water muds (<20 m) are often inhabited by deposit-feeding protobranch bivalves which intensely rework the upper 0–5 cm of deposits (Sanders, 1956; Zajac et al., 2000). Their feeding and burrowing activities increase sediment water contents, enhance erodibility, and substantially elevate overlying water turbidity (Rhoads and Young, 1970). These biogenic impacts vary seasonally so that during warmer periods of high activity, the turbidity of bottom waters in LIS can be greatly increased (Rhoads et al., 1984). The less turbid water during winter periods allows benthic photosynthesis to depths of at least 15 m in the central basin (unpublished O_2 production measurements) alters LIS particle recycling patterns, and may be a cause of the lack of correlation between $^{234}Th_{xs}$ inventories and D_B during that time (**Figure 11B**). The LIS basin scale patterns of reactive particle capture are otherwise reflective of faunal communities and their coupling to the physical sedimentation regime (**Figure 13**). Any future shifts in these faunal distributions related, for example, to progressive environmental changes, will likely alter spatial patterns of particle exchange and remineralization.

Generality of Relationships

The relationships between reactive particle capture into deposits (inventories) and bioturbation (particle mixing)

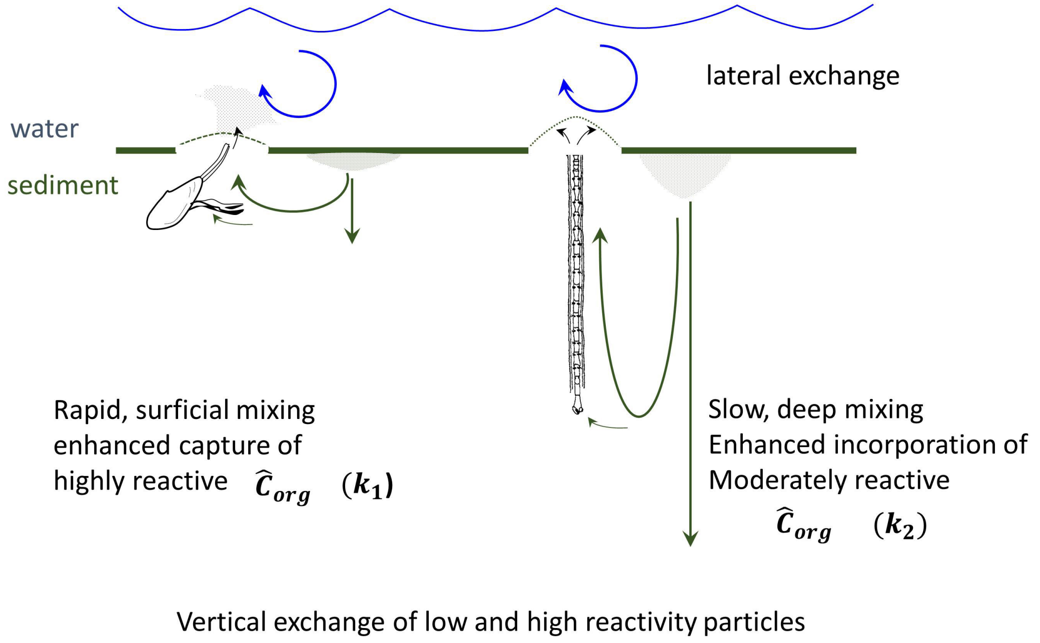

FIGURE 13 | Schematic depiction of coupling of reactive organic matter capture and particle exchange with the scaling of particle bioturbation. Pseudo-first order rate coefficients for organic matter, k_1 and k_2, represent highly labile and moderately labile C_{org} pools, respectively. Highly labile substrates are focused into the intensely mixed regions having high resuspension and exchange. The direct injection of pseudofeces and feces into the water column, and fluidization of the seabed, by protobranch bivalves enhances turbidity and promotes physically driven lateral transport – exchange (Rhoads and Young, 1970). Reactive (labile) particles are captured by vertical exchange into intensely bioturbated patches. Over longer timescales, moderately reactive material migrates and exchanges into deeper regions of more slowly mixed deposits.

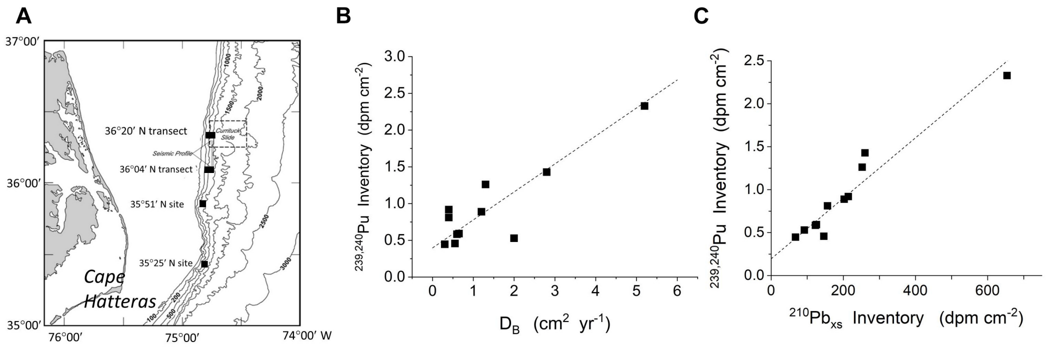

FIGURE 14 | Data from the Cape Hatteras margin demonstrate that the coupling of local bioturbation with physical transport processes to produce large scale patterns of reactive particle distribution is a general phenomenon in sedimentary environments. **(A)** Location of sites sampled by Alperin et al. (2002) along the highly productive continental margin off Cape Hatteras. **(B)** The inventory of ^{239,240}Pu varies directly with D_B estimated at the same sites (data from Alperin et al., 2002). **(C)** The close correlation between ^{239,240}Pu and $^{210}Pb_{xs}$ demonstrates that the tendency for reactive particle inventories to increase with biological mixing holds for multiple reactive components in this region (data from Alperin et al., 2002).

can be demonstrated in other systems, and in particular, in open margin environments. The highly productive margin region off Cape Hatteras has been particularly well studied in this regard (e.g., Blake and Hilbig, 1994; Blair et al., 1996; Levin et al., 1999; Green et al., 2002). Alperin et al. (2002) examined $^{210}Pb_{xs}$ and ^{239,240}Pu distributions in a series of cores at 12 sites spanning depths of 212–1004 m, with an average of 568 m (median 538). ^{239,240}Pu ($t_{1/2}$ = 24,110; 6573 years for ^{239}Pu, ^{240}Pu, respectively) was introduced into the marine system during atmospheric testing of nuclear weapons in the 1950s to ∼1963, and is a transient tracer of surface-derived reactive particles. The background bulk C_{org} pool in deposits in this region is typically 1000–2000 years old (DeMaster et al., 2002). Their data show that the inventories of both ^{239,240}Pu and $^{210}Pb_{xs}$ along the margin correlate directly with D_B, the latter calculated from an optimized mixing model of both ^{210}Pb and ^{239,240}Pu penetration patterns (**Figure 14**). As in the case of the LIS examples,^{239,240}Pu and ^{210}Pb inventories in this region do not generally correlate with net sedimentation (Alperin et al., 2002). Reactive reductant mixing mediated by bioturbation is clearly focused into bioturbated patches by the coupling of vertical (biogenic) and horizontal (physical) exchange.

SUMMARY AND CONCLUSION

Priming of C_{org} remineralization in marine deposits depends on the mixing together and juxtaposition of relatively labile and refractory substrates. The biological reworking of sedimentary deposits inherently promotes priming through local redistribution of relatively reactive particles introduced at the sediment–water interface or direct injection of reactive secretions (mucus) by fauna into otherwise refractory deposits.

The coupling of resuspension of surface sediment and lateral transport of particles with bioturbation activity exchanges sediment and increases the flux, inventory, and penetration depths of reactive C_{org} into otherwise more refractory sedimentary debris.

Total remineralization (aerobic, anaerobic) in bioturbated deposits increases due to the increased inventory of reactive C_{org} as a function of reworking rate. Thus, when coupled to physical sedimentation processes, bioturbation is self-stimulating and priming interactions are enhanced at the community level.

Bioturbation affects remineralization patterns and priming patterns across basin scales, with the scaling of reactive reductant mixing depending directly on scaling of particle bioturbation.

These relations further suggest competition for food resources between spatially separated bioturbated regions of the seafloor, that is, bioturbation patch wars.

Although the local impacts of bioturbation on priming in marine sediments must be similar to those occurring in terrestrial soils, the coupling of water column sediment transport with local bioturbation processes in marine systems results in distinctive basin-scale patterns of remineralization and potential priming interactions not common in terrestrial environments.

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the **Supplementary Files**.

AUTHOR CONTRIBUTIONS

RA and JC conceptualized the project, and participated in the field and laboratory work. RA wrote the initial version of the manuscript.

FUNDING

This synthesis utilizes data that were collected with funding from a variety of sources, including the NSF, DOE, EPA, and NOAA.

This work was supported by the NSF OCE 1737749 (to RA) and the NSF OCE 1736591 (to JC).

ACKNOWLEDGMENTS

A large number of colleagues aided with the multiple field campaigns and analyses utilized here, in particular D. Hirschberg and C. Heilbrun. J. Y. Aller aided with manuscript preparation. We thank the late K. K. Turekian for the intellectual catalysis, and also multiple additional colleagues for discussion.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2019.00157/full#supplementary-material

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.