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Rapid physical and biological particle mixing on an intertidal sandflat

by Anthony F. D'Andrea[1,2], Glenn R. Lopez[1] and Robert C. Aller[1]

ABSTRACT

Sediment mixing processes were investigated using inert tracer experiments, benthic macrofaunal community analysis, and surveys of ray feeding pits to quantify the relative rates and controls of physical and biological reworking on Debidue Flat, an intertidal sandflat in South Carolina. Sediment reworking on Debidue Flat was rapid, with both advective and biodiffusive mixing operating over different vertical spatial scales. Physical reworking by tidal currents dominated initial transport of the tracer in the top 5–10 cm on timescales of ~30 days. Although the exact mechanism of tracer transport is unclear, it is most likely due to active fluidization of surface sediments during stages of the tide followed by a density-driven settling of tracer resulting in a steady downward transport to the depth of bedform reworking. Biodiffusive mixing was evident throughout the sampled interval (~30 cm) and dominated reworking at depths greater than 10 cm. Estimated biodiffusive mixing coefficients (D_b) were high all year (0.15–0.28 cm^{2}d^{-1}), and were comparable to values reported for coastal bioturbated muds. The haustoriid amphipod *Pseudohaustorius caroliniensis* was most likely responsible for tracer dispersal in the 10–30 cm interval based on its distribution, abundance, size, and observed burrow structures. Ray pit excavation and infilling were seasonal disturbances that contributed ~12–22% to spatially averaged advective transport rates but were locally intense and capable alone of turning over the entire upper ~15 cm of the flat in ~100–1000 d. We propose that the mixing processes on Debidue Flat promote an unconstricted, open sediment matrix that maintains the high permeability required for the rapid porewater exchange to 25 cm noted for this system. Thus, in addition to redistributing organic substrates, physical and biological particle mixing play important roles in controlling permeability of flat deposits and quantification of these processes is important to understand controls on permeability and biogeochemical cycling of solutes in sandy systems.

1. Introduction

Intertidal sandflats are physically dynamic systems where tidal currents have been implicated as the dominant force controlling sediment structure (Grant 1981b, 1983). Tidal reworking and ripple movement may dominate sediment transport in many cases, but intense bioturbation can also clearly be important in sandy deposits (Rhoads, 1967;

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Howard and Dörjes, 1972; Hylleberg, 1975; Myers, 1977). Bioturbation by benthic organisms redistributes particles during feeding, burrowing, tube building, and burrow construction. These activities can profoundly affect the physical, chemical, and biological properties of the seabed (e.g. Yingst and Rhoads, 1980; Rhoads and Boyer, 1982; Aller, 1982, 2001; Martin and Sayles, 1987; Wheatcroft *et al.,* 1990). Understanding the rates and mechanisms of sediment mixing are important because mass properties, especially grain size distributions and permeability to fluid flow, partly determine their biogeochemical cycling properties (see reviews by Shum and Sundby, 1996; Huettel and Webster, 2001). Carbon remineralization in sands can be comparable to, or exceed those, found in organic rich muds, justifying a thorough understanding of material transport and biogeochemical cycling processes in sandy systems (Shum and Sundby, 1996; D'Andrea *et al.,* 2002).

Sediment particle reworking rates are typically quantified as biodiffusion (D_b), bioadvection (V_b), or nonlocal (α) transport coefficients, depending on the nature of the particle movement. Biodiffusive transport coefficients (D_b) quantify small-scale dispersion and the progressive spreading of material through transport steps that are small relative to the spatial scaling of the property of interest, for example, the distribution of fresh planktonic debris (Guinasso and Schink, 1975; Robbins *et al.,* 1979; Boudreau, 1986a; Wheatcroft *et al.,* 1990). Nonlocal transport functions quantify exchange of particles between regions of deposits separated by scales that are relatively large with respect to a given property distribution (Rhoads, 1974; Boudreau, 1986b; Rice, 1986; Robbins, 1986). The initial translation or unidirectional movement of material during nonlocal transport, such as subduction of particles downward into the sediment column, can be quantified as bioadvection independent of dispersion (Gerino *et al.,* 1998). Sediment mixing parameters are usually determined using excess activity profiles of radionuclides such as [234]Th and [210]Pb (Aller and Cochran, 1976; Wheatcroft *et al.,* 1990; Wheatcroft and Martin, 1996), concentration profiles and inventory of a reactive component such as chlorophyll *a* (Sun *et al.,* 1991; Green *et al.,* 2002), inert introduced tracers (Rhoads, 1967; Wheatcroft, 1991, 1992; Gerino *et al.,* 1998), or labeled tracers (Wheatcroft *et al.,* 1994; Blair *et al.,* 1996). There are distinct differences between sandy and muddy sediments which must be taken into account when selecting the techniques used to estimate particle movement. Permeable sands tend to be well sorted with a low proportion of silts and clays ($<10\%$). Coarse grained material makes utilization of naturally occurring excess radiotracer profiles difficult or analytically impossible due to preferential association of radiotracers with fine particles. Fine particles may also be moved differentially through pore spaces during fluid advection (Huettel *et al.,* 1996). In addition, the unsteady nature of sands may violate the steady state assumptions typically used in modeling reactive tracer profiles.

In the present study, we utilize manipulated inputs of inert particle tracers to document and quantify dynamic sediment mixing processes on Debidue Flat, an intertidal sandflat in the North Inlet estuary, South Carolina. Reworking rates are estimated using an introduced heavy mineral tracer and time series x-radiography which permitted measurement of particle redistribution *in situ* and direct observation of sedimentary structure evolution. The

tracer experiments were conducted in parallel with seasonal benthic community studies. Macrofauna community data were evaluated using the functional group concept based on feeding method, feeding selectivity, feeding depth, mobility, and sediment transport mechanisms (Jumars and Fauchald, 1977; Brenchley, 1981; Lopez, 1988). These characteristics were used to infer the styles and length scales of biological reworking and identify the likely taxa responsible for any observed bioturbation. Feeding pits formed by rays are seasonally dominant surface features on sandflats in estuaries along the southeastern U.S. (Howard *et al.,* 1977). The size (6 cm to 1 m diameter) and depth (5–15 cm) of these features represent an additional source of biological reworking that was also studied. This combination of observations was designed to distinguish physical reworking from bioturbation, and quantify the seasonal rates and spatial scales of sediment transport on Debidue Flat. These experiments were run concurrently with detailed studies of organic matter flux and reactivity (D'Andrea *et al.,* 2002) to link the dynamics of particle mixing with carbon biogeochemical cycling on Debidue Flat.

2. Methods

a. Study site

Debidue Flat is located within the North Inlet estuary near Georgetown, South Carolina (33°19'N, 79°08'W). This intertidal sand flat is within 0.5 km of the inlet and is a remnant flood tidal delta. Debidue Flat has been a stable feature for over 30 years with annual periods of erosion in early fall, deposition from March through May, and stability during the summer; these patterns are directly associated with depositional and erosional events of the nearby beaches (Humphries, 1977). The tidal channel that drains Debidue Flat is dominated by ebb-tidal currents (Kjerve and Proehl, 1979) with minimal wave action due to its location behind Debidue Island. Salinities are usually high (29–35), and freshwater runoff is negligible. The sediments on this flat are well-sorted medium-fine sand (2.35 ϕ), and have a fairly uniform porosity (mean $\varphi = 0.40$) and low organic content (<0.04% dry wt) (Grant, 1981a; D'Andrea, unpublished data). The macro-surface topography is dominated by ebb-oriented surface ripples, dasyatid ray pits, and burrows of the thalassinid shrimp *Callichirus major* and the enteropneust *Balanoglossus aurantiacus.*

b. Particle mixing experiments

Three tracer input experiments, PM1, PM2, and PM3, ran for 140, 162, and 131 days over a 16 month period from July 1997 to November 1998 (Table 1). Experiments were conducted along the mean low tide mark in the intertidal area of the sandflat. The experimental areas were exposed for as much as 4 hours during a tidal cycle. A randomized block design was used, with three replicate blocks at the same tidal height consisting of 8 or 10-1 m^2 quadrats per block. Sets of 0.5–1 cm layer of heavy mineral sand (mostly garnet with some magnetite) were frozen into 22×29 cm plates and placed in the center of each of the quadrats. The heavy mineral plates rapidly thawed on the sediment surface after

Table 1. (A) Estimated advective velocity, V, on Debidue Flat; (B) Estimated biodiffusion coefficients, D_b, on Debidue Flat.

A.	Experiment	Time period	V (mm d^{-1})	Standard error
	PM 1	Jul–Nov 1997	0.85	0.17
	PM 2	Jan–Jun 1998	0.71	0.11
	PM 3	Jul–Nov 1998	1.15	0.07

B.	Experiment	Time period	Slope $(2D_b)^{1/2}$	Standard error	D_b (cm^{2}d^{-1})	$D_b - $ SE (cm^{2}d^{-1})	$D_b + $ SE (cm^{2}d^{-1})
	PM 1	Jul–Nov 1997	0.67	0.22	0.23	0.10	0.39
	PM2	Jan–Jun 1998	0.15	.087	0.15	0.11	0.20
	PM3	Jul–Nov 1998	0.74	.11	0.28	0.20	0.37

emplacement. Slab cores (16 × 50 × 3 cm) were collected vertically from a randomly determined quadrat in each of the three blocks at each sampling time point. An additional 2–4 quadrats with a vertically as well as horizontally emplaced mineral sand layer were added in the second and third particle mixing experiment to elucidate the horizontal patterns of biological mixing that were observed in PM 1. This involved the excavation of the top 30 cm of the sediment column and emplacing a vertical heavy mineral sand plate, refilling the sediment around the plate, and adding another heavy mineral plate on the surface. The horizontal tracer in these quadrats was not considered in the quantification of particle movement because the unconsolidated nature of the sediments after excavating and refilling around the vertical tracer was different than sediments on the rest of the sandflat; rather these quadrats were used for estimating horizontal dispersion of vertically emplaced tracer. This technique was tested in PM 2 and additional slab cores were collected during PM 3 from each of the 3 blocks.

Slab cores were collected on days 0, 20, 21, 35, 95, and 140 in the PM 1; days 0, 4, 15, and 162 in PM 2; and days 0, 3, 9, 18, 30, 44, and 131 days in PM 3. Cores were returned to the laboratory and x-rayed within 6 hours of collection using a Kramex PX-20N portable x-ray unit. The x-ray protocol involved suspension of the portable x-ray unit ~1 m above an x-ray slab core placed over 18 × 44 cm type 100 x-ray film. Slab cores were x-rayed for 26 or 30 seconds at a power setting of 20 milliamps/60 kilovolts. After development, x-rays were scanned to produce positive prints of sandflat structure and tracer penetration. This provided a rapid and convenient method for visualizing sedimentary and biological structures, and following the progress of the heavy mineral sand tracer over the course of the experiments. X-radiography is sensitive to density differences and the heavy mineral sand (garnet ~3.5–4.5 g cm^{-3}, magnetite ~4.9–5.2 g cm^{-3}) was easily identified relative to the surrounding quartz sand (~2.6 g cm^{-3}). Low densities of heavy mineral sand appeared as obvious particles in x-radiographs and thus can be distinguished from surrounding sand and physical textures.

The depth penetrations of tracer layers were measured directly from x-radiographs and

used to estimate particle transport coefficients. Advective transport coefficients, V (mm d^{-1}), were estimated during each experiment by following the depth penetrations of the mean positions of tracer layers with time. Biodiffusion coefficients, D_b ($cm^2 d^{-1}$), were estimated from tracer layer dispersion patterns. On each replicate x-radiograph from a given time, 6 tracer penetration and dispersion measurements were performed. Two of the 6 measurements were located through regions with the shallowest average vertical penetration of the tracer, 2 through regions with the highest penetration, and 2 were placed randomly across the remaining tracer layer. The minimum and maximum depth penetrations of the tracer relative to the sediment surface were determined in each vertical transect as a measure of dispersion (e.g. Fig. 2). Only tracer particles clearly identifiable from the surrounding sediment fabric were used for these measurements.

We calculated the mean penetration depth and dispersion of tracer for each replicate x-ray. Least squares or weighted least squares regressions (Sokal and Rolf, 1995; Draper and Smith, 1998) of mean depth versus time were used to quantify the bioadvective velocity (mm d^{-1}). The dispersion range in each case is taken as an approximation to the deviation around the mean of a Gaussian distribution. Biodiffusion coefficients were estimated from plots of the arithmetic mean dispersion (z') of the tracer around the mean using the Einstein or Einstein-Smoluchowski relation (e.g. Boudreau, 1997):

$$z' = \sqrt{2D_b * t} \,;$$

D_b was estimated from plots of z' against $t^{1/2}$ for each of the experiments.

Deposition, erosion, and movement of bedforms on the sandflat can directly impact the measured penetration of the tracer layer, leading to either an overestimation (deposition) or underestimation (erosion) of the bioadvective velocity. One-meter stakes (4−6) were emplaced at the corners of each block. The heights of these stakes relative to the sandflat surface were measured during the second and third particle mixing experiments to account for net deposition and/or erosion during the particle mixing experiments.

c. Faunal analyses

Analysis of the benthic community supplemented determination of particle mixing rates. Macrofauna samples were collected in June 1997 (summer), September 1997 (fall), January 1998 (winter), and June 1998 (summer). Replicate, 7 cm diameter cores (3 at each timepoint) were collected within or in the vicinity of each particle mixing quadrat, 1 core per block at each time point. Each core was sectioned into 0–3, 3–10, 10–20, and 20–30 cm depth intervals. Animals were sieved from the sediment using a 500 μm sieve and stored in ~7% filtered seawater-buffered formalin. Fixed samples were later transferred to 70% ethanol. Animals were identified to the lowest taxonomic group possible, usually species. Each taxonomic group was assigned to one of the following functional groups: suspension feeder (SF), surface deposit feeder (SDF), head-down deposit feeder (HDF), organic trapper or browser (OTB); free burrowing deposit feeder (DF), or carnivore/ scavenger (C/S). Based on surficially expressed biogenic structures, the larger, deep

burrowing fauna such as *Balanoglossus* were obviously under sampled using the coring technique. Biogenic structures produced by large macrofauna were quantified during each season using two-100 meter transects at approximately the same tide level as the particle mixing experiments. One-m^2 quadrat was sampled every other meter on each transect for densities of *Balanoglossus aurantiacus* fecal mounds, *Callichirus major* burrows, *Callianassa biformis* burrows, and *Onuphis jenneri* tubes.

d. Ray pit surveys

The spatial and temporal distribution of ray pits during major periods of ray activity (May–October) were monitored using 3–100 m^2 quadrats located slightly below the mean low tide line in parallel with the three particle mixing blocks. The abundances and sizes (diameter, depth) of all ray pits within the quadrats were measured through the summer (June–August) and in the fall (September–November) over the 16 months of the particle mixing experiments. Ray pits were surveyed 4–6 days each month. New ray pits were distinguished from old pits by the presence of mounds of fresh sand on the sides of the pit. Abundances and sizes of the ray pits were combined to calculate the areal coverage and daily reworking rates of ray pits on Debidue Flat. Areal coverage was calculated using the measured diameters of ray pits to calculate total area of ray pits (m^2) relative to the total area of a quadrat (100 m^2). Daily ray pit reworking rates were calculated based on measured pit depth and diameter assuming the pit shape was an inverted cone. The volume (cm^3) was calculated as 1/3 $\pi R^2 * D$, where R = measured pit radius (cm) and D = pit depth (cm). For a given day, the volume displacement by all ray pits was combined to estimate areally averaged daily reworking per quadrat (10^6 cm^2): $\dfrac{\Sigma(1/3\ \pi R^2 D)}{10^6}$. This resulted in an estimate for ray pit reworking (mm d^{-1}) which could be directly compared to the tracer layer advection estimates.

3. Results

a. Particle mixing experiments

The particle mixing experiments were interpreted as a continuous, progressive time series detailing particle mixing processes over a 16-month period on Debidue Flat. The pattern of mixing was the same for the three experiments, regardless of season. The heavy mineral tracer initially appeared as a uniform layer on the sediment surface (Fig. 1A). Ripple migration and reworking rapidly subducted the tracer layer into the sediment. There was also evidence of bioturbation, primarily in the form of amphipod and polychaete burrows (Fig. 1B). A given tracer input continued to move down into the sediment over the first 30 days of the experiments as a distinct layer (Fig. 2A). Below 5–10 cm, the tracer was no longer found as a distinct layer; and it appeared as dispersed particles over the length of the slab cores (20–30 cm) by 95 days of the experiments (Fig. 2B).

The vertically emplaced tracer layers were added in the last two particle mixing
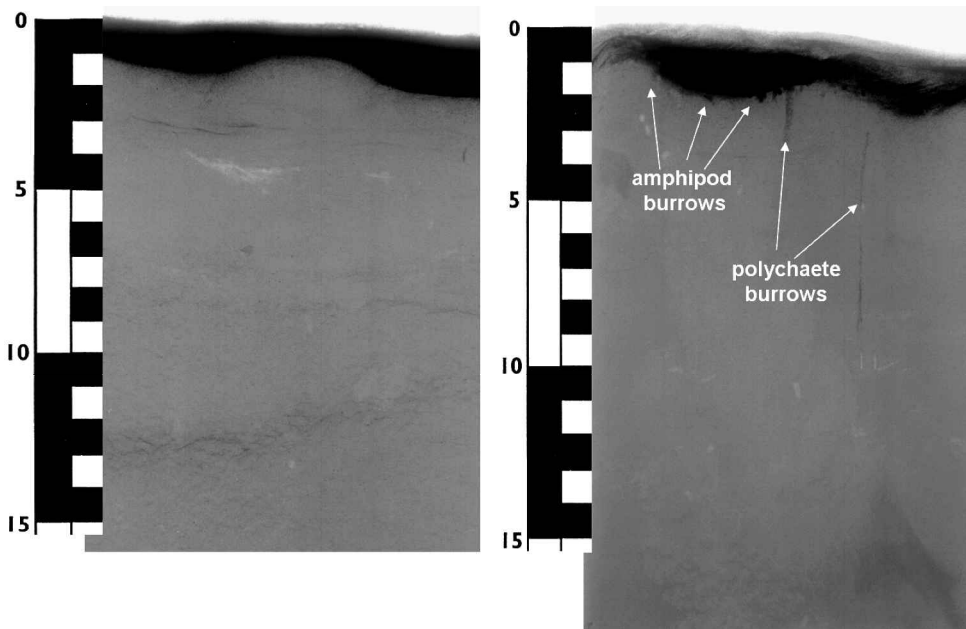
Figure 1. Positive scans of x-radiographs from slab cores taken during particle mixing experiments representing typical patterns observed in the experiments. The scale on the left side of the image is in cm. (A) Day 0 of PM 1: Note the general absence of physical and biological texture in the core and the settling of the heavy mineral plate into the natural ripple structures on Debidue Flat. (B) Day 4 of PM 3: Initial burial of the tracer layer. There are tracer particles in backfilled amphipod burrows and polychaete burrows.

experiments to help elucidate the mechanisms of this dispersal. Initially, the vertical tracer appears as a consolidated undisturbed layer, although the sediment was still somewhat porous due to the excavation necessary to emplace this layer (Fig. 3A). The tracer layer was rapidly riddled with burrows in the first few weeks of the experiments. The vertical tracer layer was never fully dispersed, but the layer was riddled with burrows to the base of the slab cores in all samples and experiments (Fig. 3B). There was no evidence of vertical tracer layers in the top 10 cm at the end of both of the experiments in which they were sampled.

The penetration and dispersion of the tracer in the particle mixing experiments were used to estimate the advective velocity and the biodiffusion coefficients for the top 30 cm of Debidue Flat. Figure 4 shows the regression for each of the particle mixing experiments; the slopes estimated the advective transport, V. Vertical transport of particles into Debidue Flat was high in all seasons ranging from 0.71–1.15 mm d^{-1}, with some annual variation from summer 1997 to summer 1998 (Table 1A). In all experiments, tracer particles placed at the surface were transported to at least 20 cm in 3–4 months, indicative of a deep mixed layer. The changes in relative sandflat height compared to the tracer penetration in PM 3
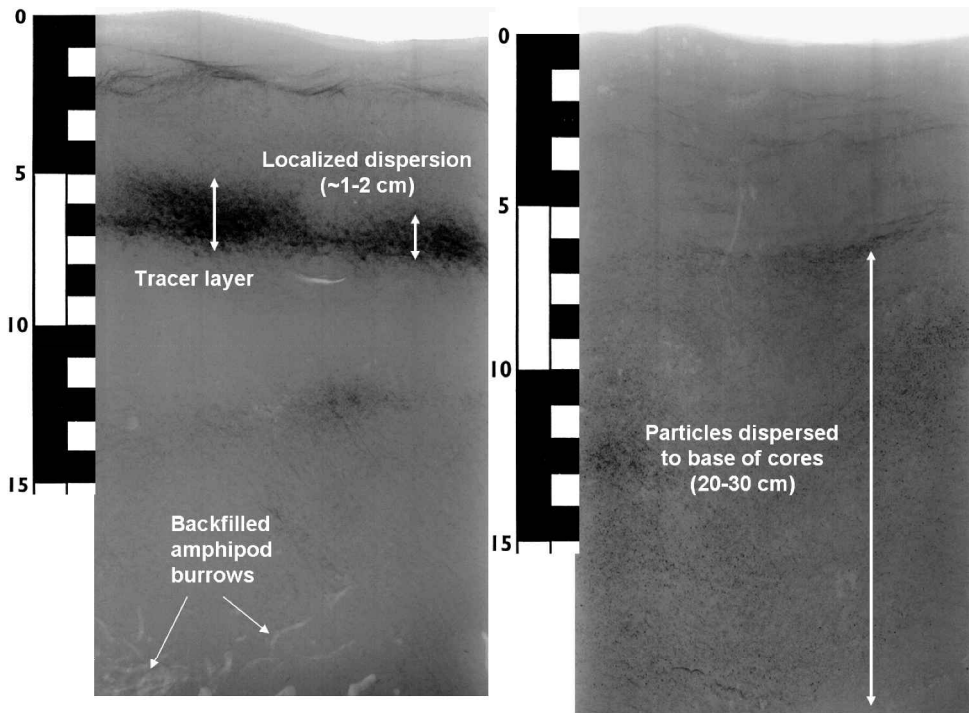
Figure 2. Positive scans of x-radiographs from slab cores taken during particle mixing experiments representing typical patterns observed in the experiments. The scale on the left side of the image is in cm. (A) Day 30 of PM 3: Burial of tracer layer to ~5–7 cm. There is still evidence for some of the tracer still interacting with bedform motion. There are backfilled amphipod burrows near the base of the core. The scale on the left side of the image is in cm. (B) Day 162 of PM 2: Tracer completely dispersed both horizontally and vertically to a depth of at least 20 cm.

showed small periods of erosion and deposition over the time period of the experiment (Fig. 5). In contrast to the steady penetration of the tracer into the sandflat, the *net* change in sandflat height over 143 days was approximately zero. The biodiffusion coefficient, D_b, was estimated by plotting the mean dispersion against the square root of time (Fig. 6). Biodiffusion coefficients on Debidue Flat were high (0.15–0.28 cm^{2}d^{-1}) and showed similar temporal patterns to advective velocity, with highest values in the summer to fall experiments relative to the winter–spring period, although there was some variability (Table 1B).

b. Benthic macrofauna

   The macrofauna of Debidue Flat included 38 species and four functional groups. Abundances were high over the 4 seasons studied with lower abundances measured only in fall 1997 (Fig. 7). The benthic community was dominated by deposit feeding haustoriid
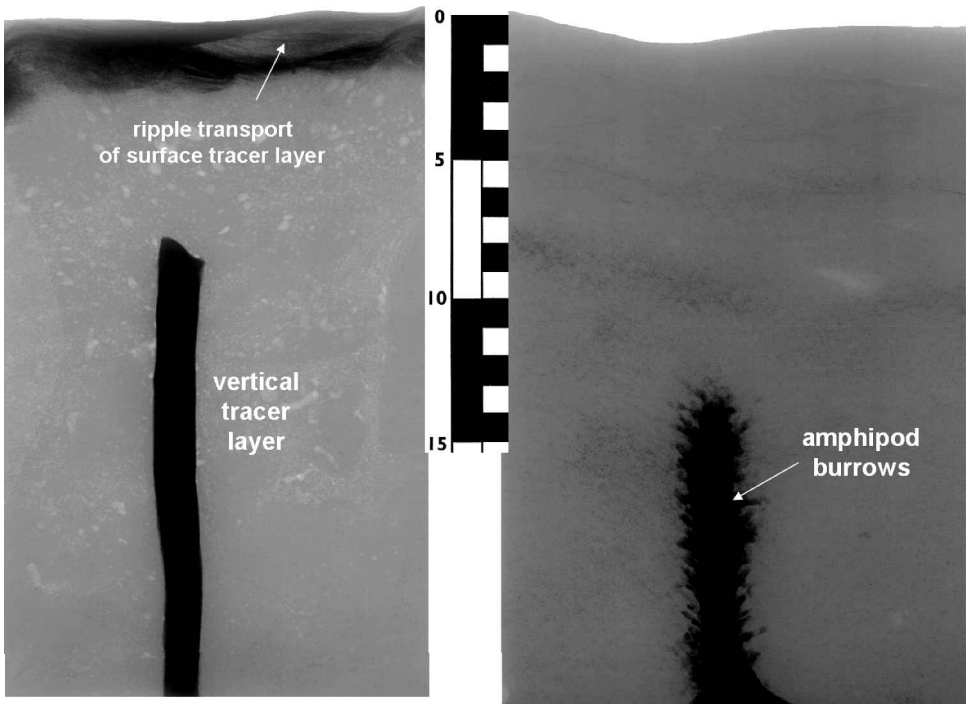
Figure 3. Positive scans of x-radiographs from slab cores collected during the vertical tracer mixing experiments. The scale on the figure is in cm. (A) Day 3 of PM 3: This is essentially day 0 of the vertical tracer experiments. There is obvious ripple laminations present at the top of the core. The light areas of the image are actual air holes still present in the sediment from the disturbance related to placing the vertical tracer layer into the sandflat. (B) Day 131 of PM 3: The vertical tracer layer is completely riddled with amphipod burrows. Note that there is no evidence of the vertical tracer shallower than 10 cm.

amphipods (*Acanthohaustorius millsi* and *Pseudohaustorius caroliniensis*) and the diatom-trapping polychaete *Paraonis fulgens*. These three species accounted for 85–93% of total infaunal abundances annually (Table 2). *P. fulgens* occurred in the top 20 cm of Debidue Flat but was concentrated in the top 10 cm (Fig. 8). Peak abundances of *P. fulgens* occurred in the summer when they accounted for 50–70% of the total benthic abundances. Haustoriid amphipods were abundant at every sampling time, with abundances peaking in the 10–20 or 20–30 cm depth intervals (Fig. 8). The amphipods were dominant in the fall and winter, accounting for ~60–65% of the total abundances. High abundances of amphipods in surface sediments (most likely *A. millsi;* see discussion) were only found in summer 1997 and winter 1998. Large macrofaunal features exhibited no seasonal change (*Balanoglossus aurantiacus*), a slight drop in the winter (*Callichirus major, Callianassa biformis*), or a slight but steady increase (*Onuphis jenneri*) over the course of the study
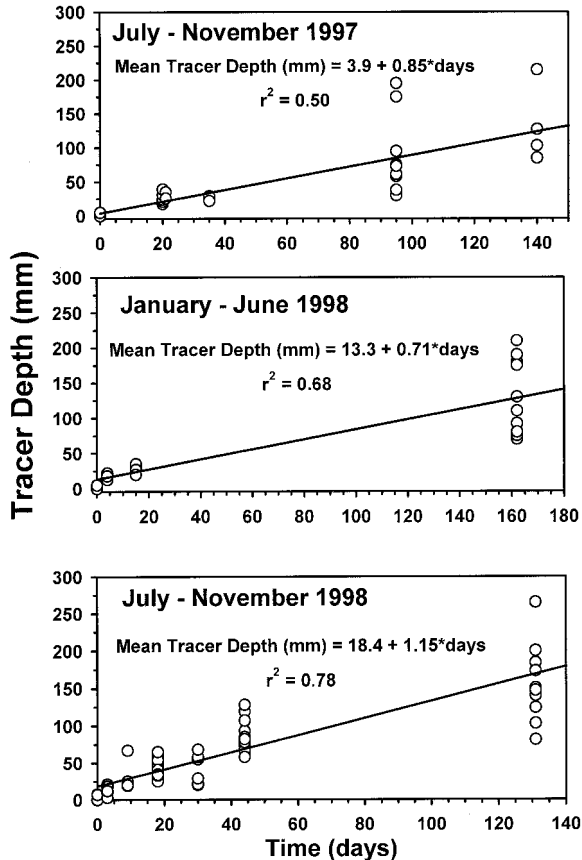
Figure 4. Regressions of tracer penetration in particle mixing experiments used to estimate advective velocity of particles, *V*. The slopes of the regressions estimate the advective velocity during the time period of the individual experiments.

(Fig. 9). Abundances of large macrofauna were always orders of magnitude less than the dominant infauna of Debidue Flat (see Table 2).

c. Ray pit surveys

Dasyatid ray pits occurred from June to November in both 1997 and 1998, with peak abundances in July (Fig. 10A). Spring periods (March–May) were not sampled but ray pits are thought to also occur at these times. Pit diameter was generally 30–50 cm, with larger ray pits occurring in late summer–early fall (Fig. 10B). Mean pit size of old pits was generally smaller than new ray pits, although none of these differences was significant. Ray pits covered 1.5–3% of the sandflat surface from June–August with new ray pits covering 0.6–0.8% of Debidue Flat (Fig. 10C). Areal reworking rates due to ray pit disturbance
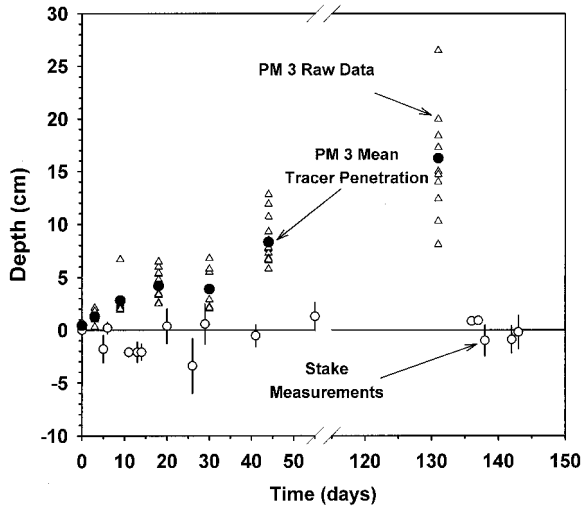
Figure 5. Plot of changes in sandflat height during PM 3 (open circles, mean ± SE). The reference line represents zero net erosion or deposition; negative values represent erosion and positive values represent deposition on Debidue Flat.

were similar during the time periods in which they were abundant (0.14–0.26 mm d^{-1}), although there was some annual variation (Fig. 10D).

4. Discussion

Mixing of tracer particles on Debidue Flat was rapid, with tidally-driven physical transport apparently dominating during the initial stages near the upper boundary and biogenic transport dominating the sand body internally. These processes resulted in the rapid burial of the tracer layer to 5–10 cm in 30 days followed by internal dispersal of the tracer particles to 30 cm in <150 days. We will treat each of these processes (advective and dispersive mixing) separately, discuss the likely physical and biological mechanisms responsible for the observed patterns, and argue that sediment reworking processes play an important role in maintaining the permeability of Debidue Flat essential for the observed rapid porewater exchange between sediments and overlying water column in this system.

a. Advective reworking on Debidue Flat

Advective transport of the tracer during the first 30 days of the particle mixing experiments resulted in the rapid subduction of a distinct tracer layer to depths of 5–10 cm. Particle transport could be the result of physical mixing or activities of deep-feeding benthic organisms. Although the exact nature of the physical transport processes remains to be resolved, there are two likely physical explanations for the observed particle transport
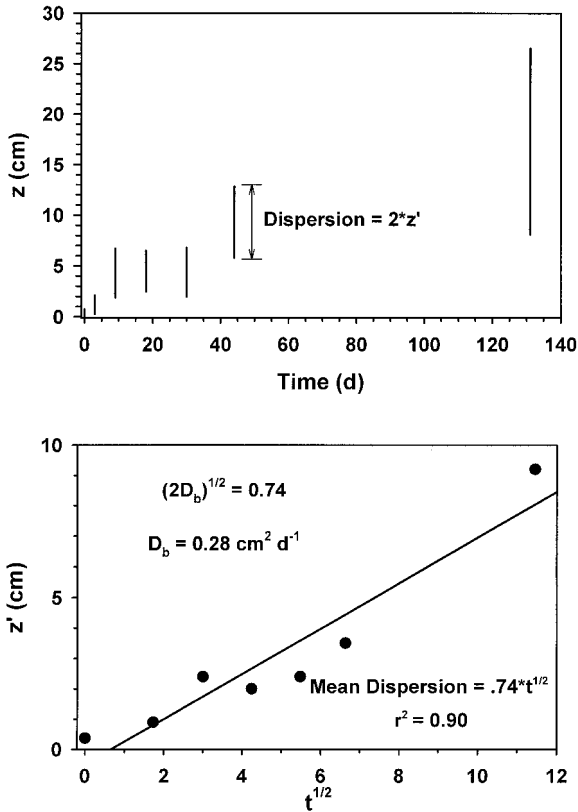
Figure 6. Plots of dispersion with time (top) and mean dispersion with $t^{1/2}$ (bottom) for PM 3. The mean dispersion (z') was calculated from the dispersion data. The slope of the regression line was used to calculate D_b using the Einstein relation.

patterns: bedform migration with leeside basal lag and density-driven settling of tracer particles through a fluidized sand bed.

Bedform migration and tidal reworking are temporally constant but spatially discontinuous features of Debidue Flat (Grant, 1981b). The daily tidal reworking of surface material was reported as ~2.5–3.3 cm during two periods of relatively low ebb tidal velocity (27–30 cm s^{-1}) (Grant, 1981b). Tidal velocities in the tidal creek which covers Debidue Flat can exceed ~90 cm s^{-1} 1 m above the bottom (Kjerfve and Proehl, 1979), with velocities as high as 2.2 m s^{-1} measured on spring tides (B. J. Kjerfve, pers. comm.). Thus, it seems plausible that physical reworking of surface sediment over the course of 30 days (2–3 spring tides) could result in an intact heavy mineral lag layer as a bottomset bed at a depth of ~5–10 cm. Intense physical disturbance in the upper decimeter could also explain the apparent shearing off of the upper portion of the vertically emplaced tracer bed (Fig. 3B). The loss of the upper portion of the vertically emplaced tracer and known
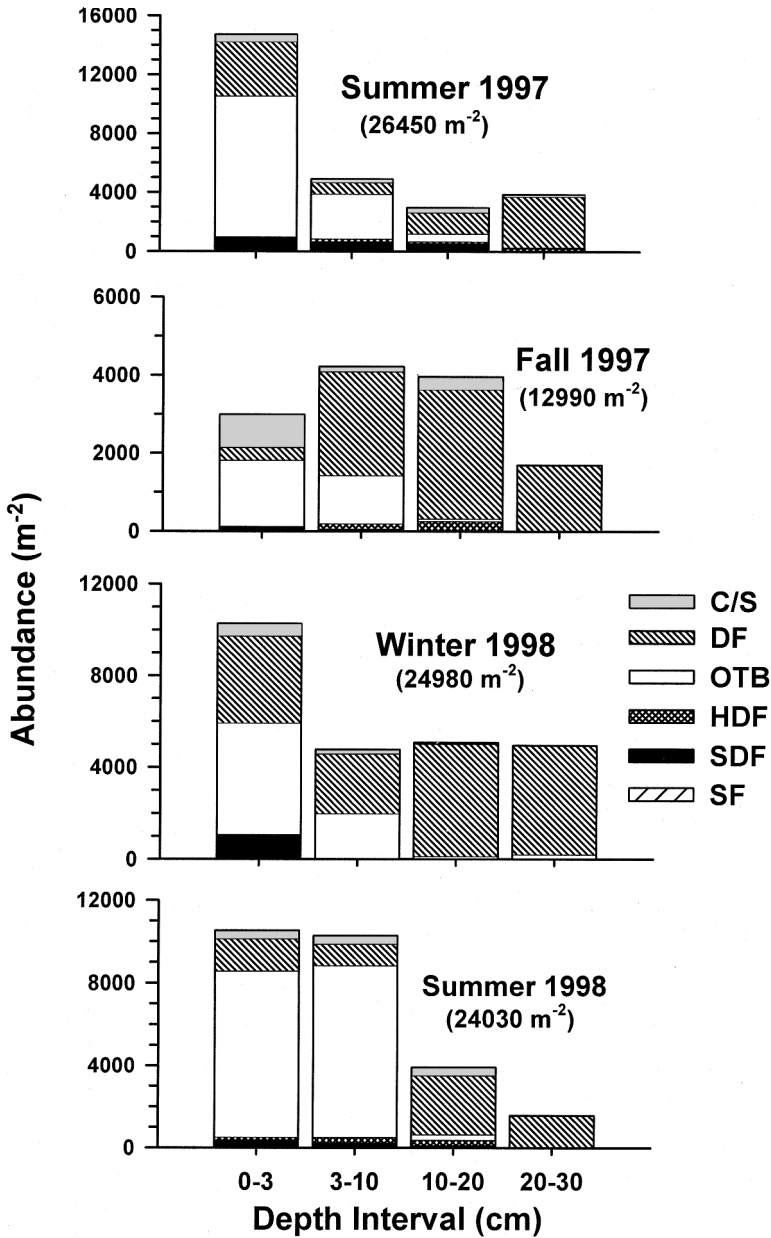
Figure 7. Mean abundances of functional groups during the four seasonal samplings. Infaunal abundances are divided into four depth intervals and cumulative abundance for a sampling is indicated on each figure. SF = suspension feeders; SDF = surface deposit feeders; HDF = head-down deposit feeders; OTB = organic trappers or browsers; DF = free-burrowing deposit feeders; C/S = carnivores/scavengers.

Table 2. Rank order, functional group, and mean abundances of major benthic fauna on Debidue Flat during the four seasonal samplings. SDF = surface deposit feeders; SF = suspension feeders; HDF = head-down deposit feeders; OTB = organic trappers/browsers; DF = free-burrowing deposit feeders; C/S = carnivores or scavengers.

Summer 1997

Species	Functional Group	Abundance (m^{-2})
Paraonis fulgens	OTB	13200
Haustoriid amphipods (2 spp.)	DF	9300
Spiophanes bombyx	SDF	520
Sigambra spp.	C/S	476
Heteromastus filiformis	HDF	433

Fall 1997

Species	Functional Group	Abundance (m^{-2})
Haustoriid amphipods (2 spp.)	DF	7990
Paraonis fulgens	OTB	2990
Dorvilleid spp.	C/S	844
Heteromastus filiformis	HDF	259
Sigambra spp.	C/S	194

Winter 1998

Species	Functional Group	Abundance (m^{-2})
Haustoriid amphipods (2 spp.)	DF	16000
Paraonis fulgens	OTB	7100
Tellina texana	SDF	649
Sigambra spp.	C/S	346
Themiste alutacea	SDF	173

Summer 1998

Species	Functional Group	Abundance (m^{-2})
Paraonis fulgens	OTB	16600
Haustoriid amphipods (2 spp.)	DF	7012
Heteromastus filiformis	HDF	389
Haploscoloplos fragilis	HDF	130
Leitoscoloplos spp.	HDF	130

mechanisms of bedform migration suggest that a portion of tracer particles may have been transported horizontally completely out of the experimental observation patch. Any such particle loss could result in underestimates of diffusive mixing during initial transport stages and overestimates of tracer layer advection rates based on the position of the layer center of mass. The generally regular progression of transport patterns with time, however, indicates that either horizontal particle loss is not a major influence on calculated rates or other processes are responsible for the subduction of the tracer layer.

A second physical process which could account for the observed tracer patterns would be preferential settling of the dense tracer particles during fluidization events of the surficial sand bed. The zone of disturbance by currents in sandy systems is characterized by a mobile, fluidized sand layer (Klein, 1970), and disturbance depth can be increased by rapid changes in bottom current velocity or infrequent large disturbances such as storms
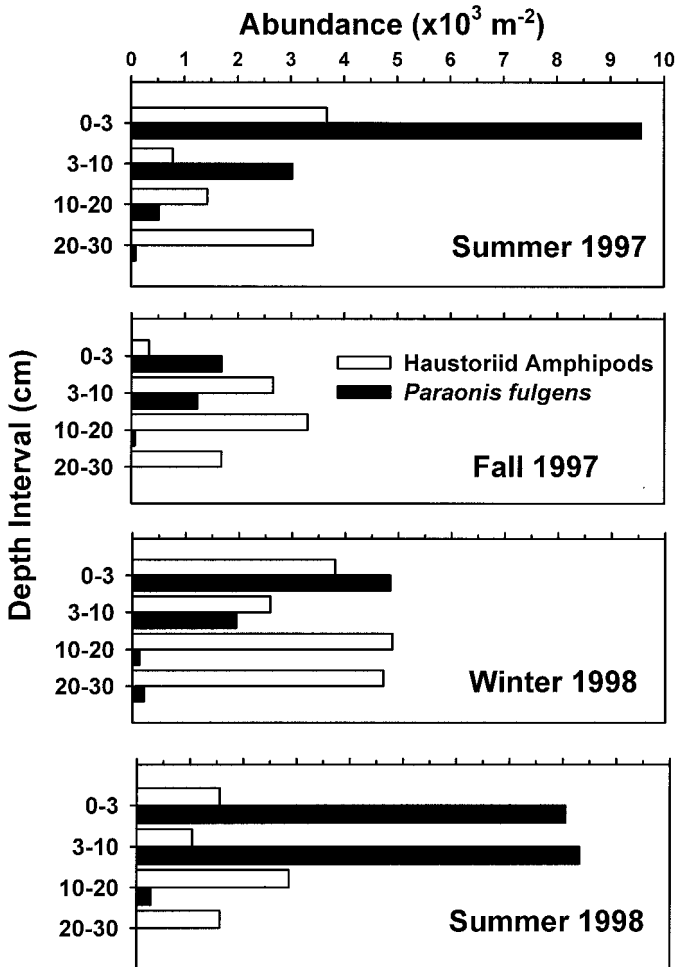
Figure 8. Mean abundances and depth distribution of haustoriid amphipods (open bars) and *Paraonis fulgens* (solid bars) during seasonal sampling on Debidue Flat.

(e.g. Klein and Whaley, 1972). If episodic, high velocity tidal and/or storm events fluidize a portion of the sand bed, a tracer could move rapidly downward in the sediment column due to the higher density of garnet sand ($3.6–4.3$ g cm^{-3}) and magnetite ($4.9–5.2$ g cm^{-3}) relative to quartz sand (~ 2.6 g cm^{-3}). Although the bedforms commonly observed at low tide on Debidue Flat are ebb-oriented surface ripples (15–20 cm wavelength, 3–5 cm amplitude, (Grant, 1983)), these bedforms could be the last stage of a tidal fluidization process as subsiding currents re-establish the ripple field.

If fluidization of the surficial sand column is the dominant physical process resulting in advection of the tracer particles, the tracer technique utilized in these experiments would
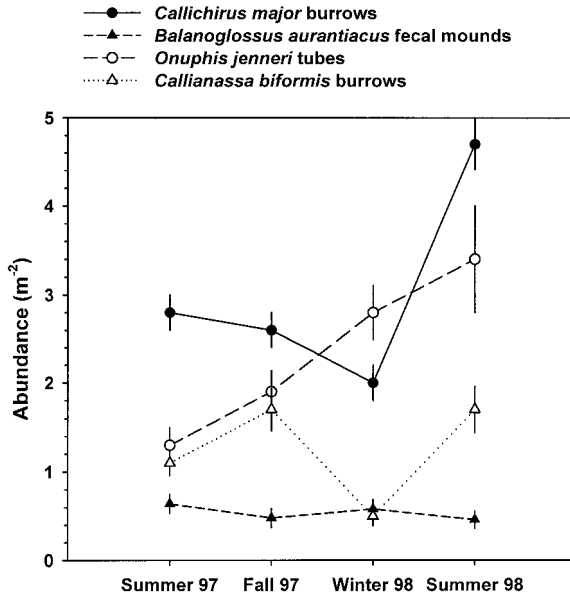
Figure 9. Mean abundances ($\pm$SE) of large macrofaunal structures on Debidue Flat.

generally overestimate net advective transport of particles other than heavy minerals or their hydraulic equivalents. Differential transport could be tested using inert tracers such as luminophores (e.g. Gerino *et al.,* 1998) or metal labeled particles (Olmez *et al.,* 1994, Wheatcroft *et al.,* 1994) in addition to or in lieu of the heavy mineral/x-radiography technique described here. These alternative techniques use particles otherwise identical to average *in situ* particles, thus overcoming artifacts resulting from particle density per se. Regardless of possible artifacts resulting from differential transport of tracer, the restricted range of rapid tracer penetration depth both seasonally and annually, and the correspondence of penetration scale to the scaling of typical bedforms or fluidized layers, implicate physical mixing of the surface ~10 cm as a dominant sediment mixing process for at least a subpopulation sand particles.

The initial subduction of tracer noted in these experiments could also reflect subsurface feeding and surface deposition (nonlocal transport) by the benthos which would be interpreted as short term advective transport (e.g. Aller and Dodge, 1974). The head-down deposit feeders identified on Debidue Flat—*Heteromastus filiformis, Haploscoloplos fragilis,* and *Leitoscoloplos* spp.—were not abundant throughout the year (Table 2) and were too small for the length scale of particle subduction observed in the x-radiographs. The component of the benthos with a burrowing or feeding mode likely to have an impact on non-local particle transport on Debidue Flat is the enteropneust *Balanoglossus aurantiacus. B. aurantiacus,* is a large acorn worm (up to 1 m long) inhabiting semi-permanent U-shaped burrows to depths of 60 cm (Howard and Dörjes, 1972; Duncan 1984, 1987).
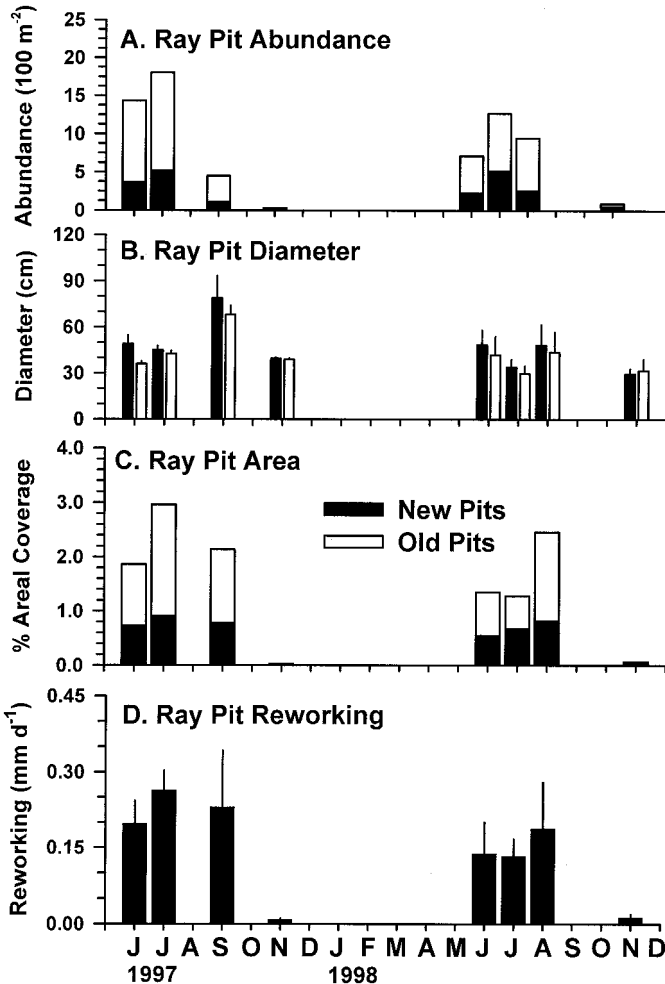
Figure 10. (A) Mean abundances, (B) diameter, (C) % areal coverage, and (D) reworking rate of dasyatid ray pits on Debidue Flat from Jun, 1997 to Nov, 1998. New ray pits are represented by the solid bars and old ray pits by the open bars. Plots B and D include the SE around the mean.

The burrow has both an anterior (funnel) and posterior (fecal cast) portion. The anterior portion of the burrow branches at 10–12 cm below the sediment surface with one narrow branch connected to the sandflat surface for ventilation and the second connected to the feeding funnel; the feeding position of *B. aurantiacus* is beneath this branching and is on the same spatial scale as the observed advective transport on Debidue Flat (Fig. 11, Duncan, 1987). *B. aurantiacus* is an active, vigorous burrower replacing almost all funnel and casting sites within 2–3 tidal cycles (Duncan, 1987). Individual reworking estimates for enteropneusts are generally high, ranging from 20–800 cm^3d^{-1} (Thayer, 1983;
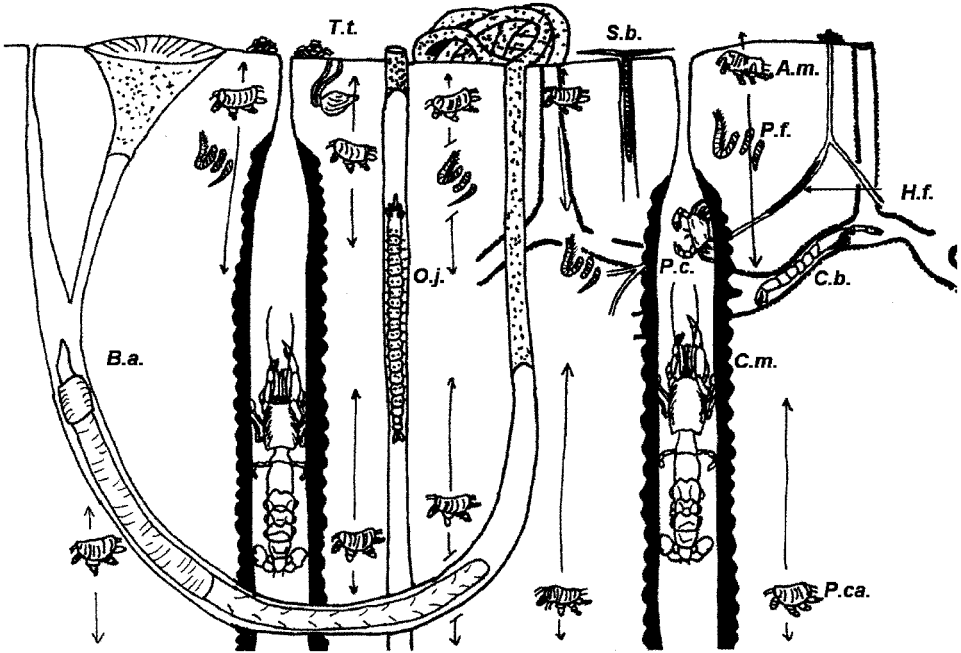
Figure 11. Zonation and distribution of the important benthic fauna in the community of Debidue
Flat (after Howard and Dörjes, 1972; Ruppert and Fox, 1988). The vertical scale is approximately
30 cm. B.a. = *Balanoglossus aurantiacus;* C.m. = *Callichirus major;* O.j. = *Onuphis jenneri;* T.t.
= *Tellina texana;* P.f. = *Paraonis fulgens;* S.b. = *Spiophanes bombyx;* P.c. = *Pinnixa cristata;*
H.f. = *Heteromastus filiformis;* C.b. = *C. biformis;* A.m. = *Acanthohaustorius millsi;* P.ca. =
Pseudohaustorius caroliniensis.

Suchanek and Colin, 1986). Reworking estimates for *B. aurantiacus* are in the lower part
of this range at 129 cm^3 ind^{-1} d^{-1} with a reworking depth from 3 to 80 cm (Duncan, 1981,
1984; Thayer, 1983). However, the densities of *Balanoglossus* over the course of this study
were quite low (0.5–0.6 m^{-2}, Fig. 9). Using the reworking rate reported for this species,
population reworking would be ~65 cm^3 m^{-2} d^{-1} which can be converted to a spatially
averaged advective velocity of ~0.07 mm d^{-1}. This value would only account for 6–10%
of the overall advective velocities observed in these experiments (Table 1). Thus, deep
nonlocal biogenic transport probably does not significantly alter the initial dominance of
physical advection inferred for transport in the top 10 cm of the sandflat but clearly
contributes to the longer term net advection of tracer below ~10 cm.

  Dasyatid ray pits are large, seasonal biological disturbances that were not well quantified
by the particle mixing experiments. Ray pits covered 1–3% of the sandflat surface during
the time period that rays were active within North Inlet estuary (Fig. 10C), in contrast to the
30% estimated by Grant (1983) in aerial photographs. After formation, ray pits rapidly
infilled with surrounding sand leaving a fairly shallow <15 cm depression which filled

completely over 1–3 days. This pattern of deep disturbance followed by infilling would effectively transport surface sediments locally to depths up to at least 15 cm into the sediment column on time scales of hours to days. Estimates of pit reworking were combined in time periods corresponding to the three particle mixing experiments. The similarity among months of ray activity in a given year were used to group reworking rates for the months ray pits were not actually sampled. A reworking rate for the time period of each particle mixing experiment was then calculated as an equivalent advective velocity for direct comparisons with tracer layer transport.

The calculated average pit reworking estimates were 0.19, 0.07, 0.14 mm d^{-1} for PM 1, PM 2, and PM 3, respectively. These average estimates lie within the range of advection rates, $V \sim 0.02$–1.5 mm d^{-1}, expected from the general range of fractional areal coverage by ray pits ($A_f \sim 0.01$–0.03), individual pit turnover or fill times ($\tau \sim 1$–3 days), and cone-shaped pit depth ($D \sim 15$ cm), where $V = 1/3\ D^*A_f/\tau$. The fractional area of the flat turned over by rays, therefore, ranges from ~ 0.003–0.03 d^{-1} ($= \tau/A_f$) suggesting that the entire flat surface could be reworked by rays in ~ 30–300 days and the upper 15 cm of the flat in ~ 100–1000 days ($= 3\tau/A_f$ assuming cone-shaped pits). When ray pits were active, pit reworking added an additional average 10–22% to the estimates for the overall advective velocity, V, from the small-scale particle mixing experiments. These results are consistent with the assertion of Grant (1983) that reworking by rays, while locally dramatic and important, is low in an overall mass balance sense compared to other sources of reworking on Debidue Flat.

b. *Biodiffusive mixing and benthic macrofauna on Debidue Flat*

Biodiffusion superimposed on nonlocal or advective transport dominated reworking deeper than 10 cm, dispersing particles to 20–30 cm depth on timescales of <140 days. This mixing process was evident from the x-radiographs (Fig. 2), burrows in the vertical tracer experiment (Fig. 3B), and the increased dispersion of the tracer around the mean tracer depth with time (Figs. 4–6). Haustoriid amphipods were present all year in high abundances at depths greater than 10 cm (Fig. 8) and create burrows that fit the criteria for biodiffusive mixing (Figs. 2A, 3B). Estimates for the biodiffusive coefficient, D_b, were similar throughout the 18 months of the experiments with some depression of biodiffusion in the winter, most likely related to lower temperatures (Table 1). These values (0.15–0.28 cm^{2}d^{-1}) fall within the middle to upper range of biodiffusion coefficient estimates measured using profiles of excess ^{234}Th in estuarine and continental margin bioturbated muds (see review in Wheatcroft and Drake, 2003).

Although extensive particle mixing studies have been conducted to quantify D_b, few of these studies have included detailed studies of the infaunal community. The abundance, depth distribution, and feeding style of the benthic community should affect the magnitude of the measured D_b and clarify the biogenic controls on sediment reworking. The macrobenthic community was consistent with other studies of this sandflat (Holland and Polgar, 1976; Holland and Dean, 1977; Grant 1981a, 1983; Fox and Ruppert, 1985) and

can be divided into shallow (<10 cm) and deep (>10 cm) components (Fig. 11). The shallow community was dominated by the haustoriid amphipod *Acanthohaustorius millsi* and the paranoid polychaete *Paraonis fulgens*. The rest of the dominant fauna in the shallow community were all either deposit feeders (the capitellid polychaete *Heteromastus filiformis* and the thalassinid shrimp *Callianassa biformis*) or species which can switch between deposit and suspension feeding (the tellinid bivalve *Tellina texana* and the spionid polychaete *Spiophanes bombyx*). The deep community consisted almost exclusively of the haustoriid amphipod *Pseudohaustorius caroliniensis.* The large macrofauna in this system— *Balanoglossus aurantiacus, Callichirus major,* and *Onuphis jenneri*—occurred across the depths of the sandflat, but only *B. aurantiacus* had a burrowing or feeding mode which was likely to have an impact on particle reworking on Debidue Flat (discussed in the previous section). The benthic organisms on Debidue Flat most likely to impact biodiffusive particle mixing on Debidue Flat included *P. fulgens* and the two species of haustoriid amphipods.

P. fulgens forms spiral mucoid feeding traces while selectively ingesting diatoms from grains in well-sorted, permeable sand (Röder, 1971; Risk and Tunnicliffe, 1978). This species occurs within 10 cm of the surface, and its feeding traces form horizontal bedding planes which can stabilize subsurface sand. *P. fulgens* does not ingest sediment grains directly, but rather moves the particles aside for diatoms (Risk and Tunnicliffe, 1978). After an individual is done with an individual trace, *P. fulgens* moves up or down within the sediment and begins spiraling outward. The traces range in size from 4–8 cm diameter and ~0.75 mm thick. Based on the sizes of these traces, Grant (1983) calculated the reworking rate of this species as $0.4–4.6 \text{ cm}^3\text{ind}^{-1}\text{d}^{-1}$, depending on the size of the trace used. He also compared these rates to physical reworking on Debidue Flat, estimating that the *P. fulgens* population could rework at ~3.6–32.4% of the physical reworking rate based on bedform movement. Over 90% of the *P. fulgens* in this study occurred in the shallow region (<10 cm) of the sandflat dominated by tidal advection (Fig. 8). The high advective transport in the upper sediment column may provide an effective mechanism for the downward transport of diatoms to *P. fulgens* feeding traces and affect the distribution of this polychaete. The low densities ($100–600 \text{ m}^{-2}$) of *P. fulgens* in deeper portions of the sediment column (>10 cm) are unlikely to significantly contribute to the high biodiffusivities measured in this system.

The back-filled burrows observed in the tracer experiments (Fig. 1B, 3B) were consistent with the abundances, feeding styles, burrowing activities and body sizes (3–5 mm long, 1 mm wide) of the two haustoriid species identified, especially *P. caroliniensis.* These species were implicated as the primary controls on biodiffusive reworking throughout the sediment column, but most important at depths greater than 10 cm. Haustoriid amphipods were dominant or co-dominant at all time points sampled (Table 2, Fig. 8). The separation of the two species on Debidue Flat is primarily vertical, with *A. millsi* found in depths less than 8 cm and *P. caroliniensis* found primarily at depths greater than 10 cm into the sandflat (Grant, 1981a; pers. obs.). *P. caroliniensis* create angular (oblique, 45°), vertically oriented burrows while searching for favorable feeding horizons in sandy

Table 3. Summary of the values and results of amphipod population reworking and rest period (Ω) calculations. Data included amphipod abundance, individual reworking rates for haustoriid amphipods (Howard and Elders, 1970), the biodiffusivity coefficient (D_b), and the step length (δ). The reworking time for the top 25 cm can be estimated by dividing the volume of the sediment column ($cm^3 m^{-2}$) by the population reworking rate ($cm^3 m^{-2} d^{-1}$). The rest period was calculated from the relationship $\Omega = \dfrac{\delta^2}{2D_b}$ (Wheatcroft *et al.,* 1990) where δ is the step length of particle movement (here estimated to be $\frac{1}{2}$ the body length of the amphipods) and D_b is the measured biodiffusivity (Table 1B).

Experiment	Haustoriid abundance[α] (m^{-2})	Population reworking[β] ($cm^3 m^{-2} d^{-1}$)	Time to rework top 25 cm (d)[γ]	D_b $cm^2 d^{-1}$	δ low[δ] (cm)	δ high[δ] (cm)	Ω low (h)	Ω high (h)
PM 1	8645	12450	20	0.23	0.15	0.25	5	3
PM 2	11506	16560	15	0.15	0.15	0.25	7	5
PM 3	7012	10100	25	0.28	0.15	0.25	4	3

[α] Combination of densities during time period of experiment (e.g. the abundance of PM 1 is the mean densities of combined summer and fall samples encompassed by the time period of this experiment).

[β] Based on laboratory reworking rate of $1.44 \ cm^3 d^{-1}$ individual^{-1} (Howard and Elders, 1970).

[γ] Calculated from the volume of the top 25 cm ($2.5 \times 10^5 \ cm^3 m^{-2}$) and estimated population reworking rate ($cm^3 m^{-2} d^{-1}$).

[δ] Low and high estimates of step length were based on the size ranges of amphipods sampled (3–5 mm) during the experiments.

sediments (Howard and Elders, 1970; Fig. 3B). Their high burrowing rates (2.6 cm min^{-1}ind^{-1}; Howard and Elders, 1970), small body size (3–5 mm), and deep distribution on Debidue Flat (Fig. 8) fit the criteria for biodiffusive mixing. Thus, *P. caroliniensis* is the likely bioturbator in the deep portions of Debidue Flat.

The role of amphipods in biodiffusive mixing can be evaluated by comparing time scales of bioturbation using the infauna data collected and published values of reworking by haustoriid amphipods. Utilizing the laboratory reworking rate of *P. caroliniensis* (1.44 cm^{3}d^{-1} individual^{-1}; Howard and Elders, 1970), we estimated a 15–25 day period for the amphipod densities we measured to rework the 25 cm sediment column (Table 3). The maximum dispersion of the vertical tracer column ($\sim$3.5 cm) was achieved by 18 days during PM 3 (Fig. 12), consistent with an amphipod control on biodiffusion hypothesis.

A second approach is to decompose D_b into the step length (δ), the distance particles are moved, and a rest period (Ω), the elapsed time between movements (Wheatcroft *et al.,* 1990). This relationship, $D_b = \dfrac{\delta^2}{2\Omega}$, can then be used to test whether it is a reasonable hypothesis that amphipods account for a large fraction of the biodiffusion measured in Debidue Flat sediments. The step lengths for amphipods collected over this study ranged from 1.5 to 2.5 mm based on the measured body sizes (3–5 mm) and assuming that
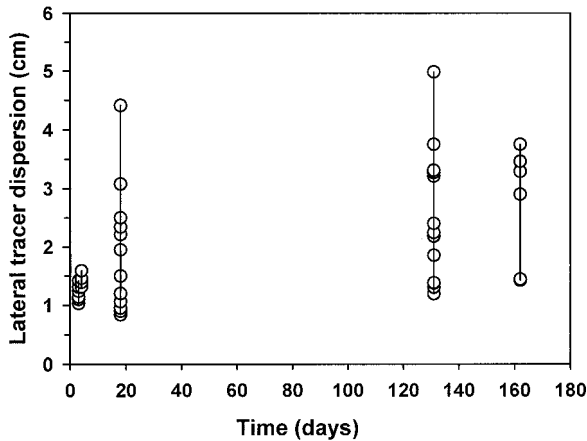
Figure 12. Plots of lateral dispersion with time in the vertically emplaced tracer experiments during PM 3.

amphipods move particles $\frac{1}{2}$ their body length during burrowing. Amphipod mixing events would have had to occur every 3–7 hours to account for the measured D_b in these experiments (Table 3). Given laboratory burrowing rates of 2.6–2.8 cm h^{-1} and reworking rates of 0.06–0.07 $cm^3 h^{-1}$ (Howard and Elders, 1970) for *Acanthohaustorius* sp. and *P. caroliniensis,* bioturbation by amphipods could account for the dispersive particle mixing observed in these experiments.

The results of the vertical tracer experiments were not consistent with the rest of the particle mixing experiments. Although dispersive mixing and amphipod burrows were observed within 18 days (Fig. 12), the magnitude of horizontal dispersion did not increase with time as was observed in the other mixing experiments. The horizontal D_b estimate for PM 3 was 5×10^{-3} cm^2 d^{-1}, less than 20% of the estimate from the horizontal tracer experiments (vertical D_b). We attribute these differences to three factors acting singly or in combination: (1) rejection of the tracer shortly after burrowing due to density differences of tracer particles relative to ambient sand; (2) altered behavior of amphipods due to abiotic nature of tracer sands; and (3) heavy disturbance of sandflat during deployment of the vertical tracer layer leading to a response by amphipod populations not comparable to the undisturbed horizontal tracer experiments. The vertical tracer technique presented here was a useful qualitative method of identifying probable bioturbators and relative time-scales of biological reworking but did not effectively quantify biodiffusive mixing in these experiments.

c. Importance of particle reworking to organic matter cycling in sands

Permeable sandflats are dynamic systems which can act like biofilters effectively filtering particulate organic material and accelerating organic matter (OM) remineralization and nutrient cycling (Huettel *et al.,* 1998; Huettel and Rusch, 2000; Huettel and

Webster, 2001). Organic matter decomposition in permeable sands is influenced by the rapid exchange of pore and overlying waters produced by advective flow within an "open" region, and an underlying "closed," diffusion-dominated region (D'Andrea *et al.,* 2002). The factors which primarily control the depth and importance of this open region include particulate organic carbon (POC) supply, sediment permeability, bottom currents, and OM lability (reviewed by Huettel and Webster, 2001). The efficiency of intertidal sands as biofilters will depend in part on physical (physical mixing, resuspension of sediments) and biological reworking processes which can help maintain the high permeabilities required for porewater exchange.

D'Andrea *et al.* (2002) demonstrated that Debidue Flat is characterized by rapid OM decomposition and exchange of solutes in the top 30 cm of the sediment column. The high permeability on Debidue Flat required for porewater exchange to occur to 30 cm is maintained by physical and biological reworking processes that prevent permanent bed stabilization and minimize clogging of pores by fine particles and organic exudates. Tidal mixing occurs to depths of 5–10 cm in less than 30 days (Figs. 1, 3), with mixing to 2–3 cm in 2 tidal cycles (Grant, 1983). This rapid mixing of surface sediments promotes high permeability of surface sediments (high porosity, winnowing of fines) and the rapid infilling of ray pit and other macrobiological structures. The high densities ($10^4\,\mathrm{m}^{-2}$; Table 2, Fig. 8) and deep burrowing depths (up to 30 cm; Figs. 3B, 8) of haustoriid amphipods, especially *P. caroliniensis,* result in high biodiffusive mixing ($0.15–0.28\ \mathrm{cm}^2\mathrm{d}^{-1}$; Table 1B) throughout the year. Bioturbation by these amphipods and their maintenance of an open sediment fabric presumably play an important role in sustaining the high permeability required to allow rapid porewater exchange to 25 cm on Debidue Flat. Thus the interplay between physical and biological mixing directly impacts the nature and magnitude of OM cycling on Debidue Flat. The quantification of particle mixing processes in permeable sands is an important step in understanding controls on permeability and coupled biogeochemical cycling in these systems.

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