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Process-specific cues for recruitment in sedimentary environments: Geochemical signals?

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ABSTRACT

The most biologically and geochemically active marine sediments are characterized by steep chemical gradients within the top centimeters of sediment (Berner, 1980). A common feature of these environments is disruptions of surface sediments by both physical and biotic forces. Growth and mortality rates for new recruits are affected by many of these surface perturbations. At the same time, these disturbances also impose a discontinuity in concentration across the sediment-water interface, and accordingly, a change in surface chemistry. In this paper we present evidence that the cue used by juveniles to distinguish between recently disturbed and undisturbed surfaces may be disruption of geochemical gradients that are typical of nearshore benthic systems. New juveniles exposed to ammonium concentrations typical of disturbed surface sediments exhibit behaviors consistent with rejection of the habitat. Conversely, new juveniles placed onto sediments containing ammonium levels typical of undisturbed surficial sediments rapidly initiate burrowing activity, a sign of "acceptability." We also present a numerical model, which assesses the dynamics of small-scale chemical shifts that accompany sediment disruption, to determine (a) what is the magnitude of surface chemistry changes associated with disturbance (i.e. what is the signal strength)? and (b) what are the spatial and temporal scales associated with the return to the undisturbed condition ("recovery")? Model results show that the signal strength, and the return to "acceptable" conditions, are strongly influenced by the initial gradient. Model predictions of the time required to "recover" indicate that times to recovery are longer than the interval between disturbance events, but are of the same temporal scale (minutes to hours). Thus, our results suggest that the dynamics of surficial gradients provide a strong signal over appropriate time scales that may reveal the intensity of disturbance and the likelihood of mortality for juveniles. As such, transport-reaction processes which govern porewater concentrations in surficial sediments may also play a role in recruitment processes.

1. Introduction

The majority of the ocean floor is sedimentary, and the most biologically and geochemically active sites are characterized by steep chemical gradients within the top centimeters of sediment (Berner, 1980). These environments are dynamic, both spatially and temporally, and are regularly disrupted by biotic and physical forces. A common feature of these

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disruptions is perturbation of the surficial sediments. Surface deposit feeding, browsing, and sediment erosion remove the top sediment layers, while defecation and sediment deposition bury the surface. These disruptions can be spatially persistent, can affect large areas of the sediment surface, and thus can have important consequences for the biology and chemistry of sediments. For example, removal of surficial sediments by erosion or deposit feeding, or deposition of sediments accompanying sediment transport or defecation, can significantly impact growth and mortality rates for settling larvae and juveniles (Wilson, 1980, 1981; Levin, 1981; Brenchley, 1982; Elmgren *et al.,* 1986; Posey, 1986; Hines *et al.,* 1989; Olafsson, 1989; Andre and Rosenberg, 1991).

Simultaneously, disturbance of surficial sediments imposes a discontinuity in concentration between sediment porewater and overlying water. For example, removal of sediments by erosion or surface deposit feeding exposes subsurface sediments which may have low or no oxygen, and concomitantly high concentrations of reduced compounds (e.g. Grant and Bathmann, 1987; Marinelli, 1992). In contrast, overlying water is typically oxic with low concentrations of reduced compounds. At the same time, deposition of feces onto the sediment surface imposes a strong suboxic signature to the sediment surface, due largely to the anoxic conditions in infaunal guts (Plante and Jumars, 1992) and the intense microbial activity noted in hindguts and in fecal pellets (Lopez and Levinton, 1987; Plante and Mayer, 1995). Even the deposition of previously eroded nearshore sediments can impose seemingly "reduced" conditions to the sediment surface, due to desorption of ammonium and possibly, desorption and decomposition of newly exposed organic material (Rosenfeld, 1979; Aller, 1994; Keil *et al.,* 1994).

The common effect of disturbance on sediment chemistry and juvenile health has important implications for recruitment. If organisms can detect the concentrations of solutes in sediment surfaces that accompany disturbance, selection should favor those recruits which integrate that information into recruitment decisions about a site. In fact, juvenile infauna can differentiate between recently disturbed sediment surfaces and undisturbed ones and do emigrate from the former. Woodin *et al.* (1995) showed that surfaces which had been disturbed by a variety of events (depositional or erosional, biotic or physical) could all be distinguished from undisturbed surfaces by several species of juvenile polychaetes and bivalves. The measure of differentiation was either failure to burrow or significant increases in burrowing times, which were correlated with higher probabilities of erosion or transport away from the settlement site.

The recruitment literature has many elegant demonstrations of the importance of species- or habitat-specific signal molecules (Highsmith, 1982; Zimmer-Faust and Tamburri, 1995; see reviews by Butman, 1987; Pawlik, 1992). However, normal constituents of seawater can also convey information via their concentration (Zimmer-Faust, 1991). For example, Cuomo (1985) previously suggested total dissolved sulfide could serve as a recruitment cue, although Dubilier (1988) offers a different explanation. Organisms capable of using habitat-specific cues, or concentration information, should be at a selective advantage. Several lines of evidence suggest that concentrations of normal

sediment porewater solutes such as ammonium, oxygen or sulfide, whose concentrations vary sharply in surficial sediments, could act as a disturbance signal for new recruits and thus would act as process-specific cues. First, disturbance of sediments imposes dramatic changes in the chemistry of a variety of solutes at the sediment surface, resulting in a potentially strong signal for organisms to use. For example, profiles obtained from field and laboratory sediments suggest that ammonium concentrations in the surficial sediments differ by a factor of 10 or more from those several millimeters below the sediment surface (Aller and Yingst, 1978; 1985; Devol and Christensen, 1993; Marinelli, 1994), a common depth of disturbance. Other covarying solutes (e.g. oxygen, sulfide, dissolved organics) exhibit similar concentration differences. Second, the "return to acceptability" of previously disturbed sediments occurs on the order of hours, both in light and in darkness (Woodin and Lindsay unpub. obser.). As we argue below, this time period is consistent with a restoration of chemical gradients by diffusion-reaction processes operating at the sediment-water interface. Third and finally, organisms are known to detect concentrations of at least two such dissolved porewater substances, ammonium and oxygen, and to alter their behavior as a function of concentration (Derby and Atema, 1982; Zimmer-Faust, 1987; Woodin and Marinelli, 1991).

In this research we present evidence that the cue used by the juveniles to distinguish between recently disturbed and undisturbed surfaces may be disruption of the geochemical gradients typical of sediments that rarely move as bedload. As discussed by Zimmer-Faust (1991), marine organisms live in very noisy chemical environments and must be able to differentiate between background noise and informative chemical signals. Such signals can take the form of species-specific or habitat-specific signal molecules as in the case of positive settlement cues (Highsmith, 1982; Zimmer-Faust and Tamburri, 1995) or can be molecules normally found in seawater but whose concentration provides information (Zimmer-Faust, 1991). Here we concentrate on responses of juveniles to ammonium which is normally found at low concentrations in seawater but at much higher concentrations in sediment porewaters.

Our approach to examining the possibility that ammonium concentrations serve as a habitat cue was two pronged. First, we conducted laboratory experiments which examined responses of new juveniles, here defined as individuals within one week of metamorphosis initiation, to sediment ammonium concentrations under different experimental conditions. We hypothesized that higher concentrations of ammonium at the sediment surface, a condition which often occurs following sediment disturbance, would result in failure to burrow or a significant delay in burrowing activity. Second, we devised a numerical transport reaction model to examine the influence of disturbance on surface ammonium concentrations and near-surface gradients, and to examine the time course of recovery of disturbed gradients to the previously undisturbed condition. The experimental study begins to evaluate the biological reality of the use of disrupted geochemical gradients as surface cues. The modeling study is to establish whether such gradients would return to relatively

undisturbed conditions within biologically relevant time periods and therefore provide a mechanism for evaluating the dynamics of recovery.

2. Materials and methods

a. Experimental study

i. Test species. Our test organisms were new juveniles of the infaunal arenicolid polychaete, *Arenicola cristata. Arenicola* lays egg masses which are initially attached to the bottom. These were collected and cultured with aeration in the laboratory until larvae (3 to 4 setigers) were released. The larvae were then transferred to 11 cm i.d. glass culture dishes and maintained until 6 setigers, approximately 600 μm in length. *Arenicola* larvae are lecithotrophic and were not fed. The juveniles were fed *Isochrysis galbana* T-ISO strain as well as a mixture of diatom species. Individuals used in experiments were within seven days of their initiation of metamorphosis. The use of new juveniles, rather than settling larvae, avoids the potentially serious problem of differentiating between competent larvae and incompetent larvae of similar size and appearance (Bachelet *et al.,* 1992).

   Arenicola will burrow into and maintain burrows in acceptable sediments at the 6-setiger stage. This species actively rejects some sediments by either initiating a crawling sequence or by elevating the anterior two-thirds of its body off the sediment surface. In flowing water such individuals are easily eroded off their attachment point (Woodin *et al.,* 1995). Sediments into which the recruits did not burrow within the observation period were classified as unacceptable.

ii. Behavioral observations. Individual juveniles were gently pipetted into the water column, and allowed to drift onto the sediment surface. Individuals which contacted the sediment surface forcefully, landed on a sand grain larger than their length, or landed in any position other than their ventral surface, were not used in the analyses. Timing of responses to the sediments began upon the contact of the individual with the sediment surface. Using a dissecting microscope, individuals were monitored continuously from their arrival on the sediment surface until they disappeared below the surface or until expiration of the designated observation period per individual, 7 min. The length of the observation period was set to a minimum of $10\times$ the mean time individuals took to initiate burrowing in preliminary observations. Only one individual was added to a test surface. Given that organisms' responses to ammonium are known to vary with acclimation (Borroni and Atema, 1988), juveniles were maintained prior to use in seawater with ammonium concentrations ≤ 5 μM.

iii. Experiments. Experimental sediments were collected in the field and immediately transported to the laboratory. Sediments were collected from the top 2 mm of the sediment surface with a paint scraper. Areas of disturbance such as fecal mounds, burrow scrapings, tubes and feeding traces were avoided. Upon arrival at the laboratory, sediments were

swirled in a bucket with seawater to remove fine fecal material. Sediments were dedicated to either suction core experiments or slurry experiments. In each experimental approach, ammonium concentrations in sediments or overlying water were manipulated to specified levels via addition of 0.45 μm-filtered seawater spiked with ammonium chloride to achieve specified concentration levels. This approach does not completely obviate the influence of other solutes, e.g. oxygen or sulfide, whose concentrations often covary with ammonium, but minimizes the potential effects of these solutes on juvenile responses to disturbance.

iv. Suction core experiments. Sediments were placed into 3.75 cm tall by 2.5 cm i.d. cores with 64 μm mesh bottoms and aged overnight in an aerated seawater table. Before use each core was placed on a large Buckner funnel and seawater of one of two ammonium concentrations (manipulated via ammonium chloride spike) was pulled through the sediment by vacuum without allowing the sediment to become dry. The seawater used in the porewater flushes was either low in ammonium (3 μM), a concentration commonly found in coastal waters (Table 1), or greatly elevated in ammonium (350 μM), a concentration often reached within the sediment porewaters (Table 1). At least 10 porewater flushes were done on every core. The flushes promoted removal of porewater ammonium (and other solutes) and perhaps some desorption and removal of exchangeable ammonium (Rosenfeld, 1979). Following the sequence of flushes, the mesh bottom of the core was wrapped with plastic wrap to prevent loss of fluid, the water remaining over the core sediment was removed, and the core was placed in a water bath at the height of the sediment within the core. The goal was to produce cores with either low (≤5 μM) or high (≥20 μM) concentrations of ammonium at the sediment surface. As shown in Table 2, surfaces of control sediments had ammonium concentrations of 3 μM, while experimentally elevated surfaces were at 25 μM.

Aerated seawater of known ammonium concentrations was then added to both the water bath and the core, keeping the head pressures in balance. At least two samples were taken from all solutions as well as from the sediment surface to confirm actual concentrations. Water samples were also taken for ammonium analysis from the overlying seawater in each dish after addition of juveniles. Four treatments were established. ''Controls'' had sediments that were flushed with 3 μM ammonium seawater and the same seawater over the top of the sediment. ''Elevated sediment'' cores had sediments flushed with 350 μM ammonium seawater and 3 μM ammonium seawater over the top of the sediment. ''Elevated water'' cores had sediments flushed with 3 μM ammonium seawater and 350 μM ammonium seawater over the top of the sediment. ''Both Elevated'' cores had sediments flushed with 350 μM ammonium seawater and 350 μM ammonium seawater over the top of the sediment. The ammonium concentration of the water bath corresponded to that of the seawater over the top of the sediment.

v. Slurry experiments. Sediments were placed in a flask with more than two times their volume of 0.45 μm filtered seawater, shaken overnight at 4°C, and then filtered until damp.

Table 1. Examples of the depth distribution of ammonium concentrations, and related environmental parameters, in nearshore sedimentary environments inhabited by representatives of benthic macroinfauna. As indicated by the "Range of values in profile," ammonium concentrations in these field environments are similar to model profiles listed in Figure 1.

Location	Depth of profile	Sediment grain size or type	% Organic content	Bottom water concentration	Range of values in profile	Infaunal occupants	Source
Narragansett Bay, RI	20 cm	clayey silt	—	<10 µM	70–200 µM (e.g. profiles 1–5 in Fig. 1)	*Maldanopsis, Nephtys Macoma, Ampelisca Ninoe, Spiochaetop-terus*	McCaffery *et al.*, 1980
Western Kattegat (station 5)	14 cm	sand	0.6–1.0%	—	40–60 µM (e.g. profile 1 in Fig. 1)	*Lanice*	Blackburn and Henriksen, 1983
Mud Bay, SC	20 cm	silt-clay	3.6%	0.2 µM	100–200 µM (e.g. pro-files 2–5 in Fig. 1)	*Heteromastus, Nereis, Macoma, Tellina*	Aller, 1980 Aller & Yingst 1985 and pers. comm.
Barnstable Harbor, MA	17 cm	sandy mud (surrounding *Amphitrite* tube)	1–2%	0.3–2.2 µM	100–400 µM (e.g. pro-files 2–9 in Fig. 1)	*Amphitrite, Clymenella,* Spionids, Nereids, *Mercenaria*	Aller & Yingst, 1978
Wadden Sea mudflats	20 cm	sand	0.4–1.2%	—	0–40 µM (e.g. profile 1 in Fig. 1)	*Arenicola marina*	Hüttel, 1990
False Bay, WA	15 cm	muddy sand (125–250 µm)	1.2%	—	0–900 µM	*Abarenicola Eupolymnia*	Marinelli, 1994
Friday Harbor, WA	30 cm	muddy sand	—	—	0–160 µM (e.g. profiles 1–3 in Fig. 1)	*Neoamphitrite, Nereis Neanthes, Diopatra Macoma*	Jahnke unpub. data; Woodin, Marinelli pers. obs.
Kysing fjord	10 cm	sand	1.3%	—	0–700 µM (Fig. 1, all profiles)	*Macoma, Nereis*	Henriksen *et al.*, 1983
Skallingen peninsula	8 cm	sand	0.3%	—	0–400 µM (Fig. 1, all profiles)	*Macoma, Nereis*	Henriksen *et al.*, 1983
Norsminde fjord	10 cm	silty-sand	2.0%	11–30 µM	0–200 µM (e.g. profiles 1–5 in Fig. 1)	*Nereis*	Kristensen, 1984

Table 2. Burrowing by juveniles of *Arenicola cristata* in suction cores flushed with normal seawater or with seawater elevated in [NH$_4$]. 'Perc. Reject' = percentage of the individuals which did not burrow within the observation period. '*N*' = total number of juveniles per treatment. Ammonium concentrations (μM) are for seawater samples from the seawater source used to flush the cores in each treatment '[NH$_4$] Flush' or from samples from the water overlying the sediment '[NH$_4$] Water' or from sediment surface samples '[NH$_4$] Surf'. 'na' = not available.

Treatment	*N*	Perc. reject	[NH$_4$] Surf	[NH$_4$] Water	[NH$_4$] Flush
Control	10	0%	3	2	2
Elevated Sed	10	0%	25	3	339
Elevated H$_2$O	10	0%	na	324	3
Elev. Sed + H$_2$O	10	0%	295	318	339

This process promoted removal of porewater ammonium and other solutes, and most likely, some additional desorption of exchangeable ammonium (Rosenfeld, 1979). The resulting sediment was divided into 200 ml fractions. Each fraction was combined with 100 mls of 0.45 μm filtered spiked seawater. The ''elevated ammonium seawater'' contained 230 μM ammonium, while the ''control seawater'' contained 5 μM ammonium. These resulting mixtures were shaken again for one hour at 4°C, warmed to 22°C, and then placed in 45 ml fractions in 11 cm i.d. glass dishes, rinsed briefly with seawater without added ammonium (approx. 5 μM), and then covered with at least 2 cm of 5 μM ammonium seawater. After the second shaking period, water samples were taken for ammonium analysis from the overlying seawater in the shaker flasks. In addition samples were taken from both the sediment surface and the sediment porewater after the sediments were placed in the dishes. Again, the goal was to produce sediment surfaces with either low or elevated ammonium concentrations but within values to which organisms would be exposed under normal field conditions (Table 1). In all cases ammonium was analyzed by the method of Koroleff (1976).

vi. Statistical analysis. All experiments were analyzed using PC SAS for OS/2 version 6.10 (SAS Institute, Cary, NC). The data were of two types: (1) times to initiation of burrowing and (2) percentages of juveniles per treatment accepting or rejecting the sediment. In the first case only those individuals which initiated burrowing were used. The burrowing times were analyzed by analysis of variance. Simultaneous comparisons among treatments were made with the Tukey's studentized range test. The times to initiation of burrowing were log$_{10}$ transformed. The percentage burrowing data were analyzed by a Fisher's Exact test.

b. Model description

Nearshore sediments are relatively high in organic matter (e.g. >1%) and are active sites of organic matter decomposition. Generally, decomposition results in the consumption of soluble oxidants such as oxygen, nitrate, and sulfate (among others) to oxidize organic

material, and the resultant production of soluble reduced compounds such as ammonium, sulfide, carbon dioxide, and phosphate. As a result of decomposition and diffusion, there are sharp gradients in concentrations of oxidants and reduced compounds over extremely small length scales (millimeters to centimeters) from the surficial sediments downward. For example, oxygen concentrations commonly change by orders of magnitude (e.g. 250 μM to near 0) within several mm depth of the sediment surface in many coastal sediments (e.g. Marinelli and Boudreau, 1996). Similarly, porewater ammonium and sulfide concentrations can increase >20 fold within the top centimeter of sediments (e.g. Aller and Yingst, 1978, 1985; Jorgensen *et al.,* 1983).

The disturbance-recovery model is a simple transport-reaction scheme which assumes that the upper sediment layers (e.g. $z = 0$–6 cm) are homogeneous with respect to organic matter content, and no bioturbation or irrigation occurs. This assumption is justifiable because, for the upper sediment layers of interest (generally 0–10 mm) diffusive transport dominates solute exchange (Marinelli, 1992). Nonlocal exchanges associated with irrigation and bioturbation are more significant at deeper depths (e.g., beyond 2 cm) in the sediment column. Under these assumptions, the equation for a dissolved solute in this system is

$$\frac{\partial C}{\partial t} = D's \frac{\partial^2 C}{\partial z^2} \pm R_0 e^{-az} \tag{1}$$

where C = concentration of the dissolved solute; z = depth into the sediment relative to the sediment-water interface; t = time; $D's$ = molecular diffusion coefficient of the solute corrected for porosity, tortuousity, and temperature; R_0 = rate of consumption or production of a solute assuming spatial dependence only; and a = depth attenuation coefficient which can reflect changes in organic matter reactivity with depth. This equation describes the net accumulation or disappearance of a solute with time due to diffusive transport in the porewaters in the vertical direction, and production or consumption of the solute via an attenuated zeroth-order reaction term. The zeroth order reaction is a kinetic scheme in which the production of a solute is independent of its concentration. This form has been used previously to describe the production of the byproducts of organic matter decomposition, including ammonium, and its use (relative to first order kinetic schemes) is justified in Aller (1980) and Boudreau and Marinelli (1994).

The goal of the model is to simulate a disturbance of porewater profiles in the upper sediment layers and to monitor recovery of the profiles to pre-disturbance levels. Thus, by definition, the model simulates transient conditions, i.e.,

$$\frac{\partial C}{\partial t} \neq 0. \tag{2}$$

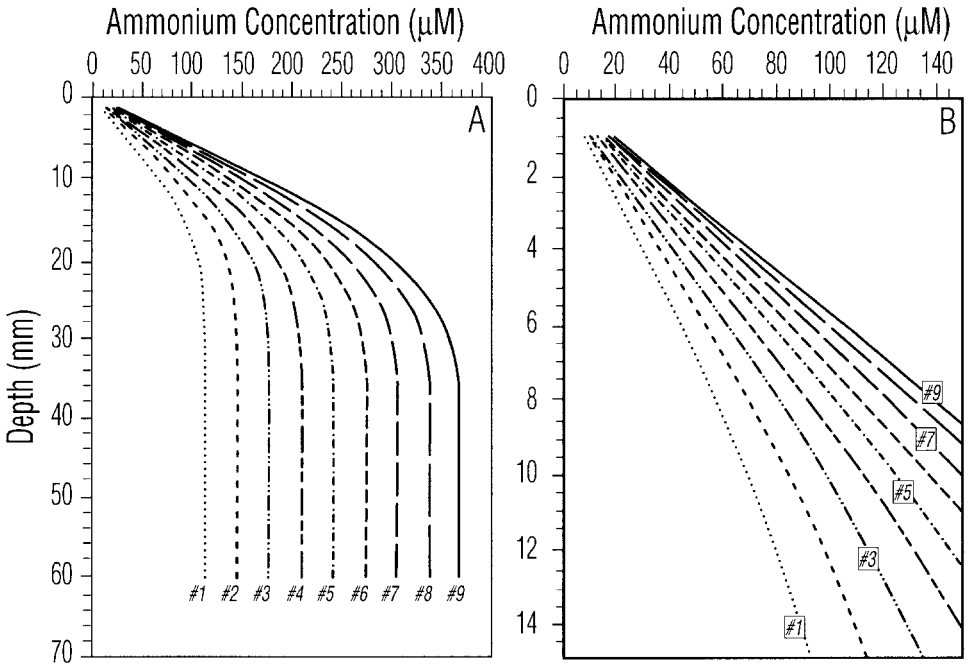This approach is appropriate for nearshore conditions, due to time-dependent processes

Figure 1. Ammonium profiles used as the initial conditions in the disturbance-recovery model. Panel A: Full view of model-generated profiles. Panel B: Detail of profile features in the top 15 mm of sediment. The profiles were generated by the transport-reaction model described by Eq. (1).

associated with the activities of animals, the deposition and utilization of organic matter, erosional events associated with tidal currents, and other dynamic processes.

We chose a case where the disturbance was defined as the removal of surficial sediments, and exposure of subsurface sediments and porewater. Such a disturbance could be physical or biological in origin. The disturbance/recovery simulation was accomplished in three steps. First, we used Eq. (1) to generate profiles that are within the concentration range of conditions observed in nearshore sediments populated by macrofauna (Fig. 1, Table 1). These profiles are smoother and thus more reflective of diffusion than the nonlocal processes of irrigation and other macrofaunal activities, but the profiles reflect the range of concentrations that exist in bioturbated habitats. (Again, because diffusive transport in the upper sediment layers (mm to 1 cm) is comparatively more important to solute exchange than nonlocal processes imposed by macrofauna, a diffusion mechanism thus is reasonable for generating profiles over these depths.) Second, we "disturbed" the profile, and simulated a sediment removal event, by shifting the position of the sediment-water interface to the specified depth of disturbance. We assumed also that the disturbed (removed) sediment and porewater are mixed into an effectively infinite water column. Finally, we allowed the disturbed profile to "recover" (according to Eq. (1)) to predisturbance levels, and monitored the time course of that recovery.

Table 3. Parameters (calculated {C}, assigned {A}, or based on experiment {E}) used in the diffusion-reaction model.

Porosity	0.85 {A}
Diffusion coefficient, Do (cm^2 s^{-1}, free solution, at 0°C) (after Van Cappellen and Wang, 1995)	9.766×10^{-6} {A}
Temperature (°C)	21 {E}
Temperature and tortuousity-corrected diffusion coefficient, based on the formulae $Do_{t°C} = (Do_{0°C})(1 + at)$, where $a = 0.041$ for ammonium (Van Cappellen and Wang, 1995), and $Ds = Do/(f*P)$ (with m = 2.8, after Ullman and Aller, 1982) (cm^2 s^{-1})	1.3565×10^{-5} {C}
Enhancement (E') of Ds in upper sediment layers due to meiofaunal activities (where $D's = E' * Ds$) (after Aller and Aller, 1992)	2.0 {A}
Overlying water concentration Co (µM) (reflecting ammonium depletion in overlying waters)	0.0 {A}
Bottom boundary gradient B (µM/cm) (see text)	0.0 {A}
Reaction rate coefficient Ro (µM min^{-1}) (see text)	2.93×10^{-3} {A}
	2.93×10^{-4} {A}
	2.93×10^{-5} {A}
	2.93×10^{-6} {A}
Attenuation coefficient a (cm^{-1}) (see text)	0.0 {A}
Timestep (sec)	12 {A}

The model domain includes the upper 6 cm of sediments, although disturbance is imposed only over a small percentage of that length scale. The boundary conditions are:

$$C_{z=0} = C_0 \tag{3}$$

$$\frac{\partial C}{\partial z_{z=6}} = B \tag{4}$$

where B is a constant. The initial condition is the initial undisturbed profile. The model was solved by explicit, forward-stepping finite difference numerical methods. Additional model parameters are given in Table 3. The range of reaction rates for ammonium production are consistent with those measured in coastal zones (Aller and Yingst, 1980, Aller and Mackin, 1989; Marinelli and Boudreau, 1996) and provide profiles which fall within the range of values observed in nearshore habitats (e.g. Table 1).

The model allowed us to specify a variety of conditions that are relevant to natural systems. For example, we modified the value of the whole sediment diffusion coefficient to include the effects of meiofaunal activities in the surficial sediments on the transport term (Table 3, based on Aller and Aller, 1992). In addition, we simulated the extent of disturbance by varying the depth of sediment removal, with greater depths of disturbance associated with a greater discontinuity in concentration at the sediment-water interface. We also varied the rate of net ammonium production, on the assumption that higher ammonium production rates would lead to longer times to recovery.

In addition, the model allowed us to specify the conditions associated with acceptability

for new recruits in two important ways. First, we varied the concentration of ammonium within the top millimeter of sediment that would prove acceptable to new recruits. This window of acceptability is based on a literature survey of studies where marine organisms were exposed to known concentrations of ammonium in seawater and responses were monitored. Among crustacea, single cell recordings indicate that some species can detect ammonium at concentrations <1 μM (Derby and Atema, 1982) and alter cell firing rates as concentrations are increased (Borroni and Atema, 1988). Behavioral responses of epifaunal and pelagic crustacea indicate a high degree of species variance, where some species flee at 20 μM and others do not respond even at 200 μM (Zimmer-Faust *et al.,* 1984; Zimmer-Faust, 1987; and Hazlett, 1990). Competent molluscan larvae respond to millimolar but not micromolar concentrations (millimolar: Coon *et al.,* 1990; Rodriguez *et al.,* 1995; micromolar: Zimmer-Faust and Tamburri, 1995). Among infaunal organisms, irrigation rates increased in response to 30 to 40 μM of ammonium in one species of terebellid polychaete but not in another (Woodin and Marinelli, 1991). Thus, we defined our ''window of acceptability'' to fall between 20–40 μM, well within the range of detectability and in the range where some species respond strongly and others do not. By using values such as these derived from the literature, we potentially avoid the usual problem of internally defining a standard and then looking for its verification via the same type of experiment. Second, we specified the depth interval over which this recovery should occur. For a complete return to undisturbed conditions, the disturbed profile would have to correspond to the predisturbance condition for all depth intervals. However, because new recruits explore primarily the sediment surface, and rarely probe to depths beyond their own length, we specified that recovery occur within a zone of exploration, which we defined as the top 1 mm. Thus, in the model study, recovery was defined as the return of the ammonium concentrations within the top mm sediment layer to a specified level between 20 and 40 μM.

3. Results

a. Experiments

i. Suction core experiments. The results from suction cores are consistent with our previous observations of *Arenicola cristata* juveniles. The juveniles appeared to be active and responsive in all treatments, and all individuals burrowed (Table 2). However, new juveniles showed significant differences in times to initiation of burrowing with the different treatments (Fig. 2). As we predicted, times to initiate burrowing were significantly slower in all of the elevated ammonium treatments (water and sediment) than in the control cores (Fig. 2) (two-way analysis of variance: treatment: $F_{3,31} = 7.03$, $MSE = 0.097$, $p < 0.001$; date: $F_{1,31} = 0.05$, $p > 0.8$; interaction: $F_{3,31} = 1.35$, $p > 0.27$). Elevated ammonium concentrations, both in the overlying water and on the sediment surface, were associated with increases in times to initiate burrowing (Fig. 2). Any individual which lay immobile on the bottom for >60 s was rejected ($<5\%$ of all individuals in all treatments).

Figure 2. Times (means and one standard error) (s) to initiate burrowing into suction cores for
    juveniles of *Arenicola cristata*. 'Control' = control cores consisting of sediments flushed with
    0.45 μm-filtered, 3 μM ammonium seawater and with overlying seawater ammonium concentra-
    tions set at 3 μM. 'Elev Sed' = cores consisting of sediments flushed with 0.45 μm-filtered,
    elevated ammonium seawater, and with overlying seawater ammonium concentration set at 3 μM.
    'Elev H$_2$O' cores consisting of sediments flushed with 0.45 μm-filtered, 3 μM ammonium seawater
    and with overlying seawater elevated in ammonium. 'Elev Sed + H$_2$O' = cores consisting of
    sediments flushed with 0.45 μm-filtered, elevated ammonium seawater and with overlying
    seawater also elevated in ammonium. Responses observed in control cores are significantly
    different from all other treatments. See Table 2 for actual ammonium concentrations.

We saw no evidence of failure to burrow as a result of juveniles anaesthetized by elevated
ammonium concentrations.

ii. Slurry experiments. In the sediment slurries, ammonium concentrations in the overlying
waters were very different in the two treatments at the end of the final sediment shaking
(control: 40 μM, elevated sediments: 357 μM). Following the final rinse and placement
into dishes, ammonium concentrations at the sediment surface were much lower, ranging
from 11 to 40 μM. The percent of juveniles which rejected sediments corresponded well to
the ammonium concentrations, both at the surface and in the underlying porewaters
(Fig. 3). A significantly higher percentage of the juveniles failed to burrow within the
observation period in the elevated ammonium sediments relative to the control sediments
(controls: 30%, elevated sediments: 80%; Fisher's Exact test, $p < 0.05$). However, 30% of
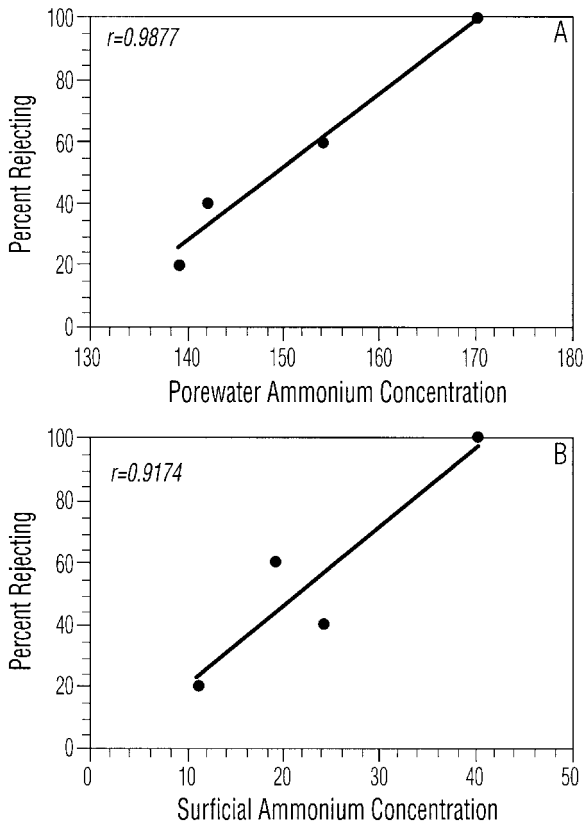the juveniles also failed to burrow in the control sediments. This is a much higher failure

Figure 3. Percentage of juveniles of *Arenicola cristata* which failed to initiate burrowing within the observation period. Sediments were slurries shaken with ammonium-enriched seawater. Panel A: Porewater (subsurface) ammonium concentrations µM. Panel B: Sediment surface ammonium concentrations (µM).

rate than we had previously observed in unshaken control sediments (Woodin *et al.,* 1995) and may reflect desorbtion of ammonium or other organic compounds into the porewater upon exposure to fresh seawater (Rosenfeld, 1979; Hedges and Keil, 1995), or alternatively, changes in the bacterial community that often accompany sieving or slurry treatments (Findlay *et al.,* 1990). So few individuals burrowed in the elevated ammonium treatment that we did not analyze the times to initiation of burrowing statistically. However, the times to initiation for those that burrowed were much longer in the elevated sediment treatments than in the controls (controls: 43.7 s, elevated sediments: 176.0 s). As in the suction core experiments, all juveniles appeared to be active and responsive in all treatments.

b. Model

We used our time-dependent numerical simulation of Eq. (1) to generate profiles which could then be disturbed and monitored for recovery (Fig. 1). These profiles (labelled 1-9)

are intended to capture the range of concentrations and conditions that might exist in nearshore sediments where macrofauna are abundant (Table 1). An example of the effect of disturbance on sediment profiles, followed by recovery of the profile to a specified condition, is provided in Figure 4.

Model results suggest that the time course of recovery of disturbed sediments is highly sensitive to two important parameters: steepness of the gradient in the disturbed region and the specified surface concentration that is deemed acceptable to new recruits. Longer recovery times are required for sediments where gradients are steep and subsurface concentrations are relatively high, compared to shallower gradients. For example, for profile #8 (a steep gradient with relatively high subsurface concentrations), the time required for sediments to return to a 30 μM concentration in the top 1 mm layer is on the order of 7 hours (Fig. 5). For profile #2 (a comparatively shallow gradient with lower subsurface concentrations), the time required for ''recovery'' to the 30 μM level is less than 1 hour (Fig. 5). This variation in recovery time is caused by the difference in surface concentrations that result when the different profiles are disturbed to the same vertical extent (4 mm sediment removal). For profile #8, the surface concentration that results when sediment is removed is much higher (60 μM) than that for profile #2 (35 μM). Thus, longer times are required for diffusive transport to restore the profile to the specified recovery concentration level (Fig. 5).

Longer recovery times are also predicted when the specified concentration that is ''acceptable'' to new recruits is decreased. For example, the time required for sediments in profile #6 to return from nearly 60 μM to 35 μM is 25 minutes, whereas the time required to return to 25 μM is nearly 5 hours. The nonlinear relationship between recovery time and surficial ammonium concentration is due to the form of the transport term. Immediately after disturbance, $\partial C/\partial z$ at the sediment water interface is greatest, resulting in more diffusive transport of ammonium out of the sediment relative to the constant production of ammonium associated with the zeroth order reaction scheme. This gradient becomes less steep with recovery (while production remains constant), resulting in gradually less diffusive transport, and therefore, longer recovery times associated with lower specified surficial concentrations.

The model results also suggest that the recovery times are greatly influenced by the depth of disturbance. When all other parameters are held constant, longer recovery times (hours to days) generally are associated with greater depths of disturbance, again due to the form of the gradient (Fig. 6). With shallower depths of disturbance, the discontinuity in concentration at the sediment-water interface is comparatively small, and less time is required for diffusive transport to restore the surface sediments to the specified concentration condition. With increasing depths of disturbance, the discontinuity in concentration is greater, and longer times are required for diffusive transport to restore the surface sediments to the specified concentration. However, where gradients lessen with depth into the sediment (e.g. profiles 1–5 between depths 10–20 mm), recovery times tend toward asymptotic values. In all cases, steep gradients produced immediately after disturbance
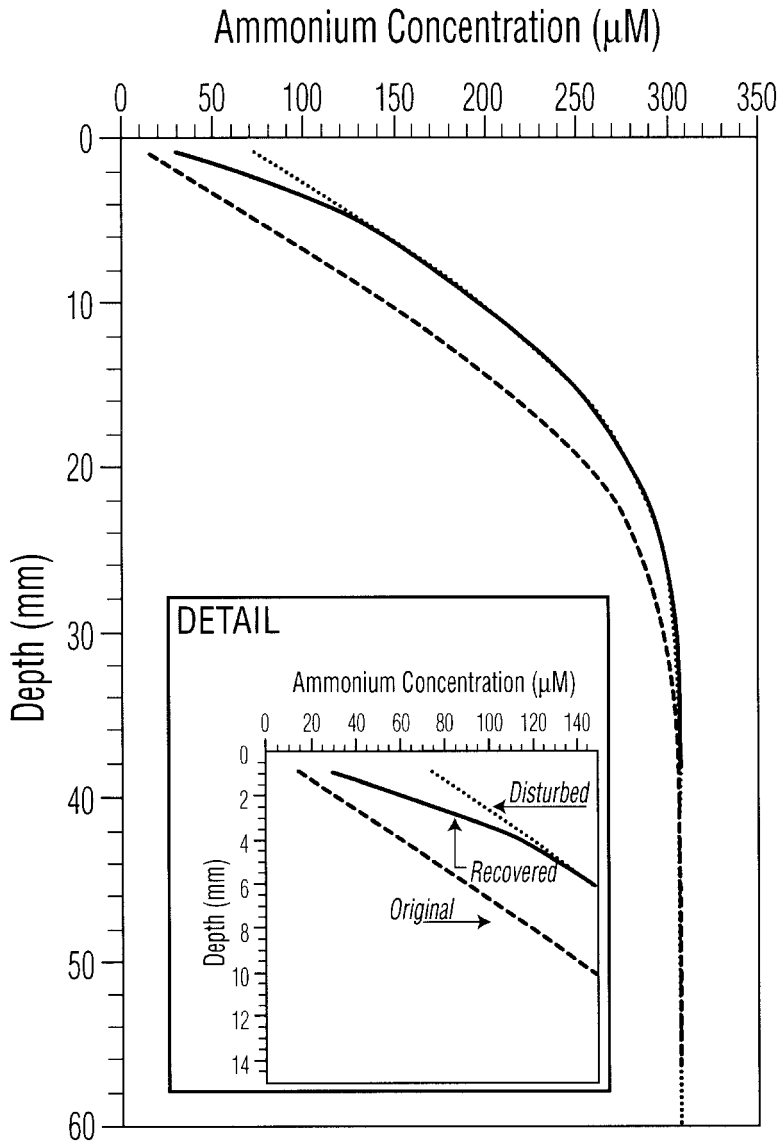
Figure 4. An example of profiles generated from the disturbance-recovery model. In this case, profile #7 was disturbed to a depth of 4 mm. The criteria for return to "acceptable conditions" included recovery of the sediment porewaters within the top 1 mm to a specified concentration of 30 μM. Detail reveals changes in surficial concentrations in the original vs. disturbed vs. recovered profiles.

promote high fluxes, and drive rapid changes in surficial ammonium concentrations in the early stages of recovery. As recovery proceeds, the rate of change in concentration diminishes, again resulting in longer times for surficial sediments to recover to a specified concentration condition.
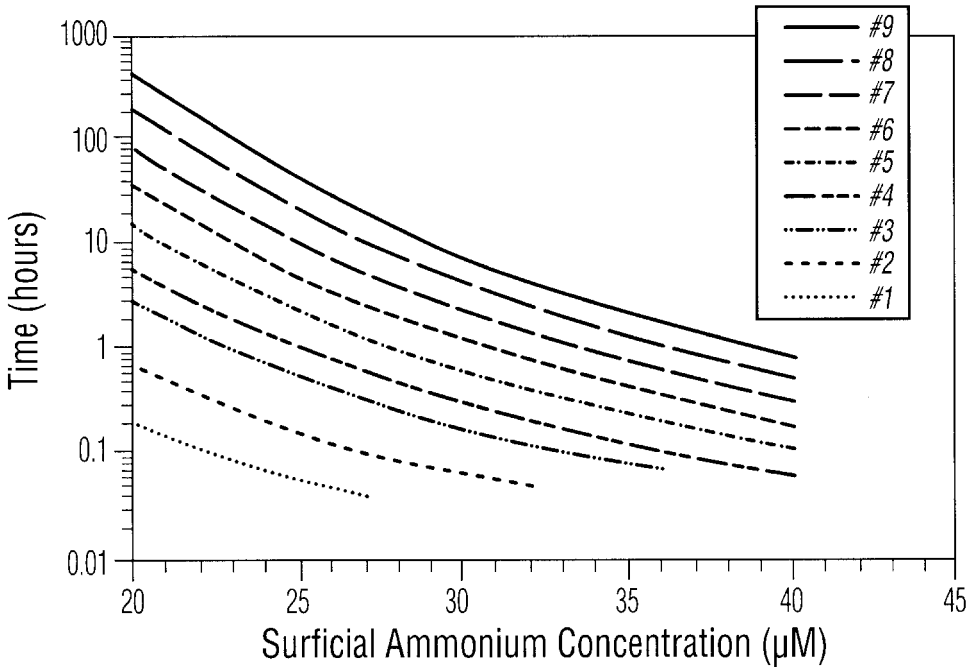
Figure 5. A comparison of the time to recovery versus specified surficial concentration for profiles #1-9. In all cases, the depth of disturbance is 4 mm, and surficial concentrations were defined as those occurring in the top 1 mm layer of sediment (the zone of exploration for new recruits).

Finally, model results predict that the value of the reaction rate term R_0 has little influence on recovery times. Under nearly all circumstances evaluated (reaction rates of 10^{-3} to 10^{-6} $\mu M/min$), ammonium production is outpaced by diffusive transport and has little influence on predicted times to return to specified surficial concentrations.

4. Discussion

Processes such as predation, erosion, sediment deposition, and defecation are commonly linked to mortality of recently settled juveniles as well as emigrating adults. These processes result in disruption of sediment surfaces, and correspondingly, disruption of solute gradients at the sediment-water interface. The newly exposed, disrupted surface therefore has a different chemical signature than an undisturbed surface. If disturbance of surficial sediments is linked to mortality, then selection should favor individuals which distinguish recently disturbed sites from those without disruption. This is particularly true if such sites are spatially extensive and spatially persistent, and if the frequency of disturbance exceeds the time required for sediments to return to the undisturbed state. As shown in Table 4A, the areal extent of biogenic disturbance of the surface is often enormous. Spatial persistence is known for very few of these species, but can be of long
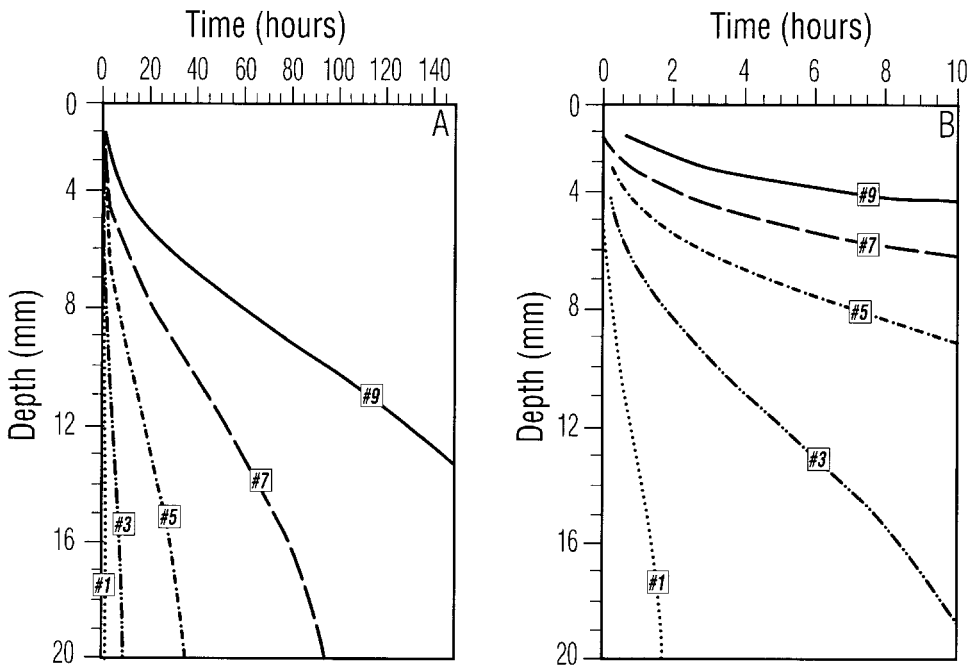
Figure 6. A comparison of the depth of disturbance versus the time to recovery for sample profiles presented in Figure 1. In all cases, the ''acceptable conditions'' for new recruits are specified as 30 μM ammonium concentrations in the top 1 mm sediment layer (the zone of exploration for new recruits). Panel A: Full view of time to recovery to 30 μM vs. depth of disturbance for profiles 1, 3, 5, 7, and 9. Panel B: Detail of panel A.

duration. For example, >50% of patches disturbed by the arenicolid polychaete, *Abareni-cola pacifica,* persist for >16 days (Krager and Woodin, 1993). Finally, disturbance frequency for feeding is on the scale of <5 min intervals, while disturbance by defecation is measured in minutes to one hour (Table 4B). Our model results indicate that recovery of surface concentrations is somewhat longer, but still on the scale of hours (Figs. 4–6). Previous work has demonstrated that infauna can differentiate among habitats that have or have not been disturbed, and accept more readily sediments that have not been disrupted (Woodin *et al.,* 1995), regardless of the nature of disturbance or the source of sediment. The present study suggests that one mechanism for distinguishing between disturbed and undisturbed sites might be the concentrations of porewater solutes such as ammonium at the site.

By manipulating the concentration of ammonium either in the surficial sediments only or in the overlying water, we altered the response of new juveniles of an arenicolid polychaete, *Arenicola cristata,* to sediments which were otherwise physically identical (similar grain composition, etc.). New juveniles of *Arenicola,* when placed onto experimental sediments with concentrations of ammonium typical of subsurface, not surface,

Table 4. Literature data on disturbance by infauna. Part A: area disturbed per individual and per population with species separated by activity type, surface feeding designated as 'Removal' and surface defecation as 'Burial.' Part B: frequency of disturbance by organisms with same separation as in Part A.

A.

Species	Size	Size area disturbed/ Ind (cm²)	Density per m²	% Area disturbed	Reference
Removal					
Macoma balthica	1.1–2.0 cm	0.1–50.3	600–2300[1]	0.6%–100%	Zwarts *et al.,* 1994
Abra nitida	0.6–1.2 cm	12.6–153.9	9–2000[2]	1.1–100%	Wikander, 1980
Scrobicularia plana	0.6–3.7 cm	0.8–153.9	2–500[3]	0.02–100%	Zwarts *et al.,* 1994
Pseudopolydora kempi japonica	0.7–4.3 mm³	3.2–7.8	4,000–33,000	100%	Miller and Jumars, 1986
Leiostomus xanthurus	juveniles	15.9–20.4	2,612 (sd 673) (pits, not fish)	100%	Billheimer and Coull, 1988
Burial					
Callianassa japonica	2.7–4.0 cm	6.9–17.1 cm² (basal mound area)	270–430	19–74%	Tamaki, 1988
Callianassa rathunae	32–65 cm	1256–2826 cm² (basal mound area)	5–7	63–100%	Suchanek, 1983
Abarenicola pacifica	1.7–4.2 cm	1.0–1.8 cm² (basal mound area)	32–104	0.3–1.9%	Krager and Woodin, 1993
Arenicola marina	1.5–100 cm	38.5–176.7 cm² (basal mound area)	2–30	0.8–53%	Brey, 1991a

[1]Brey, 1991b.
[2]Wikander, 1981.
[3]Essink *et al.,* 1991.

B.

Species	Length of active period (min, means and ranges)	Length of inactive period (min)	Reference
Removal of Surface			
Abra nitida	2.75 (1.5–4)	1.5 (1.0–2.0)	Wikander, 1980
Scrobicularia plana	2.6 (1.0–4.75)	4.1 (1.75–9.75)	Hughes, 1969
Pseudopolydora kempi japonica	7.25	1.7	Lindsay pers. obser.

Species	Period (min)	Height of mound	Reference
Burial of Surface			
Abarenicola pacific	22	0.6 cm	Krager and Woodin, 1993
Arenicola marina	20–45	4 cm[1]	Wells, 1949
Callianassa rathunae	8.7	10.3–26.7 cm	Suchanek, 1983

[1]Brey, 1991a.

sediments, either failed to burrow or significantly delayed burrowing relative to control sediments (Fig. 2 and 3). The delay in burrowing is typical of what we had observed previously for *Arenicola* when new juveniles were placed onto recently disturbed sediment surfaces (Woodin *et al.,* 1995) and is consistent with the use of disrupted geochemical gradients as surface cues by recruiting infauna. Such delays in burrowing result in significant increases in the probability of erosion (Woodin *et al.,* 1995).

Our model was designed to assess the dynamics of small-scale chemical shifts that accompany sediment disruption, to determine (a) what is the magnitude of surface chemistry changes associated with disturbance (e.g. the signal strength) and (b) what are spatial and temporal scales associated with the return to the undisturbed condition? These two questions are central to assessing whether a dissolved constituent such as ammonium, whose concentration is governed by reaction-transport processes, might provide a disturbance signal for new recruits. For a solute to be useful, the disruption of sediments must be accompanied by significant changes in solute concentration near the sediment-water interface, i.e. steep gradients must occur in the top millimeters of sediment. As shown in Figure 1, a 4 mm deep disruption results in a 10 fold or greater increase in ammonium concentration at the sediment surface even with the shallowest of our profiles (e.g. profile #1, Fig. 1). With steeper profiles, the concentration differential is even greater. Laboratory and field microelectrode measurements of oxygen and sulfide concentrations near the sediment surface show similar changes in magnitude over short distances (e.g. Jorgensen *et al.,* 1983—unfortunately no microelectrodes exist for ammonium). Thus, steep changes in solute concentrations exist over millimeter scales which could represent a strong signal for a new recruit. We acknowledge that other biogeochemical characteristics, such as microbial community composition, also change dramatically over similar length scales. However, we feel that dissolved substances are more evenly distributed (molecules move faster than bacteria!) and readily censused by recruits over the short time scales of our observation period, relative to more particle-bound and patchily distributed microorganisms. In control sediments for example, the decision to initiate burrowing is made in less than 30 s, often without movement from the initial point of contact with the sediment surface (Woodin *et al.,* 1995, Fig. 2). Note that within these profiles, representing a range of common habitats (Table 1), the impact of the depth of disturbance (and disruption of the gradient) on the time to recovery tends to fall off as gradients become less steep (Figs. 1 and 6).

A second important component for a cue to be informative is the residence time of the cue at the sediment surface relative to the the time required for the sediment surface to revert to the previous undisturbed condition, i.e. "recovery time." The feeding cycles of surface deposit feeders are often on the scale of 5 to 10 minutes; defecation cycles are also in the range of less than one hour (Table 4B); and small-scale physical disruption events of surficial sediments, either wave or tidally driven, are typically on the scale of minutes to hours (Miller and Sternberg, 1988). For a cue to provide information about the acceptability of sediments, the "recovery time" must be longer than the interval between disturbance

events. However, recovery times should not be so long that an undisturbed site is rejected if the signal associated with a process is no longer present. Recovery of ammonium profiles to where the top 1 mm is near to original surface conditions appears to occur within hours, not days, even for the steepest of the profiles modeled (Fig. 5). In addition, 'recovery time' should be a function of disturbance depth as an indication of the magnitude of the disturbance. Model results indicate this is likely to be the case (Fig. 6). Thus, our results suggest that the dynamics of surficial gradients provide a strong signal over appropriate time scales that may reveal the intensity of disturbance and the likelihood of mortality for settling juveniles. As such, transport-reaction processes which govern porewater concentrations in surficial sediments may also play a role in recruitment processes.

In conclusion, the experimental data are consistent with the hypothesis that ammonium concentrations commonly observed at the surface of disturbed sediments can be used as recruitment cues. Other solutes, such as dissolved oxygen or total sulfide, have similarly steep gradients in nearshore sediments and could also be used by infauna in this manner; they have not yet been tested. The model results show that disruption of surficial sediments results in dramatic concentration changes at the sediment surface, with "recovery times," governed by transport-reaction processes, on the order of hours (Figs. 4–6). These results are consistent with our arguments concerning the nature of recruitment cues, i.e. they should be strong and operate on biologically relevant time scales. Cues with low signal strength, or recovery times measured in days or weeks, would provide organisms with either little information or information related to the past, not the present.

The processes which disrupt the sediment surface, and the cues resulting from disturbance, are common to most nearshore areas and are strongly associated with sources of mortality. Unlike species-specific cues, they are not tied to the distribution and abundance of a particular species; thus, such process-specific cues may be much less spatially restricted. Further consideration should be given to studying which substances provide information, and the transport-reaction processes which govern their distribution, in nearshore sediments.

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