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The effect of fiddler crab burrowing on sediment mixing and radionuclide profiles along a topographic gradient in a southeastern salt marsh

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ABSTRACT

Fiddler crabs are one of the principal agents of bioturbation in intertidal salt marshes. The physical, chemical, and biological properties of sediments can be modified by fiddler crab burrowing activity. This study examined the effect of fiddler crab burrowing on sediment reworking and the distributions of ^{210}Pb and ^{137}Cs in salt marsh sediments at North Inlet Estuary, South Carolina. Fiddler crab burrow density, turnover, and volume were measured along a transect from the forest to the creek bank. Burrow density ranged between 40 and 300 burrows m^{-2} with highest densities at the creek bank. Sediment reworking is related to burrow turnover, density and size. Sediment reworking rates ranged between 4.4×10^3 and 5.7×10^4 cm^3 m^{-2} y^{-1}. Excess ^{210}Pb and ^{137}Cs profiles indicated that fiddler crab burrowing mixed the top 8 to 15 cm of sediment.

Direct field measurements of burrow density, turnover, and size were used as input to a modified version of the regeneration model of Gardner *et al.* (1987) to assess the effect of fiddler crab bioturbation on ^{210}Pb profiles. The modification takes into account the filling of abandoned fiddler crab burrows from both the infilling of surface sediment and the collapse of burrow walls. Model results were in good agreement with the observed ^{210}Pb distributions in the sediments. Overall the results of this study suggest that fiddler crabs directly influence sediment composition and biogeochemical cycles in salt marsh systems.

1. Introduction

A common feature in marine sedimentary environments is the presence of biogenic structures such as the burrows and tubes of benthic infauna. Burrowing infauna can alter the structure and distribution of sediments and increase the total surface area of oxic/anoxic boundaries available for diffusive exchange (Aller, 1988; Fenchel, 1996). The process of bioturbation, associated with the burrowing and feeding activities of infaunal macrobenthos, is one of the most important ways in which benthic macrofauna modify the

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physical, chemical, and biological properties of sediments (Rhoads, 1974; Berner, 1980; Carney, 1981; Aller, 1982).

Fiddler crabs are often the dominant macrobenthic species and one of the principal agents of bioturbation in intertidal salt marshes (Allen and Curran, 1974; Crane, 1975). The three species that occur in the temperate western Atlantic; *Uca pugnax* (Smith), *U. pugilator* (Bosc), and *U. minax* (LeConte) account for the greatest macrofaunal biomass in intertidal salt marshes (Teal, 1962). Fiddler crabs burrow actively and burrow densities range from 20 to 300 burrows m^{-2} with the highest density nearest creek banks (Katz, 1980; Ringold, 1979; Montague, 1980, 1982; Bertness and Miller, 1984; Bertness, 1985; Jaramillo and Lunecke, 1988; Genoni, 1991; Mouton and Felder, 1996). In excavating burrows, fiddler crabs transport subsurface sediments to the marsh surface. This burrowing activity of fiddler crabs affects salt marsh processes through the physical mixing of sediments and by increasing the oxic/anoxic marsh surface area by 20% to 300% (Teal and Kanwisher, 1961; Katz, 1980; McCraith, 1998). Burrowing by fiddler crabs is also known to affect primary productivity, nutrient cycling, and transfer of energy within the salt marsh system (Montague *et al.,* 1981; Montague, 1982; Hoffman *et al.,* 1984; Bertness, 1985; Gardner, 1990).

Fiddler crabs dig vertical or nearly vertical burrows from the sediment surface down-ward approximately 10 to 25 cm deep (Allen and Curran, 1974; Basan and Frey, 1977). Abandoned burrows are later filled by invasion of surface material and/or the collapse of the burrow wall. Fiddler crab burrowing transports material between widely separated points within the sediment column. This type of mixing creates unidirectional particle transport in the sediment on a scale larger than diffusive processes. Mixing of sediments by fiddler crabs is, therefore, not localized at the sediment surface but occurs throughout the entire bioturbated zone. Bioturbation by fiddler crabs is one type of nondiffusive mixing referred to as nonlocal mixing or bioadvection (Rice, 1986; Boudreau and Imboden, 1987).

In previous studies quantification of sediment reworking by bioturbation was based on fitting the parameters of a mathematical model to measured radioisotope profiles (inverse modeling). Bioturbation is often represented as analogous to molecular diffusion and models for the effect of bioturbation on sediment mixing usually describe bioturbation using diffusion equations (Goldberg and Koide, 1962; Guinasso and Schink, 1975; Berner, 1980; Officer and Lynch, 1983). This kind of diffusion model has been widely applied to describe the effect of mixing due to bioturbation on radionuclide profiles in deep-sea sediments (Guinasso and Schink, 1975; Cochran and Aller, 1979; DeMaster and Cochran, 1982; Nittrouer *et al.,* 1983/1984; Smith and Schafer, 1984; DeMaster *et al.,* 1985a, b, 1991, 1994; Pope *et al.,* 1996; Clough *et al.,* 1997), shallow nearshore sediments (Benninger *et al.,* 1979; Krishnaswami *et al.,* 1980; Turekian *et al.,* 1980; Clifton *et al.,* 1995), and lake sediments (Robbins *et al.,* 1977; McCall *et al.,* 1995). Models using transport analogies other than biodiffusion have been proposed in the literature, but are not as widely applied (Fisher *et al.,* 1980; Rice, 1986; Boudreau, 1986; Boudreau and

Imboden, 1987; Gardner *et al.,* 1987; Sharma *et al.,* 1987; Wheatcroft *et al.,* 1990; Gerino *et al.,* 1994; Soetaert *et al.,* 1996).

As an alternative to the diffusion model, Gardner *et al.* (1987) treated fiddler crab bioturbation as a regeneration process in which the process of sediment mixing is considered analogous to a regeneration effect that counteracts the effects of radioactive decay. The parameters that characterize the mixing process in the regeneration model are the frequency of burrowing events and the probability of a burrow reaching a given depth (Gardner *et al.,* 1987; Sharma *et al.,* 1987). This model has some advantages over the analogies for bioturbation assumed in other models. The regeneration model describes the mechanism for bioturbation in terms, burrowing frequency (i.e., the number of new burrows excavated in a year), and depth, that can be independently measured. The regeneration model also allows for a continuous gradient in bioturbation.

In this study we have attempted to validate the regeneration model by direct field measurement of the parameters that characterize the dynamics of fiddler crab burrowing along a salt marsh topographic gradient. These field measurements are used as input parameters in the regeneration model to produce predicted radioisotope profiles (direct modeling) and then compared to measured profiles.

By mapping the location of fiddler crab burrows for one year and measuring ^{210}Pb profiles in salt marsh sediments, we were able to address the following questions: Do fiddler crab burrows show temporal/spatial persistence? Are burrows randomly distributed, evenly dispersed, or in clumps? Are all areas within the salt marsh disturbed equivalently or are some more likely to experience more sediment mixing due to higher rates of burrow formation by fiddler crabs? In addition, detailed information is presented on the distribution of the atmospherically deposited radionuclides ^{210}Pb ($t_{1/2} = 22$ y) and ^{137}Cs ($t_{1/2} = 30$ y), in salt marsh sediments in relation to fiddler crab activity.

2. Study site

This study was conducted in the Bly Creek marsh, at North Inlet Estuary, Georgetown County, South Carolina (33°17′30″ N, 79°12′30″ W) (Fig. 1). The site is bordered to the east by barrier islands, to the south by Winyah Bay, and to the west and north by a mixed oak and pine maritime forest. The Bly Creek drainage, which is interspersed by tidal creeks, oyster reefs, and mudflats; is dominated by the cord grass, *Spartina alterniflora.* Saltwort (*Salicornia virginica*), sea oxeye (*Borrichia frutescens*), and black needle rush (*Juncus roemerianus*) are the dominant types of vegetation found on higher elevations of the marsh (Gardner *et al.,* 1989).

In 1993, a transect was established from the forest to the creek bank across the Bly Creek marsh. Five sampling sites were chosen along the transect on the basis of habitat and vegetation type. Throughout this paper the five sites will be referred to as *Juncus, Borrichia, Salicornia,* short *Spartina,* and creek bank sites. The *Juncus, Borrichia,* and *Salicornia* sites comprised the high marsh sites which were only flooded by the highest spring tides. These sites were characterized by a sandy substrate and were inhabited by the sand fiddler crab (*U. pugilator*). The short *Spartina* and creek bank sites comprised the low
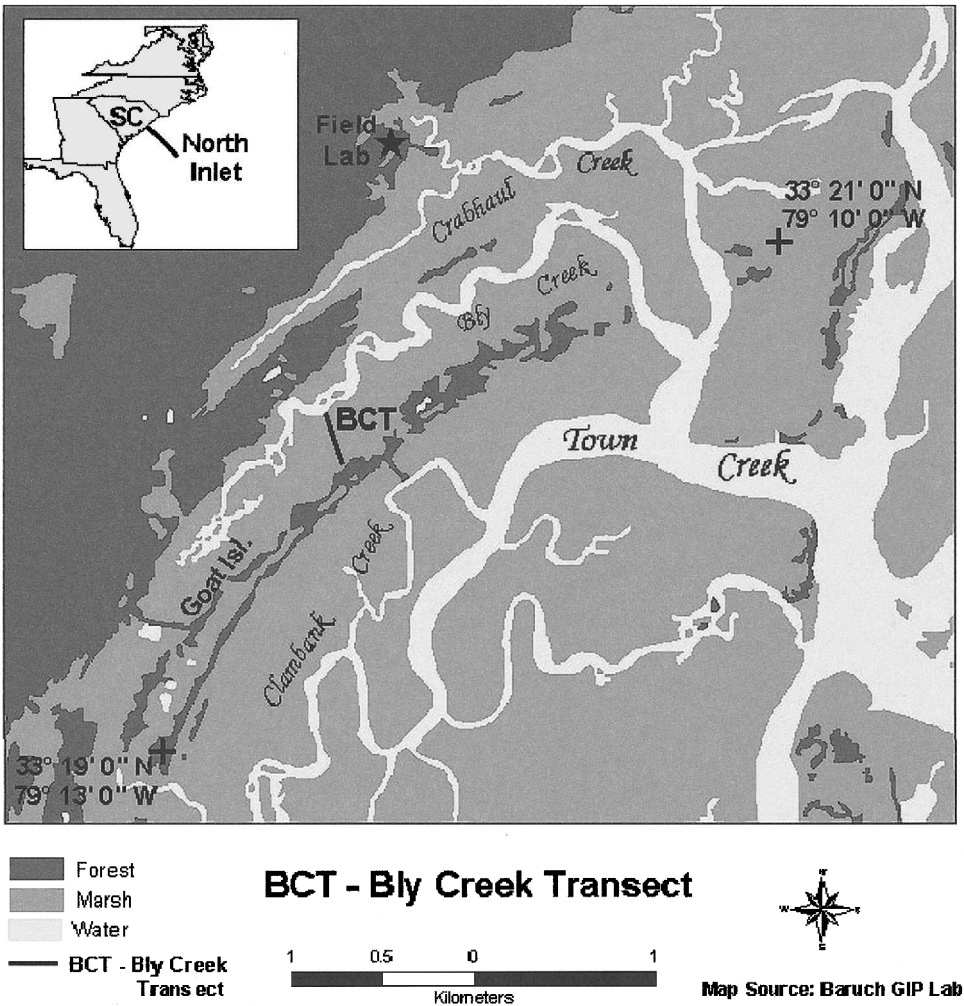
Figure 1. Map of North Inlet Estuary showing the location of the Bly Creek marsh transect. BCT =
    Bly Creek transect.

marsh sites which were regularly flooded by the tide. The short *Spartina* site was
characterized by a dense growth of short-form *S. alterniflora* growing in sandy mud. The
creek bank levee was characterized by a dense growth of tall form *S. alterniflora* growing
in silty mud. The two *Spartina* sites were inhabited by the mud fiddler crab (*U. pugnax*).

3. Methods

a. Fiddler crab burrow abundance, distribution, and new burrow formation rates

To quantify the distribution and abundance of fiddler crab burrows on the marsh, eight
permanent 0.25-m^2 quadrats were placed at approximately 5 m intervals in each of the

Juncus, Borrichia, Salicornia, short *Spartina* and creek bank sites. (Quadrats at the creek bank site were 0.06 m^2 due to the large number of burrows.) In each of the quadrats all burrows with a surface diameter > 7 mm were counted, measured with calipers to the nearest millimeter, assigned x, y coordinates, and individually marked with numbered survey flags. Quadrats were censused weekly or biweekly from June 1994 through June 1995. On each census previously identified burrows were recorded (persistent burrows), markers were removed if the burrow was no longer present (filled burrows), and newly created burrows were measured, mapped, and marked. As expected, given the presence of emergent vegetation and reports of fiddler crab acclimation to plant stems (Bertness and Miller, 1984), the small wires (2 mm in diameter $\times$ 53.5 cm long) supporting the flags (6.6 cm $\times$ 7.8 cm) used to mark burrows did not appear to affect fiddler crab burrowing or activity. The wires were pushed into the sediment so that the flags did not extend above the height of the vegetation at any of the sites with the exception of the *Salicornia* site where the plants are only 7 cm tall. Flags were placed approximately 1 to 2 cm from the burrow edge. Burrows were counted in the same quadrats at three of the sites the following year after this study was completed and the flags had been removed for one year. The numbers of burrows were similar whether flags were present or not (*t*-test: *Borrichia: df* = 7, *t* = 0.90, *P* = 0.40; short *Spartina: df* = 7, *t* = -1.36, *P* = 0.22; creek bank: *df* = 7, *t* = 0.28, *P* = 0.78).

b. Fiddler crab burrow structure

The below ground burrow structure of fiddler crab burrows was examined during the summer of 1995 by making fiberglass resin (Bondtite™) castings of a representative size range of burrows at each sampling site. Burrows were randomly chosen and filled with resin. Hardened casts were excavated by hand. Burrow diameter, maximum depth of penetration, length, and volume were determined for each burrow cast.

c. Burrow excavation pellets

Burrow excavation pellets were collected during May and June 1996 as a direct measurement of the volume of sediment turned over by fiddler crab burrowing. All pellets were removed from the 0.25 m^2 quadrats at the *Borrichia* and short *Spartina* sites immediately after the area was exposed by the receding tide. Before the rising tide flooded the site, all burrow excavation pellets within a quadrat were collected. Pellets were weighed and dried at 65°C to a constant weight.

d. Measurements of ^{210}Pb and ^{137}Cs

To determine ^{210}Pb and ^{137}Cs activities in the sediments, sediment cores were collected using a thin-walled aluminum tube 15 cm in diameter. The cutting edge of the core tube was sharpened to facilitate cutting through the root mat. Total belowground biomass (live and dead roots and rhizomes) in the top 20 cm of sediment ranged from 200 g m^{-2} at the *Juncus, Borrichia,* and *Salicornia* sites to 1250 g m^{-2} at the short *Spartina* site. Total

belowground biomass in the top 20 cm of sediment at the creek bank site was approximately 700 g m^{-2}. In October 1994, one 30-cm long core was extracted from each of the *Juncus, Borrichia, Salicornia,* and short *Spartina* sites. In order to obtain enough dry sediment for the analysis, two cores were extracted from the creek bank site. Each core was sectioned into 1-cm intervals and homogenized in the laboratory within 24 hours of collection. Sediment from equivalent depths of the creek bank cores was combined.

Water content and dry bulk density were determined on all sediment samples by weighing a known volume of wet sediment and drying it at 65°C to a constant weight. Sediments were ground to a powder with either a mortar and pestle or a soil mill. The percent weight of silt + clay was determined by wet-sieve analysis using a 45-μm mesh sieve. Aliquots were analyzed for organic carbon by the dry combustion method with a Perkins Elmer CHN analyzer. Samples were prepared for CHN analysis by dissolving sediment in phosphoric acid and then sonicating.

Sediments from each core were dried, ground, sealed in 70-cm^3 plastic petri dishes using electrical tape, and analyzed for ^{210}Pb and ^{137}Cs by non-destructive gamma ray spectrometry. Samples analyzed for ^{210}Pb and ^{226}Ra were counted directly on an intrinsic germanium detector. Samples analyzed for ^{137}Cs were counted directly on either a germanium lithium detector or an intrinsic germanium detector. ^{210}Pb and ^{137}Cs were determined from gamma emissions at 46.5 and 661.6 keV, respectively. ^{226}Ra was determined from the weighted average of its daughters ^{214}Bi and ^{214}Pb. ^{214}Bi was determined from gamma emissions at 609 keV and ^{214}Pb was determined from gamma emissions at 295 and 351.9 keV. The self-absorption factor was estimated as the transmission of a ^{210}Pb standard through the sample relative to an empty sample container (Cutshall *et al.,* 1983). Excess ^{210}Pb was determined by subtracting ^{226}Ra activity from the total ^{210}Pb activity for each sample. All sediment ^{210}Pb and ^{137}Cs data were corrected for the contribution of sea salt to sediment mass assuming porewater salinity to be 30‰. The error estimate for each radionuclide analysis (±2 σ) was calculated by propagation of errors associated with sample and background counting rates.

To determine ^{210}Pb and ^{137}Cs activity in surface sediment, samples were collected from each site in August and November 1994. Each sample consisted of the top 0.5 cm of sediment within a 0.1 m^2 quadrat. (This size quadrat allowed collection of enough sediment for analysis.) Quadrats were placed opportunistically and the surface sediment was scraped up using a metal spatula. Surface sediment samples were analyzed for organic carbon, percent weight of silt + clay, water content, ^{210}Pb, and ^{137}Cs as described above. The ^{210}Pb surface activity from the August and November samples were similar and the samples were combined to obtain a mean ^{210}Pb surface activity for each site (*t*-test: short Spartina: *df* = 6, *t* = 2.32, *P* = 0.08; creek bank: *df* = 14, *t* = 1.1, *P* = 0.30).

e. Statistical analysis

Data were analyzed using SAS statistical procedures (SAS Institute Inc., 1989). To examine the effects of site and month on fiddler crab burrow abundance, a two-way

analysis of variance was used. Only burrows >7 mm surface diameter were used in the analysis. Numbers of burrows per month were summed for each quadrat. All statistical analyses were performed using the summed data. A one-way analysis of variance was used to examine the effect of site on new burrow formation rates. To determine the effect of site on burrow diameter, depth, length, and volume; a one-way analysis of variance was performed on the burrow cast data. One of the assumptions for an analysis of variance is that the data are normally distributed. Prior to analysis of variance the data were examined for both heterogeneity of variances and normality. The burrow census data and the burrow cast data were not normally distributed, and therefore, square root transformations were used for the burrow census data and log transformations for burrow cast data.

Fiddler crab burrow survival was estimated using the lifetest procedure (SAS Institute Inc., 1989). This procedure was used to compute nonparametric estimates of the burrow survival differences among the different habitats. This analysis method includes right-censored observations (i.e., burrows that were still remaining at the termination of the study) as well as noncensored observations. This analysis determines whether two or more survival curves are random samples from the same underlying survivorship curve (Krebs, 1999).

The spatial distribution pattern of fiddler crab burrows in study quadrats was evaluated using Clark and Evans (1954) nearest-neighbor measure, R, which can range from 0 (perfect aggregation) to 2.1491 (regular hexagonal pattern). An R-value of 1.0 indicates a random distribution. The standard normal variate z was used to test the statistical significance of R. Sinclair (1985) has criticized this test for failing to account for edge effects (the nearest neighbor of an individual near an edge may be outside the quadrat), therefore, for this analysis the Donnelly (1978) correction to the Clark and Evans test statistic was used. Only quadrats with at least 7 burrows per sampling time were used in the analysis.

4. Modeling

An apparent sedimentation rate can be calculated from excess ^{210}Pb profiles. If one is willing to assume that the rate of accumulation of sediment and the input of excess ^{210}Pb have been constant, and the deposit has been undisturbed, then the apparent steady-state sedimentation rate can be calculated from the relationship:

$$\frac{dA}{dz} = \frac{-\lambda A}{S} \tag{1}$$

where A is excess ^{210}Pb activity (dpm g^{-1}), λ is the decay constant of ^{210}Pb (0.03114 y^{-1}), S is the sedimentation rate (cm y^{-1}), and z is depth in the sediment (cm). The sedimentation rate (S) is proportional to the slope of the plot of log excess ^{210}Pb activity with depth (McCaffery and Thomson, 1980; Bricker-Urso *et al.,* 1989). Because fiddler crab bioturbation disturbs the sediments in our study, the resulting

,sedimentation rates may overestimate the true sedimentation rate (Benninger *et al.,* 1979; Nittrouer *et al.,* 1983/1984); and therefore, Eq. (1) requires modification. The models presented below add terms to account for biological mixing.

The dominant processes affecting the distribution of ^{210}Pb in a sediment column are physical and biological mixing, sediment accumulation, and radioactive decay. Fiddler crab burrowing may result in the replacement of sediment particles at depth by surface material. To the extent that this is true, fiddler crab burrowing does not meet the requirements of random and local mixing inherent in the diffusion model. The regeneration model assumes that fiddler crab bioturbation is analogous to a regeneration reaction that counteracts the effects of radioactive decay (Gardner *et al.,* 1987; Sharma *et al.,* 1987). If constant input concentration, bulk density, and porosity are assumed, the steady-state equation that describes the processes of decay, sedimentation, and fiddler crab bioturbation is as follows:

$$\frac{d^{210}\text{Pb}}{dz} = \frac{-\lambda^{210}\text{Pb}}{S} - \frac{K_B(^{210}\text{Pb})e^{(-z/U_B)}}{S} + \frac{K_B(^{210}\text{Pb}_0)e^{(-z/U_B)}}{S} \tag{2}$$

where z is depth (cm) in the sediment, S is the sedimentation rate (cm y^{-1}), λ is the decay constant of [210]Pb (0.03114 y^{-1}), $^{210}\text{Pb}_0$ is the surface activity of excess [210]Pb (dpm g^{-1}), ^{210}Pb is the activity of excess ^{210}Pb at depth z (dpm g^{-1}), K_B is the burrowing frequency (y^{-1}), and U_B is the mean burrow depth (cm). The exponential function, $e^{(-z/U_B)}$, is the probability of a burrow reaching or exceeding depth z (Gardner *et al.,* 1987; Sharma *et al.,* 1987). The first term on the right-hand side of Eq. (2) describes the steady-state decay of ^{210}Pb as in Eq. (1). The second term in Eq. (2) describes removal of ^{210}Pb by fiddler crab burrowing as a function of the burrowing frequency (K_B) and the probability of a burrow reaching or exceeding depth z. The third term in Eq. (2) describes replacement of the sediment from depth (^{210}Pb) with surface sediment ([210]Pb$_0$) as a function of burrowing frequency (K_B) and the probability of a burrow reaching or exceeding depth z.

The regeneration model (Eq. 2) fits the case where all filling of burrows results from in-filling with surficial material with no collapse of the burrow wall. As will be shown in the discussion below, Eq. (2) does not provide a good fit to the observed ^{210}Pb profiles using direct field measurements of burrowing frequency (K_B), burrow depth (U_B), and ^{210}Pb surface activity. This discrepancy may be due to the fact that fiddler crabs dig burrows in soft sediments so that filling of abandoned burrows probably results from both infilling of surface sediment and the collapse of burrow walls. Mixing of burrow wall sediment with surface sediment would decrease the ^{210}Pb activity at depth compared to the case where only surface sediment fills the burrows. To account for this effect, we modified the original regeneration model (Eq. 2) by expanding the third term in the model to take into account the lateral filling of burrows through burrow wall collapse:

$$\frac{d^{210}\mathrm{Pb}}{dz} = \frac{-\lambda^{210}\mathrm{Pb}}{S} - \frac{K_B{}^{210}\mathrm{Pb}e^{(-z/U_B)}}{S}$$

$$+ \frac{K_B[^{210}\mathrm{Pb}_0(1 - z/(z + U_B)) + {}^{210}\mathrm{Pb}\ z/(z + U_B)]e^{(-z/U_B)}}{S} \tag{3}$$

In this equation the term $^{210}\mathrm{Pb}_0(1 - z/(z + U_B))$ describes infilling of burrows with surface sediment and the term $^{210}\mathrm{Pb}\ z/(z + U_B)$ describes the replacement of excavated sediment with sediment from the collapse of burrow walls. For the term $^{210}\mathrm{Pb}_0(1 - z/(z + U_B))$, when $z = U_B$ then one-half of the replacement $^{210}\mathrm{Pb}$ comes from the infilling with surface sediment while the remaining half comes from the collapse of burrow walls. For $z < U_B$, replacement $^{210}\mathrm{Pb}$ is dominated by surficial sediment; whereas for $z > U_B$, replacement is dominated by collapse of burrow walls.

Data were collected from field measurements so that each model parameter at each site along the Bly Creek marsh transect could be calculated directly. Burrowing frequency (K_B) has been calculated from fiddler crab new burrow formation rates. Mean burrow depth (U_B) was determined from measurements of casts made of fiddler crab burrows. $^{210}\mathrm{Pb}$ surface activity $(^{210}\mathrm{Pb}_0)$ was measured in surface sediment samples. The sedimentation rate (S) is problematic, as it was not measured directly. The sedimentation rate used in the model simulations is a mean sedimentation rate calculated from previously reported sedimentation rates for North Inlet Estuary ($n = 8$, range: 0.14 to 0.49) cm y^{-1}) (Sharma *et al.*, 1987; Vogel *et al.*, 1996). These earlier profiles were obtained from mid marsh areas that had low fiddler crab population densities. The mean sedimentation rate 0.28 ± 0.11 cm y^{-1}, is in good agreement with the historic rate of sea level rise (0.3 cm y^{-1}), determined from long-term tide gauge records at Charleston, South Carolina (Kjerfve *et al.*, 1978). In the discussion below we examine the sensitivity of the model to this parameter (S). The symbolic algebra (modeling) program, Maple V (Monagan *et al.*, 1996), was used to simulate $^{210}\mathrm{Pb}$ profiles using Eqs. (2) and (3). Model generated profiles were compared with observed $^{210}\mathrm{Pb}$ profiles from salt marsh sediment cores collected at each site along the Bly Creek marsh transect.

5. Results

a. Fiddler crab burrow abundance and distribution

Fiddler crab burrows were categorized as newly created, persistent, filled and total (new + persistent). To compare mean burrow abundances across time and space, a two way ANOVA was performed for the four burrow categories. The two-way interaction (month $\times$ site) was significant for each burrow category (newly created: $df = 47$, $F = 11.90$, $P < 0.0001$; persistent: $df = 47$, $F = 19.00$, $P < 0.0001$; filled: $df = 47$, $F = 21.33$, $P < 0.0001$; total: $df = 47$, $F = 19.51$, $P < 0.0001$), indicating that burrow abundance varies both spatially and temporally. Burrow abundances for all categories followed a similar temporal pattern with highest burrow abundance in spring and summer
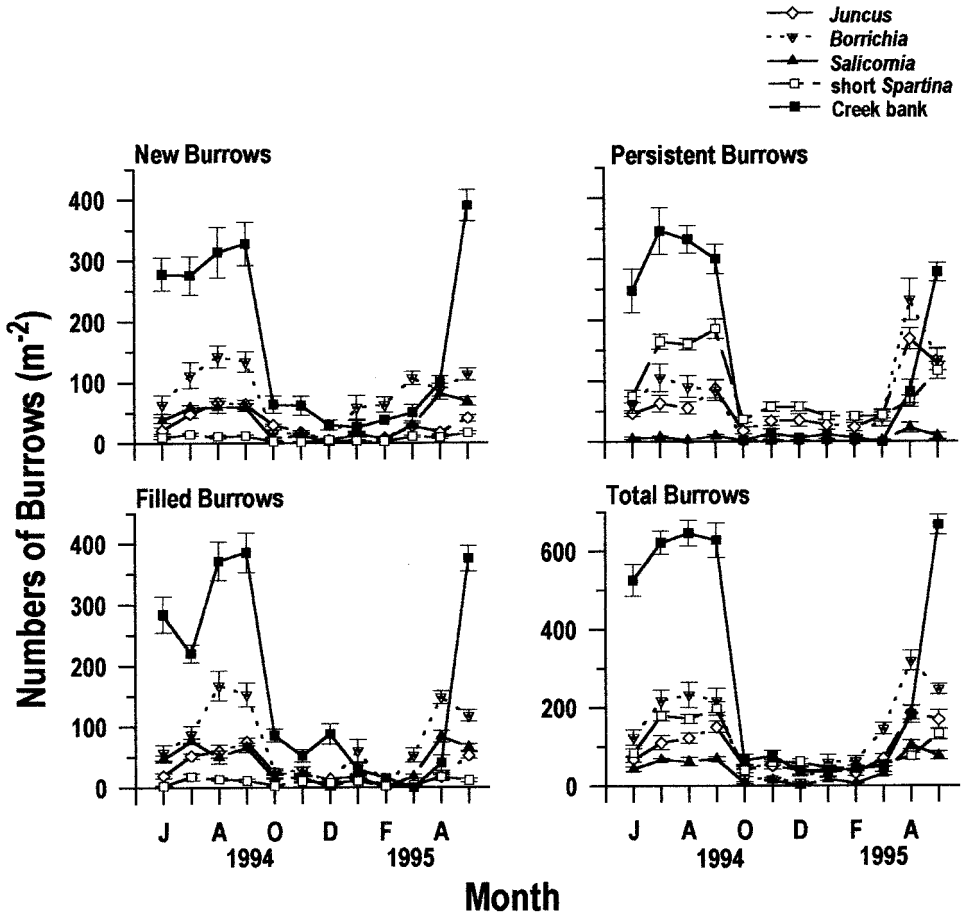
Figure 2. Numbers of new, persistent, filled, and total fiddler crab burrows (mean ± standard error of the mean) for sites on the Bly Creek marsh transect.

and lowest burrow abundances in fall and winter (Fig. 2). Burrow abundances in all categories were highest at the creek bank site (Table 1A). The *Borrichia* site had the second highest abundance of newly created, filled, and total burrows, but not persistent burrows. The short *Spartina* site had the lowest abundance of newly created and filled burrows and the highest numbers of persistent burrows. The *Salicornia* site had the lowest abundance of persistent and total burrows (Table 1A).

Clark and Evans' nearest neighbor analysis indicated that fiddler crab burrows are randomly distributed throughout the year at all sites along the transect (Fig. 3). Fiddler crab burrows were randomly distributed in at least 75% of the quadrats at all sites, with the exception of the short *Spartina* site where burrows were randomly distributed in 50% or more of the quadrats (Fig. 3). Nearest neighbor distances ranged from 5 to 12 cm (Table 1B). Burrows were closest together at the creek bank and farthest apart at the short *Spartina* site.
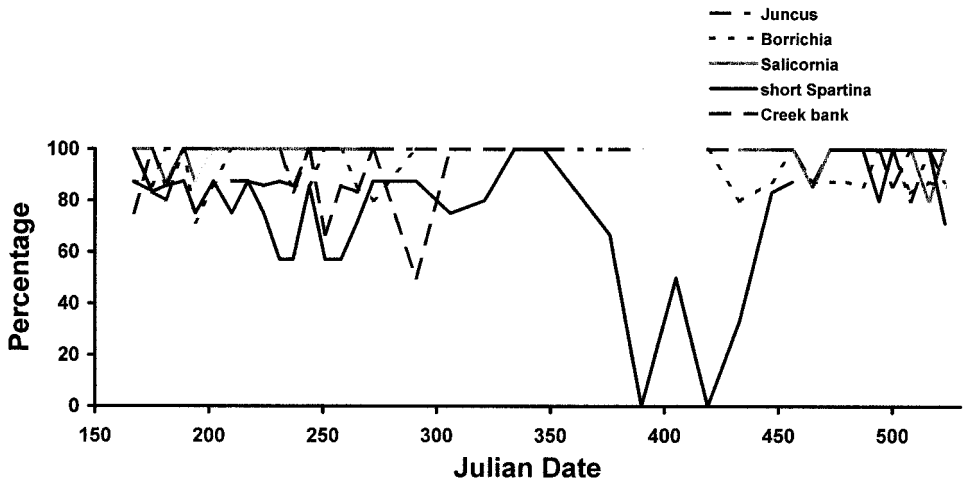
Figure 3. Percentage of quadrats with random distribution of burrows for sites on the Bly Creek marsh transect.

Table 1. Mean ($\pm$ standard error of the mean) numbers of new, persistent, filled, and total burrows (A) and new burrow formation rate, fiddler crab burrow survival estimates, and nearest neighbor distances (B) for each site along the Bly Creek marsh transect. Sites arranged from highest tidal site (*Juncus*) to lowest (creek bank). Means with the same letter are not significantly different ($\alpha = 0.01$).

A. Site	Numbers of new burrows (m^{-2})	Numbers of persistent burrows (m^{-2})	Numbers of filled burrows (m^{-2})	Numbers of total burrows (m^{-2})
Juncus	29 ± 2	57 ± 5	29 ± 2	86 ± 6
Borrichia	72 ± 6	59 ± 8	73 ± 6	132 ± 11
Salicornia	34 ± 3	5 ± 1	36 ± 3	39 ± 4
short *Spartina*	9 ± 1	82 ± 6	9 ± 1	91 ± 6
Creek bank	168 ± 15	140 ± 15	166 ± 16	308 ± 28

B. Site	New burrow formation rate (burrows $m^{-2} y^{-1}$)	Burrow survival estimate (days)	Nearest neighbor distances (cm)
Juncus	374 ± 22^c	29 ± 1	9 ± 0.2
Borrichia	941 ± 84^b	16 ± 0.3	8 ± 0.1
Salicornia	443 ± 26^c	9 ± 0.2	10 ± 0.2
short *Spartina*	116 ± 9^c	96 ± 6	12 ± 0.2
Creek bank	2012 ± 117^a	17 ± 0.4	5 ± 0.1

b. New burrow formation rates

A one-way ANOVA was performed to examine the effect of site within the salt marsh on rates of new burrow formation (number of newly created burrows $m^{-2} y^{-1}$). New burrow formation rates were significantly different among sites ($df = 39$, $F_{4,35} = 128.36$, $P < 0.0001$). New burrow formation rates were greatest at the creek bank site and lowest at the short *Spartina* site (Table 1B). Tukey's studentized range test ($\alpha = 0.01$) indicated that new burrow formation rates were significantly higher at the creek bank site than at the other sites (Table 1B), and that new burrow formation rates at the *Borrichia* site were significantly higher than at the *Juncus, Salicornia,* and short *Spartina* sites (Table 1B).

c. Burrow survival

Burrow survival estimates, a measure of burrow persistence, ranged from 9 to 96 days (Table 1B). The *Salicornia* site had the shortest burrow survival estimate and the short *Spartina* site had the longest burrow survival estimate. Burrow survival at the *Borrichia* and creek bank sites was the same. The *Juncus* site had a longer burrow survival than the *Salicornia, Borrichia,* and creek bank sites (Table 1B). The plot of the proportion of burrows surviving against time indicates that the sites differed primarily at longer survival times (Fig. 4). The lifetest procedure compares the equality of survival functions across sites using the log-rank, Wilcoxon and likelihood ratio tests. All three tests indicate strong evidence of a significant difference among survival curves for the five salt marsh sites (Log Rank: $df = 4$, $\chi^2 = 1076$, $P < 0.0001$; Wilcoxon: $df = 4$, $\chi^2 = 673$, $P < 0.0001$; Log Likelihood: $df = 4$, $\chi^2 = 1703$, $P < 0.0001$).

d. Fiddler crab burrow casts

Burrow morphology differed among sites. Burrows of *U. pugilator* (*Juncus, Borrichia,* and *Salicornia* sites) were either J- or L-shaped. *U. pugnax* burrows at the short *Spartina* site were straight or slightly J-shaped. In contrast, *U. pugnax* burrows at the creek bank site were more complex with one or more branches off the main burrow shaft. Burrows at this site frequently interconnected with other *U. pugnax* burrows or with mud crab (*Eurytium limosum*) burrows.

Measurements of fiddler crab burrow casts indicated variation in burrow size among salt marsh sites (Table 2). Burrow diameter, length and the depth of burrow penetration into the substrate differed significantly among sites (one-way ANOVA diameter: $df = 4, 70$; $F = 7.03$, $P < 0.0001$; length: $df = 4, 72$; $F = 8.54$; $P < 0.0001$; depth: $df = 4, 72$; $F = 8.75$; $P < 0.0001$). Tukey's studentized range test ($\alpha = 0.05$) indicated that burrows at the creek bank and *Salicornia* sites had significantly smaller diameters than burrows from the other sites (Table 2). Burrows from the *Juncus* site were significantly longer and deeper than burrows from the other sites (Table 2). Burrow length and depth at the *Borrichia, Salicornia,* short *Spartina,* and creek bank sites were not significantly different from one another (Table 2).

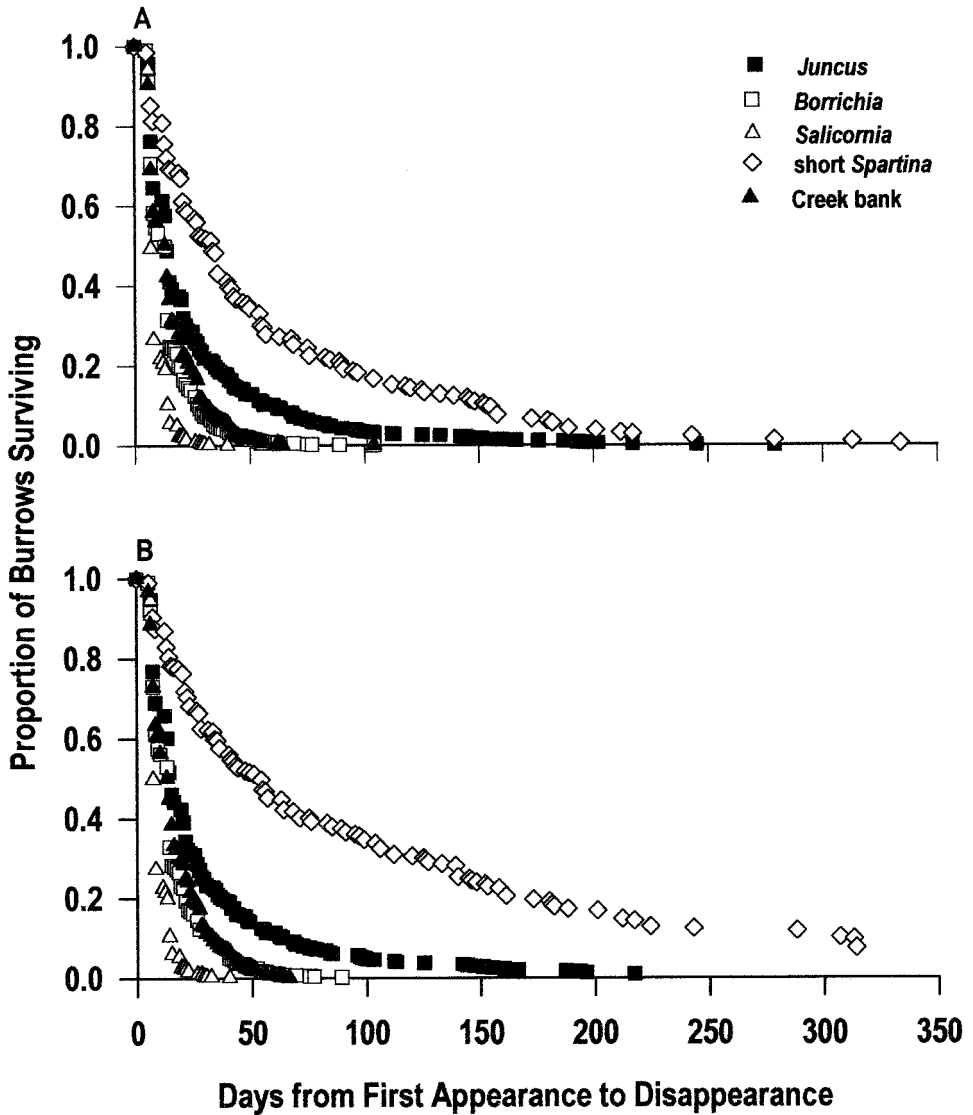Burrow volume differed significantly among sites (one-way ANOVA $df = 4, 70$; $F =$

Figure 4. Fiddler crab burrow survival estimates (days) from direct field measurements (A) and from the life test statistical model (B) for sites on the Bly Creek marsh transect.

8.85; $P < 0.0001$). Burrow volume was significantly larger at the *Juncus* site than at the other sites (Tukey's studentized range test, $\alpha = 0.05$) (Table 2). Burrow volume at the *Juncus* site was twice as large as burrow volume at the *Borrichia* and short *Spartina* sites. Burrow volume at the *Juncus* site was three times larger than burrow volume at the creek bank site and four times larger than at the *Salicornia* site (Table 2).

Table 2. Mean ($\pm$ standard error of the mean) burrow diameter, burrow length, burrow depth, and burrow volume from burrow casts collected at each site on the Bly Creek marsh transect. Means with the same letter are not significantly different at $\alpha = 0.05$.

Site	n	Diameter (cm)	Length (cm)	Depth (cm)	Volume (cm^3)
Juncus	13	1.9 $\pm$ 0.1[a]	28 $\pm$ 4[a]	21 $\pm$ 3[a]	81 $\pm$ 14[a]
Borrichia	12	1.8 $\pm$ 0.1[a]	12 $\pm$ 2[b]	9 $\pm$ 2[b]	35 $\pm$ 5[b]
Salicornia	19	1.3 $\pm$ 0.0[b]	12 $\pm$ 1[b]	8 $\pm$ 1[b]	18 $\pm$ 2[b]
short *Spartina*	15	1.9 $\pm$ 0.1[a]	11 $\pm$ 1[b]	10 $\pm$ 1[b]	38 $\pm$ 7[b]
Creek bank	18	1.4 $\pm$ 0.1[b]	12 $\pm$ 1[b]	8 $\pm$ 1[b]	28 $\pm$ 8[b]

e. Sediment reworking rates

Sediment reworking rates were calculated by multiplying new burrow formation rates by burrow volume (Table 3A). Sediment reworking rates ranged between 4.4×10^3 cm^3 m^{-2} y^{-1} and 5.7×10^4 cm^3 m^{-2} y^{-1}. The highest sediment reworking rate was at the creek bank site and the lowest at the short *Spartina* site. The sediment reworking rate at the creek bank site was greater than that at the *Juncus* and *Borrichia* sites by a factor of two and greater than that at the *Salicornia* and short *Spartina* sites by factors of seven and thirteen, respectively (Table 3A).

Sediment reworking rates measured from burrow excavation pellets ranged from 2100

Table 3. Mean ($\pm$ standard error of the mean) burrow turnover rate, burrow volume and sediment reworking rates for each site on the Bly Creek marsh transect (A); and mean ($\pm$ standard error of the mean) sediment reworking rates from burrow casts and sediment reworking rates from burrow excavation pellets at the *Borrichia* and short *Spartina* sites (B).

A. Site	New burrow formation rate (burrows m^{-2} y^{-1})	Burrow volume (cm^3)	Sediment reworking rate (cm^3 m^{-2} y^{-1})
Juncus	374 $\pm$ 22	81 $\pm$ 14	30366 $\pm$ 1810
Borrichia	941 $\pm$ 84	35 $\pm$ 5	33227 $\pm$ 2985
Salicornia	443 $\pm$ 26	18 $\pm$ 2	8178 $\pm$ 479
short *Spartina*	116 $\pm$ 9	38 $\pm$ 7	4405 $\pm$ 354
Creek bank	2012 $\pm$ 117	28 $\pm$ 8	57040 $\pm$ 3312

B. Site	Month	Sediment reworking rate (cm^3 m^{-2} month^{-1})	
		Burrow casts	Burrow pellets
Borrichia	May	3990 $\pm$ 344	3850
	June	2259 $\pm$ 542	2090
short *Spartina*	May	534 $\pm$ 91	140
	June	381 $\pm$ 112	690

Table 4. Mean burrow depth ($\pm$ standard deviation) and percent of sediment reworked annually for each site along the Bly Creek marsh transect.

Site	Burrow depth (cm)	Sediment reworked (%)
Juncus	21 ± 12	9
Borrichia	9 ± 6	22
Salicornia	8 ± 4	7
short *Spartina*	10 ± 3	3
Creek bank	8 ± 4	48

to 3800 $cm^3 m^{-2} month^{-1}$ at the *Borrichia* site and from 140 to 690 $cm^3 m^{-2} month^{-1}$ at the short *Spartina* site (Table 3B). Sediment reworking rates directly measured from the burrow excavation pellets were similar to the sediment reworking rates calculated from new burrow formation rates and burrow volumes (Table 3B).

Due to the variation in burrow depth among sites, a direct comparison of volumetric sediment reworking rates may be misleading, therefore, the approximate amount of sediment reworked yearly has been expressed as a percent. Assuming that fiddler crab burrowing was restricted to the mean burrow depth $\pm$ one standard deviation (Table 4), the approximate percent of sediment turned over yearly can be calculated as follows:

$$\frac{\text{sediment reworked } (cm^3 \ m^{-2})}{\text{burrow depth (cm)} \times 10^4 \ cm^2 \ m^{-2}} \times 100 \tag{4}$$

The percent of sediment reworked annually is highest at the creek bank and *Borrichia* sites and lowest at the short *Spartina* site (Table 4).

f. Sediment properties

Percent silt + clay varied from 4 to 95% among sites (Fig. 5). Percent silt + clay was low in the predominantly sandy sediments found at the *Juncus, Borrichia,* and *Salicornia* sites. Percent silt + clay at the short *Spartina* site gradually declined with depth. Sediments from this site became more sandy with depth. Overall, percent silt + clay was higher at the short *Spartina* site compared to the *Juncus, Borrichia,* and *Salicornia* sites. Sediment from the creek bank site had the highest percent silt + clay of all the sites. Percent silt + clay was relatively constant with depth at the creek bank site (Fig. 5).

Organic carbon content varied from 0.3 to 6.6% among sites (Fig. 6). The mean organic carbon content of sediments from the *Juncus, Borrichia,* and *Salicornia* sites was lower than the organic carbon content of sediments from the short *Spartina* and creek bank sites by a factor of 2 to 4 and 5 to 8, respectively. Organic carbon content at the short *Spartina* site decreased gradually with depth. Sediments from the creek bank site had the highest organic carbon content (Fig. 6).

Sediment water content varied among sites from 18 to 71% (Table 5). Water content of sediments from the *Juncus, Borrichia, Salicornia,* and creek bank sites was relatively
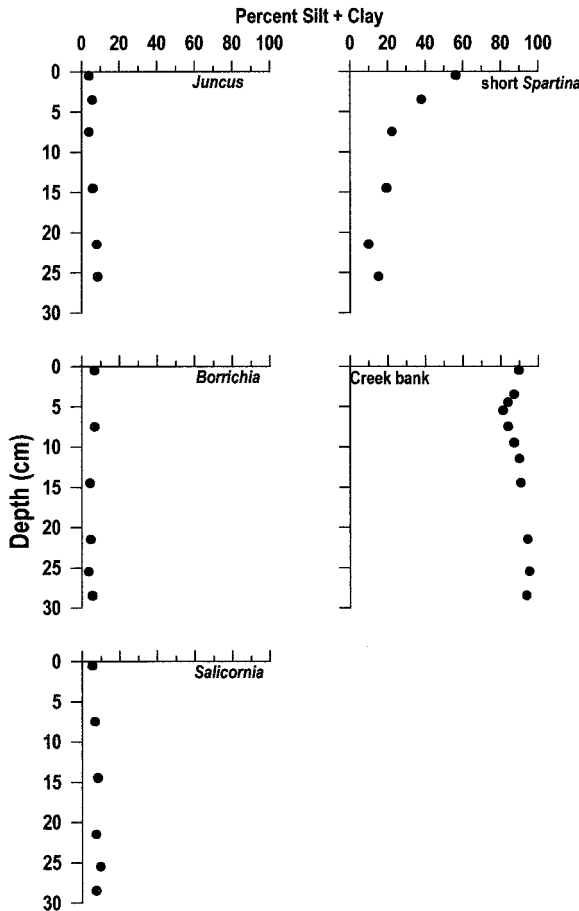
Figure 5. Depth profiles of percent silt + clay for each site on the Bly Creek marsh transect.

constant with depth (Table 5). Water content at the short *Spartina* site decreased with depth as the sediment became more sandy (Table 5).

Porosity and bulk density were relatively constant with depth at the *Juncus, Borrichia, Salicornia,* and creek bank sites (Table 5). Porosity decreased with depth at the short *Spartina* site, whereas bulk density increased with depth as the underlying sandy substrate was reached (Table 5).

g. ^{210}Pb

Mean excess ^{210}Pb activity in surface sediment samples ranged from 0.54 to 11.69 dpm g^{-1} (Table 6). Surface sediment from the creek bank site had the highest excess ^{210}Pb activity. Excess ^{210}Pb activity in surface sediments decreased with increased distance from the creek bank (Table 6). There was a significant relationship between excess ^{210}Pb activity
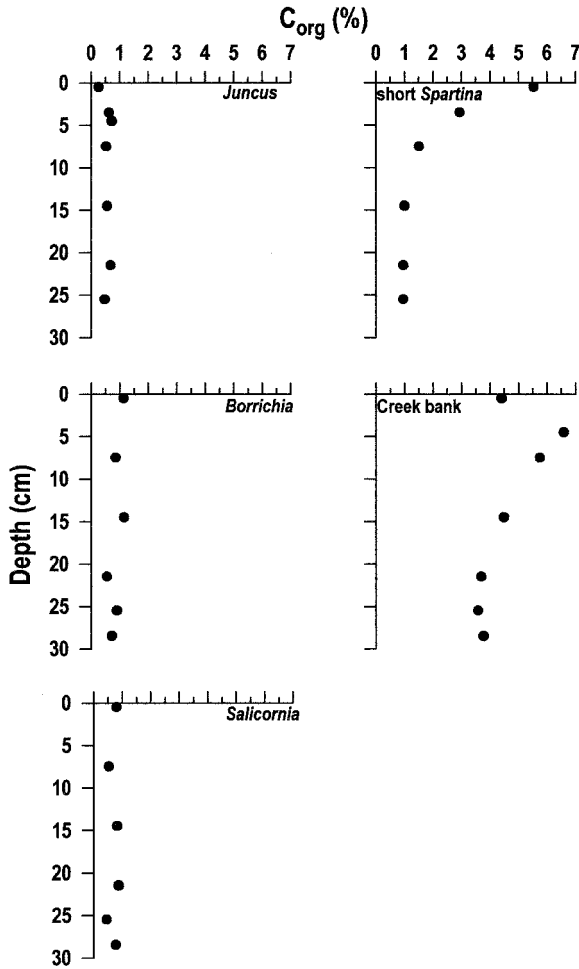
Figure 6. Depth profiles of percent organic carbon for each site on the Bly Creek marsh transect.

and the silt + clay content of the surface sediments (Fig. 7A). Excess ^{210}Pb activity was positively correlated with silt + clay content of the sediments. Ninety-four percent of the variability in excess ^{210}Pb activity at all the sites can be explained by the silt + clay content of the sediment. Sixty percent of the variability in excess ^{210}Pb activity at the short *Spartina* and creek bank sites can be explained by the silt + clay content of the sediment (regression: $y = 0.06x + 5.95$, $R^2 = 0.60$, $P < 0.0001$). If all sites are considered excess ^{210}Pb activity was significantly correlated with organic carbon content of the surface sediments (Fig. 7B). However, more than 70% of the samples were only from the short *Spartina* and creek bank sites. Excess ^{210}Pb activity was not significantly correlated with organic carbon content of the surface sediments at the short *Spartina* and creek bank sites (regression: $n = 12$, $P = 0.19$).

Table 5. Excess ^{210}Pb, silt + clay, organic carbon, water content, porosity, and bulk density for Bly Creek marsh sediment cores.

Site	Depth (cm)	^{210}Pb$_{exc}$ (dpm g^{-1})*	Silt + clay (%)	C_{org} (%)	% Water (g H$_2$O g^{-1} wet sediment)	Porosity (cm^3 water cm^{-3} wet sediment)	Bulk density (g dry cm^{-3})
Juncus	0–1	0.41 ± 0.05	4	0.27	21	0.40	1.48
	7–8	0.45 ± 0.06	4	0.53	23	0.52	1.50
	14–15	0.29 ± 0.06	6	0.56	22	0.46	1.36
	21–22	—†	8	0.68	22	0.36	1.11
	25–26	0.27 ± 0.05	8	0.48	22	0.41	1.23
Borrichia	0–1	0.55 ± 0.08	7	1.14	26	0.28	0.82
	7–8	0.60 ± 0.06	7	0.86	29	0.44	1.10
	14–15	0.48 ± 0.07	4	1.15	28	0.38	0.95
	21–22	0.41 ± 0.06	5	0.55	28	0.44	1.12
	25–26	0.14 ± 0.04	4	0.90	28	0.47	1.17
	28–29	0.26 ± 0.05	6	0.73	28	0.40	1.04
Salicornia	0–1	0.50 ± 0.08	5	0.80	29	0.27	0.65
	7–8	0.73	7	0.53	30	0.44	1.00
	14–15	0.32 ± 0.06	8	0.82	28	0.51	1.27
	21–22	0.25 ± 0.06	7	0.87	28	0.53	1.37
	25–26	0.27 ± 0.06	10	0.45	27	0.47	1.24
	28–29	0.25 ± 0.05	7	0.77	29	0.49	1.18
short *Spartina*	0–1	6.30 ± 0.40	56	5.54	61	0.52	0.33
	3–4	—	38	2.94	61	0.73	0.47
	7–8	1.23 ± 0.10	22	1.51	48	0.76	0.82
	14–15	0.23 ± 0.09	19	1.00	43	0.71	0.92
	21–22	0.13 ± 0.04	10	0.96	29	0.63	1.52
	25–26	0.23 ± 0.05	15	0.95	29	0.62	1.51
Creek bank	0–1	10.96 ± 0.62	90	4.41	67	0.80	0.46
	3–4	10.17	87	—	70	0.85	0.42
	4–5	8.69	84	6.59	71	0.86	0.34
	5–6	7.60	81	—	72	—	0.41
	7–8	5.64 ± 0.41	84	5.75	70	0.90	0.39
	9–10	5.44	87	—	69	0.92	0.43
	11–12	4.44	90	—	69	0.93	0.41
	14–15	4.31 ± 0.20	91	4.49	69	0.94	0.43
	21–22	2.49 ± 0.16	94	3.69	67	0.91	0.45
	25–26	2.31 ± 0.26	95	3.58	66	—	0.53
	27–28	2.41 ± 0.15	94	3.77	66	0.85	0.58

*Errors are from counting statistics. See text for explanation.
†— indicates missing data.

Table 6. Mean ($\pm$ standard error of the mean) excess ^{210}Pb, ^{137}Cs, silt + clay, organic carbon, and water content of surface sediment samples for each site on the Bly Creek marsh transect.

Site	^{210}Pb$_{exc}$ (dpm g^{-1})	^{137}Cs (dpm g^{-1})	Silt + Clay (%)	C$_{org}$ (%)	% Water (g H$_2$O g^{-1} wet sediment, as %)
Juncus	0.54 $\pm$ 0.06	0.06 $\pm$ 0.04	4.4 $\pm$ 1.5	0.28 $\pm$ 0.04	15 $\pm$ 0.7
(*n*)	(3)	(2)	(2)	(2)	(2)
Borrichia	0.60 $\pm$ 0.04	0.10 $\pm$ 0.02	9.8 $\pm$ 0.3	0.70 $\pm$ 0.28	23 $\pm$ 1.3
(*n*)	(4)	(4)	(4)	(2)	(8)
Salicornia	0.51 $\pm$ 0.12	0.04 $\pm$ 0.04	4.4 $\pm$ 0.6	0.40 $\pm$ 0.08	18 $\pm$ 0.8
(*n*)	(4)	(2)	(4)	(2)	(8)
short *Spartina*	10.03 $\pm$ 0.44	0.36 $\pm$ 0.04	55.0 $\pm$ 3.0	5.5 $\pm$ 0.04	70 $\pm$ 2.5
(*n*)	(8)	(8)	(8)	(2)	(8)
Creek bank	11.69 $\pm$ 0.20	0.41 $\pm$ 0.06	89.9 $\pm$ 0.7	4.5 $\pm$ 0.08	67 $\pm$ 0.5
(*n*)	(16)	(15)	(16)	(10)	(16)

Excess ^{210}Pb activity was very low in core samples from the *Juncus, Borrichia,* and *Salicornia* sites (Fig. 8). Excess ^{210}Pb activity at the short *Spartina* and creek bank sites decreased exponentially with depth reaching constant values at approximately 14 to 15 cm and 21 to 22 cm depth, respectively (Fig. 8). In contrast to the creek bank site, excess ^{210}Pb activity approached supported levels below 15 cm depth at the short *Spartina* site indicating that ^{210}Pb is almost in secular equilibrium with ^{226}Ra at depth in the sediment (Gascoyne, 1992).

Due to the differences in sediment composition among the sites and the resulting dilution of ^{210}Pb activity in sandy sediments, excess ^{210}Pb activity was normalized to weight percent silt + clay (Fig. 9). Normalization of ^{210}Pb activity to weight percent silt + clay was chosen because of the significant correlation of excess ^{210}Pb activity and silt + clay content in surface
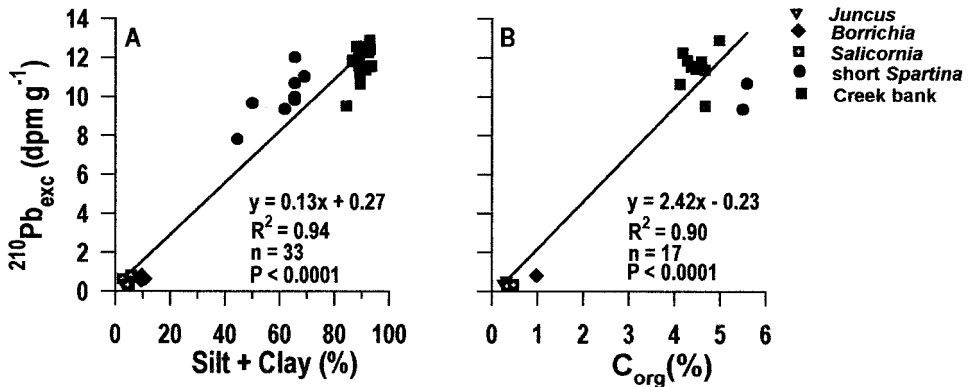

Figure 7. The relationship between ^{210}Pb activity and weight percent silt + clay (A) and organic carbon content (B) in surface sediments from all sites on the Bly Creek marsh transect.
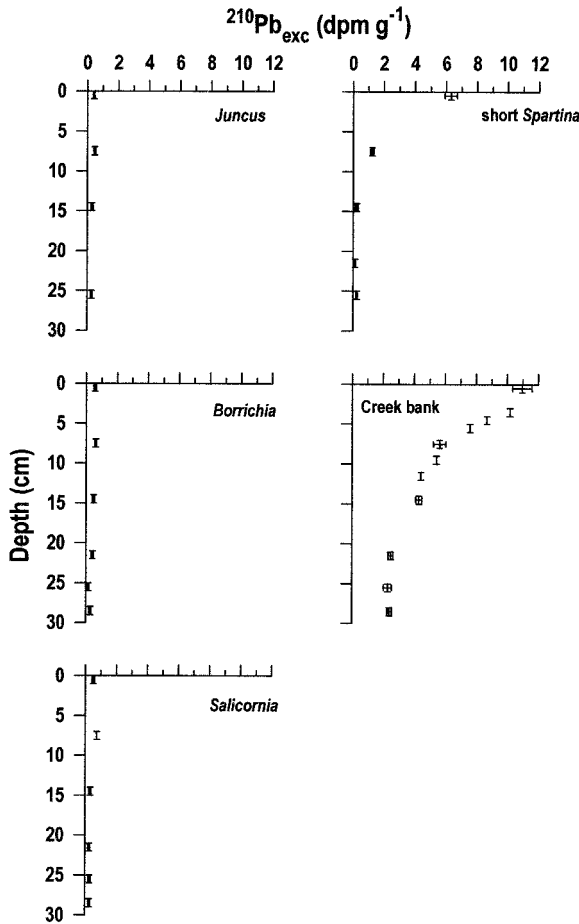
Figure 8. Depth profiles of excess ^{210}Pb activities (dpm g^{-1}) for each site on the Bly Creek marsh transect. Errors are from counting statistics.

sediments (Fig. 7A, B). Excess ^{210}Pb activity of the silt + clay fraction was uniform in the top 7–8 cm of the cores from the *Juncus* and *Salicornia* sites (Fig. 9). Excess ^{210}Pb activity of the silt + clay fraction at the *Borrichia* site was nearly uniform in the upper 21 cm of sediment. The distributions of excess ^{210}Pb for the silt + clay fraction at the short *Spartina* and creek bank sites exhibited exponential decay with depth (Fig. 9).

The apparent sedimentation rates (*S*) calculated from the excess ^{210}Pb activity-depth profiles (Eq. 1) for the short *Spartina* and creek bank sites were 0.3 and 0.5 cm y^{-1}, respectively.

h. ^{137}Cs

Mean ^{137}Cs activity in surface sediment samples ranged from 0.04 to 0.41 dpm g^{-1} (Table 6). Surface sediment from the creek bank site had the highest ^{137}Cs activity. ^{137}Cs
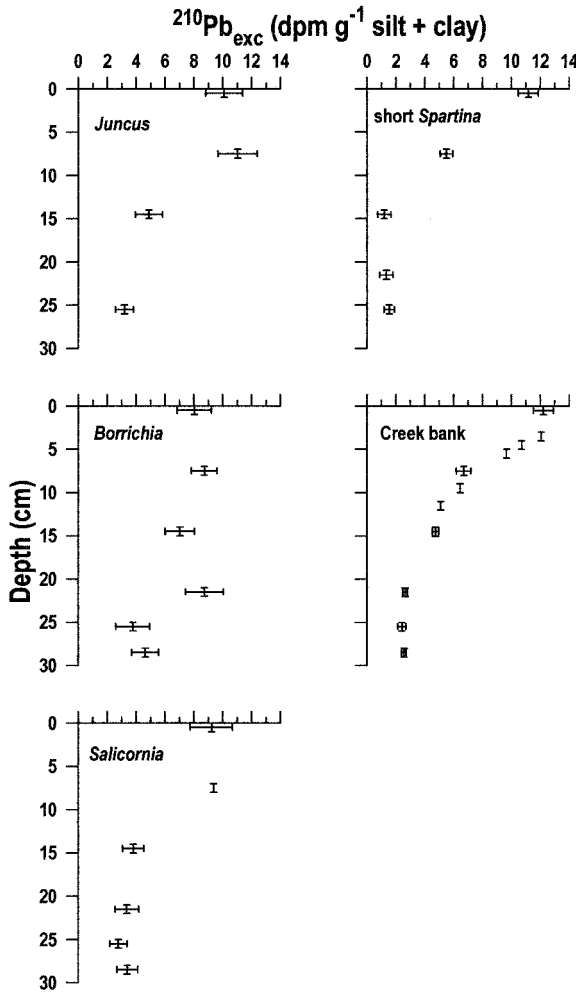
Figure 9. Depth profiles of excess ^{210}Pb activities (dpm g^{-1} silt + clay) of the silt + clay fraction for each site on the Bly Creek marsh transect. Errors are from counting statistics.

activity in surface sediments was significantly correlated with silt + clay and organic carbon content at all sites (Fig. 10A and B). However, more than 70% of the samples were from the short *Spartina* and creek bank sites. ^{137}Cs activity at the short *Spartina* and creek bank sites was not significantly correlated with either silt + clay (regression: $n = 22$, $P = 0.92$) or organic carbon content of the surface sediments (regression: $n = 10$, $P = 0.40$).

^{137}Cs was present to a depth of 30 cm at all sites with the exception of the short *Spartina* site (Fig. 11). The distribution of ^{137}Cs in sediment from the *Juncus, Borrichia,* and *Salicornia* sites was nearly constant with depth (Fig. 11). However, ^{137}Cs was not present in the top centimeter of sediment from the *Salicornia* site. The ^{137}Cs profile from the short
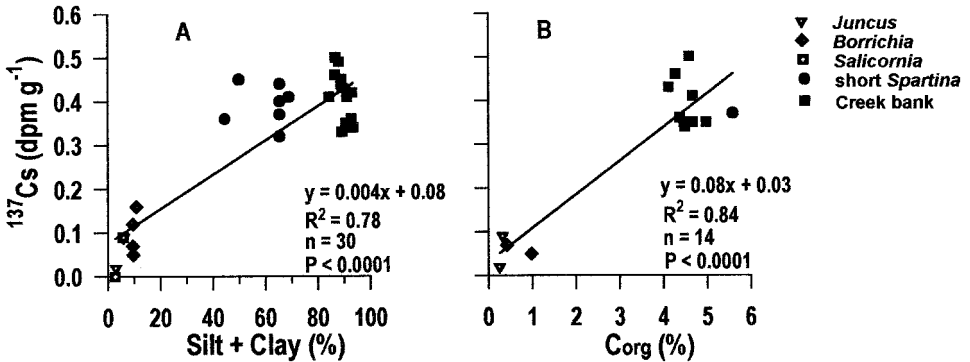
Figure 10. The relationship between ^{137}Cs activity and weight percent silt + clay (A) and organic carbon content (B) in surface sediments from all sites on the Bly Creek marsh transect.

Spartina and creek bank sites exhibited broad peaks in activity from the sediment surface to approximately 8 to 10 cm depth (Fig. 11).

6. Discussion

Fiddler crab burrow dynamics vary both temporally and spatially across salt marsh habitats (Table 1; Fig. 2). The variation in burrow dynamics among habitats is most likely related to root mat density as dense root mats are known to inhibit the burrowing ability of crustaceans (Ringold, 1979; Brenchley, 1982; Bertness and Miller, 1984). Fiddler crab burrowing activity in southeastern salt marshes seems to show the same general relationship of decreasing activity with increasing root mat density as in northeastern salt marshes (Katz, 1980; Bertness and Miller, 1984). However, in northeastern marshes root mat density is related to tidal height, whereas in southeastern marshes root mat density is not related to tidal height. (McCraith, 1998). The effect of fiddler crab bioturbation in southeastern salt marshes appears to be primarily a function of habitat type rather than tidal height within the salt marsh.

Our results indicate that fiddler crabs had the most significant influence on sediment reworking in habitats where burrows occurred in large numbers, new burrows appear frequently, and burrows are relatively short-lived (Table 1; Fig. 4). Bioturbation by fiddler crabs largely determines sediment reworking rates in the creek bank and Borrichia habitats. Additionally, fiddler crabs strongly influence sediment reworking rates in all other habitats across the salt marsh. Fiddler crabs are the dominant burrowing macrofauna in these habitats and consequently are the major source of sediment reworking (Teal, 1962). In comparison to other salt marsh habitats, the effect of fiddler crab bioturbation was minimized in the short *Spartina* habitat where new burrow formation rates were low, and burrows persisted for longer periods of time than other habitats (Table 1; Fig. 4). Fiddler crab burrowing at this site was probably inhibited by a hard, compact substrate and a dense root mat (McCraith, 1998).
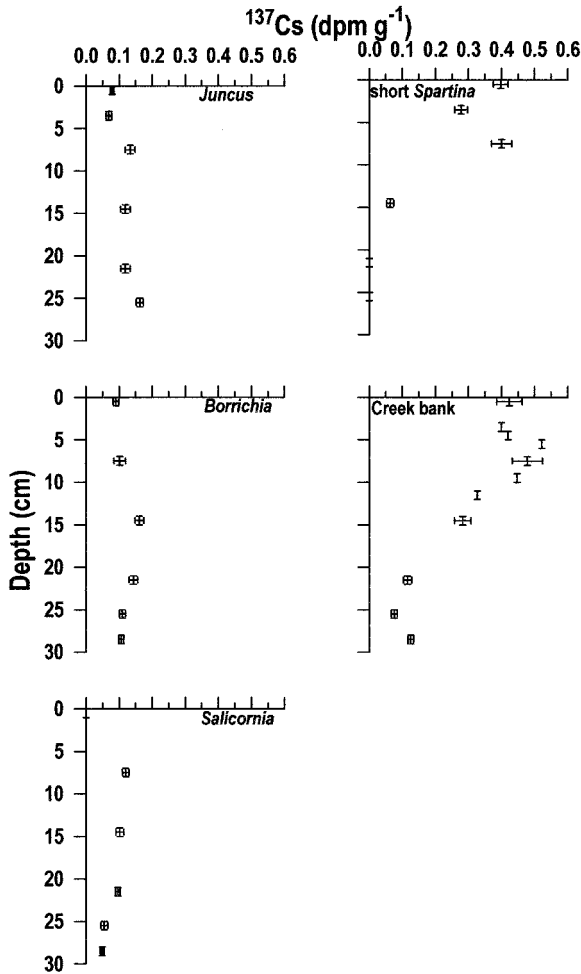
Figure 11. Depth profiles of ^{137}Cs activities (dpm g^{-1}) for each site on the Bly Creek marsh transect. Errors are from counting statistics.

In addition to the large scale spatial patterns of burrow distribution, the small scale distribution of burrows is also a relevant measure of sediment reworking. If the distribution of fiddler crab burrows within a habitat were clumped, fiddler crab burrowing activity would only be important in small patches within the salt marsh system. However, fiddler crab burrows were randomly distributed within all habitats across the salt marsh (Fig. 3) and the maps of burrows indicated that new burrows were made at positions different to those where previously made burrows had collapsed. These results indicate that fiddler crab bioturbation plays a decisive role in sediment reworking across the salt marsh on both large and small spatial scales.

The high rates of sediment reworking by fiddler crabs appear to affect the distribution of excess ^{210}Pb and ^{137}Cs in sediment from the salt marsh sites (Figs. 8, 9 and 11). However, caution must be used in interpreting these results for the high marsh sites. Both ^{210}Pb and ^{137}Cs adsorb on clay particles in sediments (Scrudato and Estes, 1975; Rickard and Nriagu, 1978; Ritchie and McHenry, 1990; Comans and Hockley, 1992; Brown and Bell, 1995; Smith and Comans, 1996). Sediments at the high marsh sites are sandy and contain only small amounts of clay (Fig. 5). This results in low ^{210}Pb activity in the sediments from these sites (Fig. 8). Excess ^{210}Pb distributions of the silt + clay fractions at these sites suggest that mixing occurs in the top 8–15 cm which is in good agreement with the mean depth of burrows found at these sites.

The presence of ^{137}Cs throughout the sediment cores from the three high marsh sites would seem to suggest that sediment mixing by fiddler crabs governs ^{137}Cs distribution in these sediments (Fig. 11). However, ^{137}Cs is known to be mobile in sediments with low concentrations of clay minerals (Evans *et al.,* 1983). The release of ^{137}Cs to interstitial water and the subsequent downward diffusive transport of ^{137}Cs may result in ^{137}Cs penetration to depths that are greater than from sediment mixing alone (Beasley *et al.,* 1982; Sholkovitz *et al.,* 1983; Nittrouer *et al.,* 1983/1984; Comans *et al.,* 1989; Sugai *et al.,* 1994). A combination of sediment reworking by fiddler crabs and porewater advection probably determines the distribution of ^{137}Cs at the high marsh sites.

Intense sediment reworking by fiddler crabs has affected the distribution of ^{210}Pb in sediments at the creek bank site (Table 3; Figs. 8 and 9). Sediment mixing by fiddler crab burrowing redistributes higher activity sediment from surficial sediments downward and lower activity sediment from depth upward. This effectively lowers the surface activity and increases activity at depth.

Although the excess ^{210}Pb distribution at the short *Spartina* site resembles that of the creek bank site, fiddler crab bioturbation is much less intense at this site (Table 3; Figs. 8 and 9). The distribution of excess ^{210}Pb in sediments from the short *Spartina* site is in agreement with the much slower rate of sediment reworking at this site. Excess ^{210}Pb activity reaches background levels at approximately 14 cm depth in the sediment, indicating that sediment reworking occurs above this depth. This depth is in good agreement with the mean depth of fiddler crab burrows in this habitat indicating that even though fiddler crab burrowing activity is limited in this habitat, fiddler crab bioturbation strongly influences sediment reworking rates in this habitat.

The near-surface enrichment in ^{137}Cs at the creek bank and short *Spartina* sites is typical for bioturbational mixing of an impulse tracer (Comans *et al.,* 1989). If mixing is negligible the observed ^{137}Cs penetration below the surface layer is solely the result of sediment accumulation (Nittrouer *et al.,* 1983/1984; Zuo *et al.,* 1991). However, mixing of sediments by fiddler crab burrowing will cause deeper penetration of sediment particles (and ^{137}Cs) than is predicted by the apparent ^{210}Pb sedimentation rate alone. The depths of predicted ^{137}Cs penetration from ^{210}Pb sedimentation rates (Table 7) is approximately 8 cm for both the short *Spartina* and creek bank sites. However, the observed depths of

Table 7. Mean ($\pm$ 95% confidence interval) of field measurements for each of the fiddler crab bioturbation model parameters.

Site	$^{210}Pb_0$ (dpm g^{-1} silt + clay)	Parameter		
		K_B (y^{-1})	U_B (cm)	S^* (cm y^{-1})
short *Spartina*	16.6 ± 1.1	0.02 ± 0.003	10 ± 1.6	0.28 ± 0.11
(*n*)	(16)	(8)	(15)	(8)
Creek bank	13.0 ± 0.4	0.2 ± 0.02	8 ± 1.7	0.28 ± 0.11
(*n*)	(16)	(8)	(18)	(8)

*From data in Sharma *et al.* (1987) and Vogel *et al.* (1996).

Note: Due to the discrepancy between surface ^{210}Pb activity and the ^{210}Pb activity in the top 0.5 cm of the core at the short *Spartina* site, the model was initialized using the surface ^{210}Pb activity from the creek bank site.

^{137}Cs penetration are much deeper at both sites (Fig. 11). These results suggest that bioturbation by fiddler crabs probably governs ^{137}Cs distribution at these sites (Fig. 11). In addition, porewater advection also probably influences ^{137}Cs distribution in the low marsh.

Our results suggest that fiddler crab bioturbation is one of the most important factors affecting the vertical distribution of atmospherically deposited radionuclides in salt marsh sediments. We used the original and modified regeneration models (Eqs. 2 and 3) to assess these effects. The short *Spartina* and creek bank sites are the only sites in the present study that meet the model assumptions of a constant sedimentation rate and a constant input concentration of ^{210}Pb. Therefore, the model was applied only to these two sites and not to the *Juncus, Borrichia,* and *Salicornia* sites. The three high marsh sites, *Juncus, Borrichia,* and *Salicornia,* are only flooded on the highest spring tides, and consequently, are not exposed to overlying tidal waters on a regular basis, thus eliminating one of the major sources of ^{210}Pb. To minimize any dilution of ^{210}Pb activity from sandy sediments present at depth at the short *Spartina* site, the model was applied to excess ^{210}Pb activity normalized to weight percent silt + clay.

Both the original regeneration model (Eq. 2) and the modified regeneration model (Eq. 3) were initialized using ^{210}Pb data for surface sediment (Table 7). The model was run substituting direct field measurements ($\pm$95% confidence level) into Eqs. (2 and 3) for parameter values: $^{210}Pb_0$, K_B, and U_B (Table 7). A mean sedimentation rate calculated from ^{210}Pb profiles from earlier studies (Table 7) was substituted for the parameter value (S).

The original regeneration model simulations (Eq. 2) for both the creek bank (Fig. 12A) and short Spartina sites (Fig. 12C) predict higher ^{210}Pb activities than observed in ^{210}Pb depth profiles. Also, the model-simulated profile for the creek bank site has a more vertical shape than the observed ^{210}Pb profile. The original regeneration model produces simulated profiles for the simple case of all filling of burrows from infilling with surface sediment only, and does not account for sediment replacement due to collapse of burrow walls. The

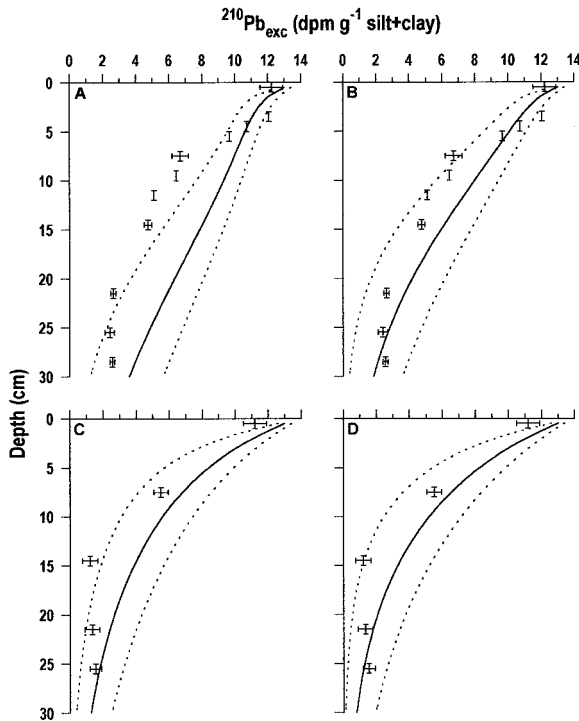$$^{210}Pb_{exc} \text{ (dpm g}^{-1}\text{ silt+clay)}$$

Figure 12. Model results using the original regeneration model (Eq. 2) for the creek bank (A) and short *Spartina* (C) sites and model results using the modified regeneration model (Eq. 3) for the creek bank (B) and short *Spartina* (D) sites. Depth profiles from sediment cores collected in 1994 (+). Predicted excess ^{210}Pb profiles (solid line) ($\pm$ 95% confidence intervals [dotted line]) from the regeneration model using direct field measurements of burrowing frequency (K_B), burrow depth (U_B), surface ^{210}Pb, and sedimentation rate for parameter values (see Table 7).

modified regeneration model (Eq. 3) does take into account the effect of burrow wall collapse on burrow filling. The simulations using the modified regeneration model (Eq. 3) fit the observed ^{210}Pb depth profiles better than those from the original regeneration model. The modified regeneration model simulations are in good agreement with the observed ^{210}Pb depth profiles (Fig. 12B and D). The model-simulated profile for the creek bank site is essentially exponential at all depths with a steep slope. The ^{210}Pb profile from the model simulation at the creek bank site is nearly identical to the observed excess ^{210}Pb profile from this site (Fig. 12B). The simulated ^{210}Pb profile from the short *Spartina* site is nearly identical in shape to the observed excess ^{210}Pb profile in the sediments, however, the model-simulated profile predicts higher ^{210}Pb activities than those observed at this site (Fig. 12C).

The regeneration model was also run using a range of values for the sedimentation rate (S; 0.05 to 0.38 cm y^{-1}) while using the mean values for all other parameters (K_B, U_B,

$$^{210}\mathrm{Pb_{exc}}\ (\mathrm{dpm}\ \mathrm{g}^{-1}\ \mathrm{silt+clay})$$

Creek Bank
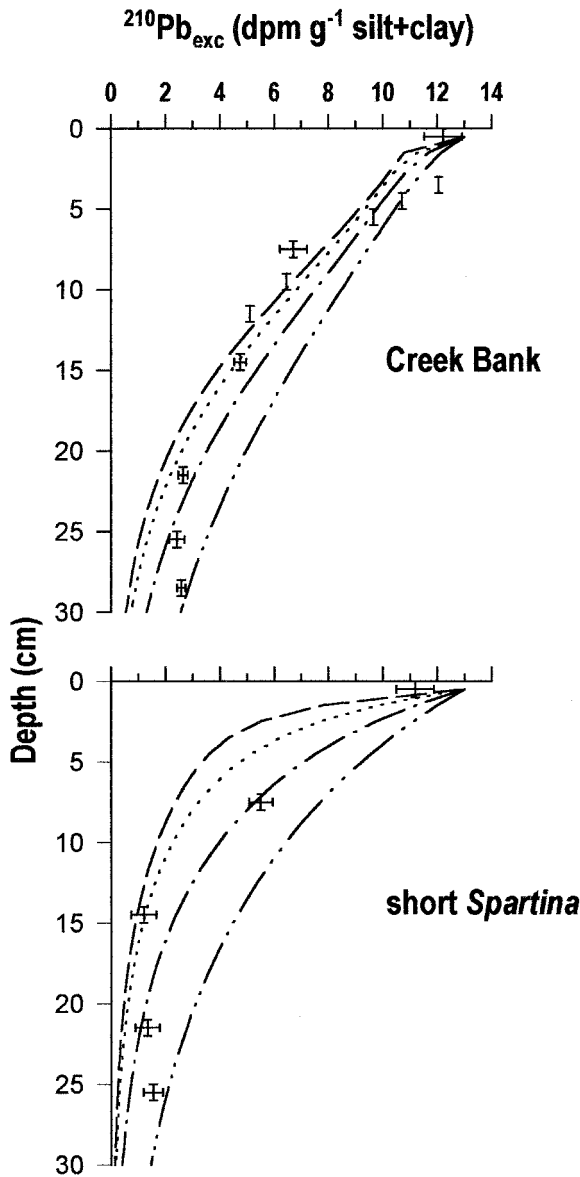
short *Spartina*

Depth (cm)

Figure 13. Model results for the creek bank and short *Spartina* sites using the modified regeneration model (Eq. 3) with a range of sedimentation rates. Depth profiles from sediment cores collected in 1994 (+). Predicted excess ^{210}Pb profiles from the regeneration model using direct field measurements of burrowing frequency (K_B), burrow depth (U_B), surface ^{210}Pb (Table 7), and sedimentation rates (S) of 0.05 (– – –), 0.1 (· ·), 0.2 (– · – · –), and 0.38 (– · · – · · –) cm y^{-1} for parameter values.

$^{210}Pb_O$; see Table 7). The simulated ^{210}Pb profiles for both the creek bank and short *Spartina* sites appear to be affected by small changes in the sedimentation rate (Fig. 13). These results suggest that the sedimentation rate at these sites may be lower than what has been previously measured due to the effect of biological mixing by fiddler crabs on ^{210}Pb distribution in these sediments. Model results from both the creek bank and short *Spartina* sites suggest that the sedimentation rate is approximately 0.2 cm y^{-1} (Fig. 13). This is two and one-half times lower than the sedimentation rate calculated for the creek bank site using the diffusion model (Eq. 1) and it is one and one-half times lower than the sedimentation rate calculated for the short *Spartina* site. These results suggest that in habitats where fiddler crab burrowing activity is high (Table 1; Fig. 2), and consequently, their influence on sediment reworking is the greatest (Tables 3 and 4) that the modified regeneration model (Eq. 3) can be used to determine the sedimentation rate.

The significance of the regeneration model lies in its ability to directly relate the effect of bioturbation by fiddler crab burrowing to ^{210}Pb distribution in sediments and its potential to determine sedimentation rates in biologically mixed sediments. The ability to use direct field measurements of fiddler crab burrow density, turnover, and depth is another important aspect of this model. For the first time, direct field measurements of fiddler crab burrowing activity have been used in a mathematical model to describe the effects of fiddler crab bioturbation on mixing of salt marsh sediments. Fiddler crab burrowing frequency (i.e., new burrow formation rates) may be useful as a predictor for ^{210}Pb distribution in salt marsh sediments. The model results demonstrate that the "burrow and fill" mechanism of fiddler crab bioturbation directly influences sedimentary and diagenetic processes in salt marsh systems. Thus fiddler crabs, as one of the most abundant macrofaunal components of the salt marsh, play a major role in determining the sediment composition of salt marsh systems.

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