Experimental evidence for linkages between infaunal recruitment, disturbance, and sediment surface chemistry

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Abstract

In prior studies, we have argued that changes in sediment surface chemistry driven by biotic and physical disturbance affect recruitment decisions of infauna. Here, we provide additional data for oxygen concentrations and infaunal recruitment behavior and a time-dependent numerical model of oxygen concentration in disturbed sediments to further support our proposed linkage between disturbance, sediment chemistry, and recruitment decisions. We evaluated the recruitment responses of the polychaete *Arenicola cristata* and the bivalve *Mercenaria mercenaria* to sediments that were undisturbed, disturbed, and allowed to recover for a specified period of time. We also obtained fine-scale measurements of oxygen concentration in surficial sediments and profiles in the upper sediment layer that new recruits explore. Undisturbed sediments were characterized by high oxygen levels and were readily accepted by recruiting organisms. Disturbance caused dramatic changes in surface and subsurface oxygen concentrations and was accompanied by nearly complete rejection of habitats by new recruits. Oxygen concentrations in cores that were disturbed and allowed to recover are consistent with the time scales of recovery as predicted by a transport–reaction numerical model. In addition, organism responses to recovering cores varied with oxygen concentration in the surface and subsurface sediments of these cores. The rapid recovery of cores suggests that diagenetic transport–reaction processes that determine pore-water composition drive the acceptability of sediments to new recruits.

Recruitment is the process that determines the rate of addition of individuals to a given habitat. With the successful addition of new individuals come implications for gene flow, biological interactions, and habitat properties, all of which structure community dynamics. Although there is significant evidence linking the presence of infaunal species with the larger scale physicochemical properties of habitats (e.g., Sanders 1958; Rhoads 1973; Woodin 1974; Weinberg and Whitlatch 1983), the cause and biological significance of these associations are complex. In the ultimate sense, transport processes govern the distribution of sediment grains and organic matter (e.g., Hedges and Keil 1995), the resultant food quality and concentration conditions within a site, and the arrival of organisms to that location (Butman 1989). All of these elements are essential to provide an organism the opportunity to inhabit a given locale. However, these elements alone do not explain the more proximate factors recruits use to differentiate among habitats.

Assuming an organism arrives at a site, the factors that guide the decision to accept or reject are potentially complex and often interrelated. There is compelling evidence that bi-

ological interactions among extant residents and exploring recruits have significant influences, both positive and negative, on recruitment patterns (Pawlik 1992; Olafsson et al. 1994). Sediment biogeochemical properties such as organic content and pore-water gradients are frequently manipulated by organisms, thereby changing the physicochemical landscape on local scales. For example, deposit-feeding organisms can ingest or ''cache'' organic matter, thereby altering its distribution and availability within the sediment column (e.g., Levin et al. 1997). Burrow-dwelling organisms that irrigate their abodes alter nutrient and metabolite concentrations in surrounding sediments (e.g., Aller 1978). Surface deposit feeders remove surficial sediments and expose suboxic or anoxic layers with markedly different chemical signatures that are transient on time scales of hours to days (Marinelli 1992). These alterations represent disturbances that affect the nutritional and physiological environment of sediments, and consequently faunal distributions, on the scales of individuals (mm to cm; e.g., Meyers et al. 1988; Marinelli 1994; Levin et al. 1997).

We have shown that pore-water substances can significantly influence recruitment decisions by polychaetes and bivalves (Woodin et al. 1998). We directly manipulated ammonium concentrations in surficial sediments to mimic undisturbed environments, as well as recently disturbed environments, and found that the disturbed sediments were routinely rejected by new recruits. This led us to hypothesize that processes that control pore-water composition (i.e., diagenetic processes) could convey important information about habitat quality and disturbance history in sedimentary environments. Our hypothesis is strengthened by the following

observations. (1) Most biologically and chemically active sediments are characterized by steep solute gradients in the upper layers that organisms inhabit and new recruits explore. These gradients provide a potentially strong chemical signal to resident organisms and new recruits. (2) Disturbances of surficial sediments impose a dramatic change in surface chemistry that recruits may detect as they explore the sediment surface. (3) Solute gradients that result from organic matter decomposition reveal important information about the organic matter content and flux, and resultant concentration conditions, within the sediment column. For example, steep gradients and low concentrations of oxygen usually are indicative of high organic loading and perhaps other forms of disturbance. (4) Organic matter oxidation–reduction processes are a feature of nearly all sedimentary environments, both past and present, that are biologically interesting. Thus diagenetic cues such as elevated ammonium and lowered oxygen concentrations are geographically widespread and have been important over evolutionary time (e.g., Larson and Rhoads 1983; Thayer 1983).

In prior studies, sediments that were disturbed, or manipulated such that solute concentrations mimicked disturbed systems, all were rejected by new recruits (Woodin et al. 1995). However, naturally disturbed sediments become acceptable again to new recruits after several hours. This rapid recovery of sediments is best explained by changes in solute concentrations in the sediment surface driven by molecular diffusion/chemical reaction processes, which typically restore surficial sediment gradients within a few hours (Woodin et al. 1998). Other cues relating to changes in the bacterial or diatom populations require significantly longer times for recovery (e.g., Craven and Karl 1984; Marinelli unpubl. data). Numerical simulations of changes in surface chemical concentrations of ammonium confirm that time scales required to restore surface concentrations are consistent with the time required for disturbed sediments to become acceptable to new recruits (Woodin et al. 1998). The model for ammonium thus provided a predictive framework for determining how recruits may respond to disturbed sediments as a function of transport–reaction processes.

Herein, we provide further evidence that new recruits for two previously unevaluated species of infauna, a polychaete and a bivalve, respond to pore-water substances in surficial sediments that are consistent with the disturbance history of the sediment. We chose oxygen rather than ammonium because, like ammonium, it is physiologically important to organisms and has strong gradients in surficial sediments. Unlike ammonium, oxygen can be measured on small length scales using microelectrodes. This study advances our prior hypothesis by providing fine-scale measurements of surficial solute concentrations during disturbance and recovery and allowing more detailed comparisons of infaunal behavior with solute concentration. Our specific predictions are that (1) surficial oxygen concentrations would be low immediately following disturbance; (2) surficial oxygen concentration recovery would be consistent with, and thus driven by, transport–reaction processes; and (3) the acceptance of surfaces by recruits would correspond to their surficial oxygen concentration.

Materials and methods

Test organisms—Our test organisms were new juveniles of the infaunal bivalve *Mercenaria mercenaria* and the infaunal arenicolid polychaete *Arenicola cristata*. The use of new juveniles of both species, 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) and is consistent with the importance of secondary site selection in infaunal species (Emerson and Grant 1991).

Mercenaria mercenaria pediveligers were obtained from Sea Perfect Atlantic Sea Farms. *Mercenaria* were raised at approximately 26°C on a diet of *Isochrysis galbana* and were 11 d old when used in experiments. The spat had lost their velum within the preceding 12 to 24 h and were competent to establish a benthic existence. *Arenicola cristata* juveniles were raised from egg masses collected in May 1997 at the University of South Carolina's Baruch Field Station. Culturing was as described in Woodin et al. 1998.

Sediment core preparation—Sediment was collected from Oyster Landing at the University of South Carolina's Baruch Field Station. Oyster Landing hosts a diverse infaunal community that includes *Mercenaria* and *Arenicola,* spionid and onuphid polychaetes, and fiddler crabs as the dominant members of the macrofauna. Collection was confined to the top one-half centimeter of sediment (thereby avoiding collection of active adult macrofauna), and areas of disturbance such as fecal mounds, burrow scrapings, tubes, and feeding traces were avoided. Sediments were transported to Skidaway Institute of Oceanography within several days of collection and maintained at ambient seawater temperature with constantly aerated overlying water until used in experiments. For the *Mercenaria* experiment (March 1997), sediments contained a high load of fine particles and fecal pellets relative to the types of muddy sands that *Mercenaria* typically inhabits. Thus, the sediment was modified slightly by swirling and decanting a small fraction of the fine material. Apparently because of local differences in grain size distribution, the sediment collected for the *Arenicola* experiment (May 1997) had less fine material, and it was not necessary to modify the sediment matrix. Sediments were sampled for grain size and carbon and nitrogen analysis. Grain size analysis was conducted according to Folk and Ward (1957). Carbon and nitrogen analysis was conducted on acidified (to remove calcium carbonate) and unacidified samples using a Fisons model 1500 elemental analyzer.

Sediment cores were made by homogenizing sediment and gently pouring the mixture into plastic cores (length = 4.0 cm, 2.5 cm i.d.) with bottoms covered by 64-μm nitex mesh. Cores were allowed to equilibrate for 24 h in constantly aerated, 3-μm filtered seawater prior to use in experiments. Calculations using Einstein's equation

$$x = (D_s t)^{1/2} \qquad (1)$$

where

x = length or distance (cm)
D_s = diffusion coefficient (cm² s⁻¹)
t = time (s)

suggest that the 24-h time period was sufficient to allow natural chemical gradients to develop in the upper millimeters of the exposed sediment surface, but not so long as to allow establishment of gradients through the bottom nitex mesh, which might affect the character of the upper surface gradients. For this calculation we assumed that diffusion in one direction, from overlying water to sediments, was of interest. However, consideration of diffusion in two directions does not appreciably alter the length scale calculation relative to the depth of the core. Overlying water was changed every few hours to ensure that ammonium and other metabolites did not accumulate and influence developing gradients. Periodic checks of ammonium and oxygen concentration suggested that low levels (1 μM) of ammonium and high concentrations of oxygen (200 μM) prevailed throughout the equilibration period.

Sediment cores were subsequently manipulated to achieve three conditions: Disturbed, Recovering, and Control. In Disturbed cores the top 3 mm of surficial sediment was removed using a small spatula. Disturbances such as removal of surficial layers are commonly achieved by surface deposit feeders (e.g., venerid bivalves, which vacuum the sediment surface with their siphon, or terebellid polychaetes, which use their labial palps to remove the surficial layer over a 5–10-cm radius) or tidally driven erosional events. In Recovering cores, the sediments, which were disturbed according to the method described above, were allowed to "recover" (i.e., re-equilibrate) for a specified time period. Recovering cores were held in aerated, 3-μm filtered, circulating seawater during the re-equilibration time. Recovery times were specified in advance to range from 2 to 8 h, but then were modified based on behavioral responses of the test organisms (see below). Control cores were undisturbed and were maintained in aerated, circulating seawater until used in experiments. For Disturbed cores, behavioral responses to the sediment surface were recorded immediately after the disturbance event. For Recovering cores, behavioral responses were assessed after a specified recovery time.

Behavioral observations—*Arenicola* will burrow into and maintain burrows in acceptable sediments at the six-setiger stage. This species actively rejects some sediments by elevating the anterior two-thirds of its body off the sediment surface. Similarly, in acceptable sediment, *Mercenaria* spat nestle down just below the surficial sediment, secrete byssus threads, and typically initiate feeding. Active rejection of habitats by *Mercenaria* is manifested by failure to burrow and persistence on the sediment surface. In flowing water, new juveniles that persist on the sediment surface are easily eroded off their attachment point (Woodin et al. 1995). Sediments into which recruits did not burrow within the observation period were considered unacceptable.

To determine behavioral responses of juveniles to sediments, individual juveniles were gently pipetted into the water column and allowed to drift onto the sediment surface. 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. Details of the observational methods can be found in Woodin et al. (1998). The experiments with *Mercenaria* had six replicate cores for each treatment, with one individual observed on each core surface. The *Arenicola* experiment had seven replicate cores and observations each for the Control and Disturbed treatments and eight replicate cores and observations for the Recovering treatments. To have cores available for observations at the same time, cores assigned to the Recovering treatments were disturbed in advance. At the end of the recovery period, these cores were tested with a corresponding Control and Disturbance core to achieve a randomized block design. Juveniles were maintained in fresh, oxic seawater (31‰, <2 μM ammonium, and ≈200 μM oxygen) prior to use.

The logistical constraints of adding new juveniles to cores, monitoring behavior, and making electrode measurements (below) required that we conduct experiments and observations in still water conditions. However, in the field, new recruits experience both still water (e.g., at slack tides or in quiescent locales) and flowing water conditions. Recent evidence from experimental and model studies suggests that benthic recruits may preferentially settle at slack tide when water is quiescent (Whitlatch and Osman 1998; Gross et al. 1992). In addition, the behaviors seen in still water correspond to those seen in flowing water that result in transport away from the site (Woodin et al. 1995). Hence, our observations under still water have validity in the context of the fluid dynamic regime in natural environments.

Oxygen microelectrode measurements—Initially, our goal was to determine the response of new juveniles to oxygen concentrations in surficial sediments that were either intact (controls), newly disturbed, or in some stage of recovery. For the *Mercenaria* experiments, we measured oxygen concentrations at the sediment surface at four locations in each sediment core using Clark-style oxygen microelectrodes purchased from Diamond General. With six replicate cores per treatment, there were a total of 24 measurements of surficial oxygen concentration for each of the Control, Disturbed, and Recovering (I and II) manipulations. The exact location of the sediment–water interface was determined by examining the electrode position through a dissecting microscope at ×10 magnification. Oxygen measurements were conducted within 10 min of the behavioral observations. The locations of the oxygen measurements coincided with the area of the sediment surface where the behavioral observations were made. The oxygen measurements were obtained under low light conditions, and manipulation of the light field did not greatly influence oxygen values. Hence, benthic photosynthesis by microalgae did not contribute substantially to the oxygen concentrations measured in the cores. We also observed no evidence of development of a stagnant boundary layer (i.e., reduction in oxygen concentrations in the millimeters above the sediment surface) during our measurements, suggesting that our procedure for storing cores did not produce significant experimental artifacts.

Our results from the *Mercenaria* experiments (see below) suggested that the oxygen gradient can also affect the be-

havior of new recruits. Thus, for the *Arenicola* experiments, we obtained two measurements of oxygen concentration at the sediment–water interface and then one complete sediment oxygen profile (which included a surface value measurement). Oxygen profiles were determined at submillimeter depth intervals until the anoxic sediment zone was reached. Thus, for the *Arenicola* experiments, we obtained 21 surface oxygen concentration measurements and seven oxygen profiles for each of the Control and Disturbance treatments and 24 surface oxygen concentration measurements and eight profiles for the Recovery treatment. Again, we observed no evidence that a stagnant boundary layer developed during our experimental procedures.

The oxygen microelectrode was calibrated every few hours during each experiment. Calibration was accomplished by measuring amperometric values of either unamended seawater or seawater that had been nitrogen-bubbled for various periods of time and regressing the amperometric reading against the actual concentration of the test solution, as determined by Winkler titration. Four values at minimum were used to construct each calibration curve. The regression statistic (r^2) usually ranged from 0.98 to 0.99 for all calibrations.

Numerical model of disturbance–recovery—To determine whether the time scales associated with the change in oxygen concentration (C) in Recovering cores are consistent with the time scales associated with restoration of gradients via transport–reaction processes (as opposed to bacterial coatings, microalgal production, or other cues), we conducted a numerical simulation of disturbance–recovery for oxygen in the experimental sediments. The disturbance–recovery model used is the same as in Woodin et al. (1998) and is a simple transport–reaction scheme that assumes that the upper sediment layers (e.g., depth into sediment $z = 0–6$ mm, relative to the sediment–water interface) are homogeneous with respect to organic matter content and that no significant bioturbation (beyond small-scale diffusive mixing and attendant effects imposed by meiofauna) or irrigation occurs. The equation for a dissolved solute in this system is

$$\frac{\partial C}{\partial t} = D'_s \frac{\partial^2 C}{\partial z^2} \pm R_o e^{-az} \tag{2}$$

A list and explanation of model parameters is given in Table 1 as well as in Woodin et al. (1998).

We used Eq. 2 to fit a reaction rate R_o and generate a profile that was representative of the oxygen concentrations observed in relatively undisturbed sediments from the study site. R_o is a heterogeneous reaction rate, which includes a range of reactions (e.g., oxidation of organic matter and compounds in both solid and reduced phases) that may affect oxygen concentration over the depth interval enveloped by the model. A numerical solution was used because the analytical solution requires more detailed knowledge of other constituents reacting with oxygen (see calculations and assumptions in Marinelli and Boudreau [1996]), which we lacked. The initial condition was based on profiles from disturbed sediments as observed in our measurements. We did not consider nonlocal processes such as irrigation or macrofaunal activities, as diffusive transport in the upper sedi-

Table 1. Parameters (calculated [C], assigned [A], or based on experiment [E]) used in the diffusion–reaction model.

Symbol	Description	Value
ρ	Porosity	0.85 (A)
D_o	Diffusion coefficient (cm² s⁻¹, free solution, at 0°C)	9.386×10^{-6} (A)
T	Temperature (°C)	26 (E)
D'_s	Temperature and tortuosity-corrected diffusion coefficient, based on the formulae $D_{o_{T°C}} = (D_{o_{0°C}})(1 + \alpha T)$, where $\alpha = 0.06$ for oxygen (Van Cappellen and Wang 1993) and $D_s = D_o/(f\rho)$ (with $m = 2.8$, where m is an empirically defined coefficient, after Ullman and Aller 1982) (cm² s⁻¹)	1.79×10^{-5} (C)
E	Enhancement of D_s in upper sediment layers due to meiofaunal activities (where $D'_s = ED_s$) (Aller and Aller 1992)	2.0 (A)
C_o	Overlying water oxygen concentration (μM)	200.0 (A)
B	Bottom boundary gradient (μM cm⁻¹)	0.0 (A)
R_o	Heterogeneous reaction rate coefficient (μM min⁻¹)	5.0×10^{-5} (C)
a	Attenuation coefficient (cm⁻¹) (assumes upper sediment column is well-mixed)	0.0 (A)
t	Time step (s)	12 (A)

ment layers (millimeters to 1 cm) is comparatively more important to solute exchange than nonlocal processes imposed by macrofauna (e.g., Marinelli 1992). We stress that our goal is not to obtain an exact model of geochemical processes affecting the oxygen gradient, but to attain a general approximation of the profile and, in particular, the time scales associated with recovery. To calculate recovery times, we ''disturb'' the profile and simulate a sediment removal event by shifting the position of the sediment–water interface to the specified depth of disturbance. This Disturbed profile represents the initial condition of the recovery process (*see* Fig. 1). Finally, we allow the Disturbed profile to ''recover'' (according to Eq. 2) to predisturbance levels and monitor the time course of that recovery.

The model domain includes the upper 10 mm of sediments. The boundary conditions are

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

$$\frac{dC}{dz_{z=6}} = B \tag{4}$$

where C is an average overlying water concentration observed in experiments, and B is set to zero (no oxygen gradient) (Table 1). The model was solved by explicit, forward-stepping, finite difference numerical methods.

Statistical analysis—The data for the organisms consist of times to initiate and complete burrowing of those that ac-
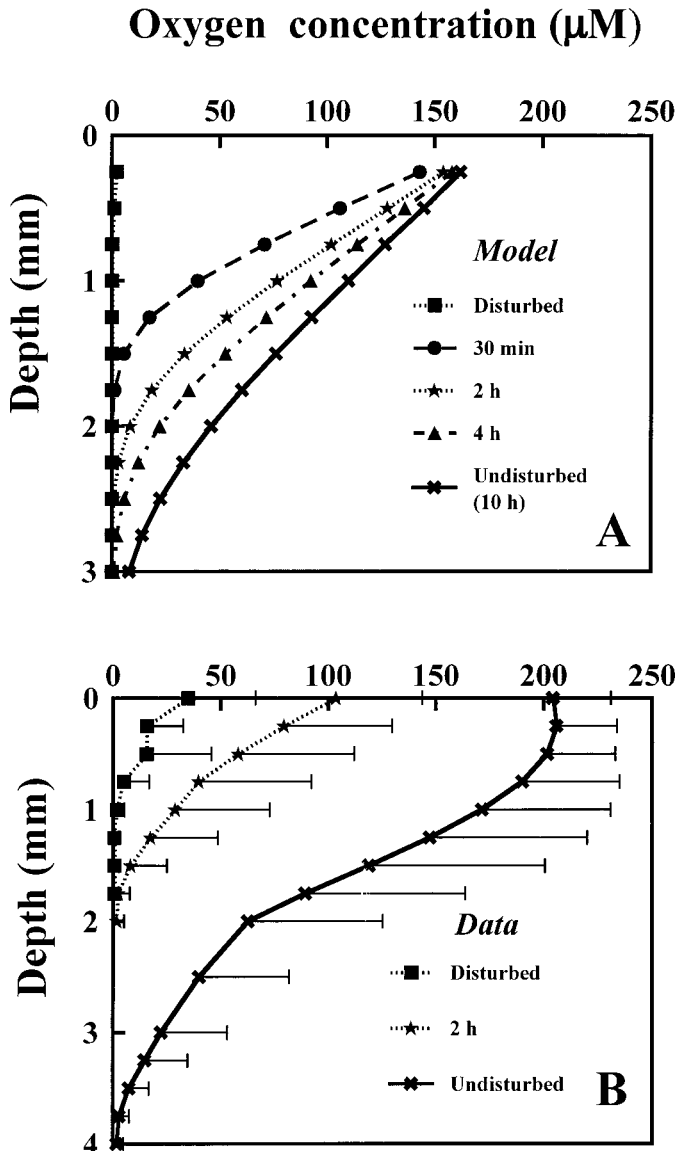
Oxygen concentration (µM)

Fig. 1. (A) Results of numerical model of oxygen concentration in nearshore sediments. The model depicts oxygen profiles in sediments that have been disturbed (e.g., top 3 mm removed) and the time course of recovery of the oxygen profile, assuming no further disturbance. The profile at 10 h is essentially at full recovery. (B) Oxygen profiles (means + 1 SD) obtained from experimental cores during the *Arenicola* experiment. The sequence of undisturbed, disturbed, and recovering profiles (2 h) is similar in general features (i.e., overall concentration with depth and gradient steepness) to that depicted by the model.

cepted the sediment by burrowing and the frequencies of burrowing individuals by treatment. To accommodate the combination of times to initiate burrowing of those that actually burrowed and those that failed to burrow within the observation period, the data on initiation of burrowing were analyzed with the nonparametric Jonckheere–Terpstra ordered alternatives test. This ranking test allows one to designate the expected order of results by treatment (Daniel 1990). The data on times to completion of burrowing by

burrowing individuals were analyzed with a Wilcoxon test, using only those treatments where three or more individuals burrowed. The data on frequencies of burrowing individuals by treatment were analyzed by a Fisher's exact test. The data on surficial oxygen concentrations by treatment were analyzed by analysis of variance. Significance was assigned to those results that had a probability of 0.05 or less.

Results

Sediment characteristics—Although sediments for both experiments were collected from the same location (Oyster Landing, Baruch Institute, Georgetown South Carolina), sediment characteristics varied, in part due to natural processes and in part due to the decantation procedure employed in the *Mercenaria* experiment. Sediments used in the *Mercenaria* trials (some fine particles decanted) had an organic carbon content of $0.09 \pm 0.001\%$ and nitrogen content of $0.007 \pm 0.0002\%$ (unamended sediment $0.7\% \pm 0.17\%$ organic carbon, $0.05 \pm 0.01\%$ nitrogen). The median grain size of the sediments was between 375 and 500 µM, and sediments were moderately sorted (no appreciable change in grain size occurred with decanting). In the *Arenicola* experiment, sediment organic carbon content was higher, averaging $0.36 \pm 0.01\%$ with a nitrogen content of $0.03 \pm 0.002\%$. Accordingly, the median grain size of the sediments was smaller, 250 µM, and sediments were moderately sorted.

Model predictions—Oxygen profiles generated by the transient numerical model show rapid changes in surficial gradients in the zone of exploration for new recruits (top millimeters) (Fig. 1A). The "10-h" profile approximates the steady state profile typical of an undisturbed region in nearshore sediments (e.g., Jahnke et al. 1990; Marinelli and Boudreau 1996). The Disturbed profile is dramatically different. There are large concentration changes (e.g., 0–150 µM) within the top 1 mm immediately following disturbance, and these changes are still dramatic 30 min (40–140 µM), even 2 h (75–155 µM) after the disturbance (Fig. 1A). Thus, the model predicts that disturbance alters both the surficial concentrations and the upper concentration gradient in sediments, and that Recovering profiles have steeper gradients than undisturbed sediments.

Measured oxygen values—Surficial oxygen concentrations obtained in the *Arenicola* and *Mercenaria* experiments are consistent with predictions of low concentrations in Disturbed sediments, high concentrations in Control sediments, and intermediate concentrations in Recovering cores (Figs. 2A, 3A). In the *Mercenaria* experiments, the oxygen concentrations in the controls and the 9-h Recovering cores were not significantly different from each other, but both were significantly different from the disturbance cores. Oxygen concentrations in 4-h Recovering cores were intermediate: not significantly different from 9-h Recovering cores or disturbance cores but significantly different from Control core values (Fig. 3A) (analysis of variance: $F_{3,19} = 8.31$, MSE = 1,283.7; followed by Tukey test with experimentwise $\alpha = 0.05$). In the *Arenicola* experiments, the oxygen concentrations in the three treatments (Control, 2-h Recovering, and
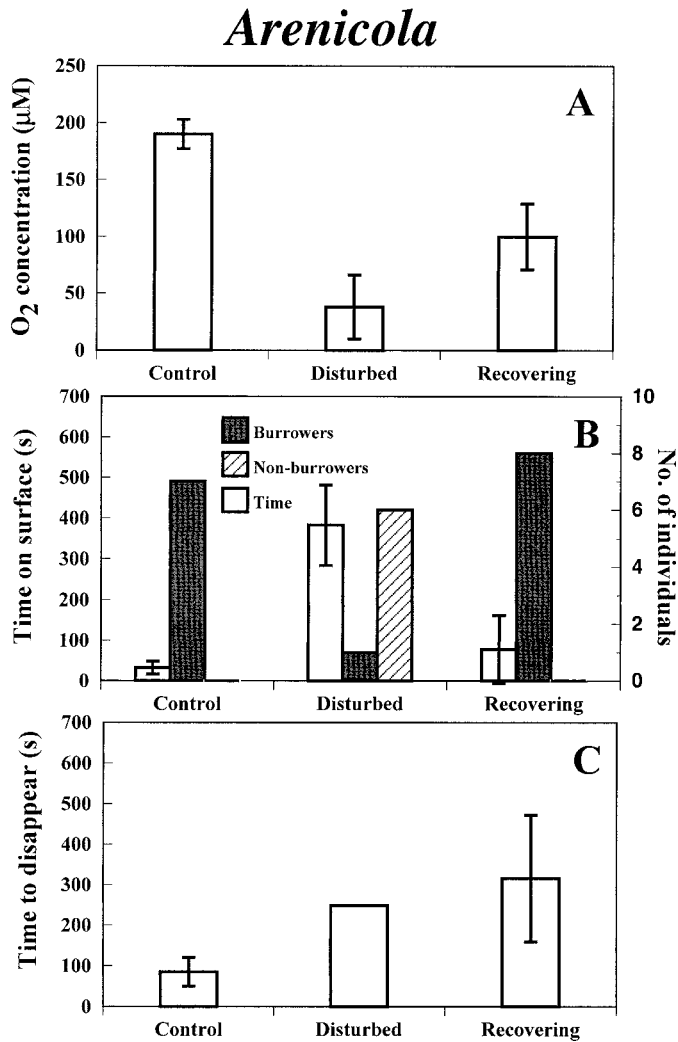
Arenicola

Fig. 2. *Arenicola* experiments. (A) Surficial oxygen concentrations (mean ± SD) in Control, Disturbed, and Recovering cores. All treatments were significantly different from one another, as determined by analysis of variance ($P \ll 0.05$). (B) Time spent on surface (± SD) in Control, Disturbed, and Recovering cores (i.e., the amount of time an organism explored the surface during the observation period). Organisms either burrowed (burrowers) or remained on the sediment surface for the entire observation period (nonburrowers). In Control cores, all organisms rapidly burrowed. In Disturbed cores, only one individual burrowed. In Recovering cores, all individuals elected to burrow but took significantly longer to initiate burrowing. (C) Burrowing times in Control, Disturbed, and Recovering cores (i.e., the duration of time an organism spent exploring the subsurface habitat before accepting it). In Control cores, organisms rapidly burrowed and established a benthic existence. In Disturbed and Recovering cores, the amount of time taken by an organism before adopting a habitat was significantly longer, suggesting a hesitance to establish a more permanent existence in these sites.

Disturbed) all were significantly different from one another (analysis of variance: $F_{2,19} = 66.9$, MSE = 612.1; followed by Tukey test with experimentwise $\alpha = 0.05$).

The oxygen profiles obtained during the *Arenicola* experiment for the Control, Disturbed, and 2-h Recovering cores
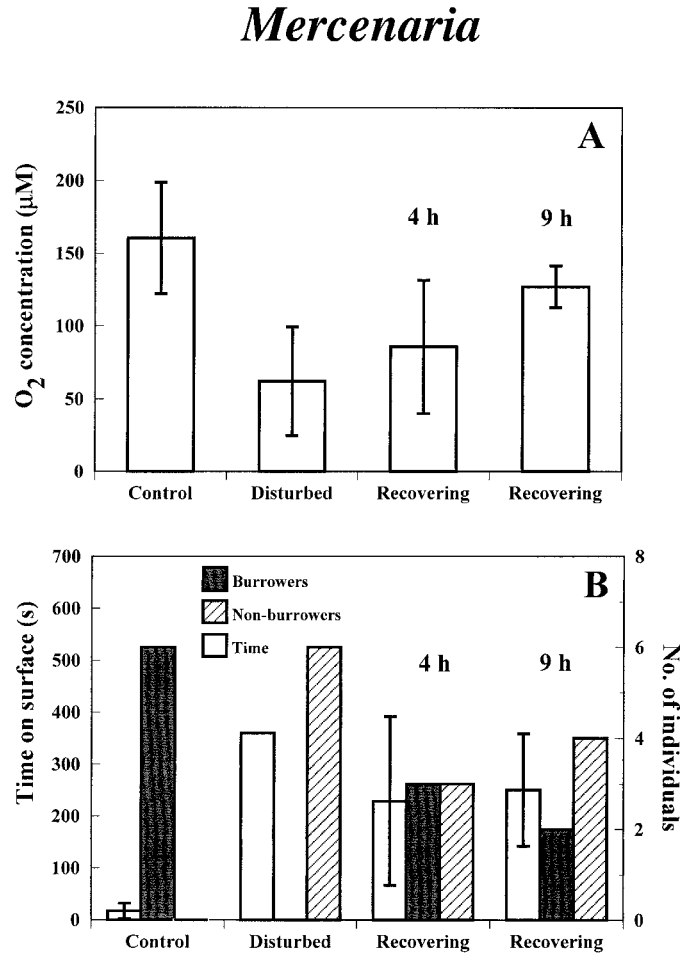
Mercenaria

Fig. 3. *Mercenaria* experiments. (A) Surficial oxygen concentrations (mean ± SD) in Control, Disturbed, and two stages of Recovering cores, Recovering T1 = 4 h, Recovering T2 = 9 h. Analysis of variance revealed significant differences among treatments ($P < 0.05$). (B) Time spent on surface (± SD) in Control, Disturbed, and two stages of Recovering cores (T1 = 4 h, T2 = 9 h; i.e., the amount of time an organism explored the surface during the observation period). Organisms either burrowed (burrowers) or remained on the sediment surface for the entire observation period (nonburrowers). In Control cores, all organisms rapidly burrowed, whereas in Disturbed cores, none burrowed. In Recovering cores, burrowing behavior was highly variable, with some organisms electing to burrow after long exploratory times on the sediment surface.

have features similar to those generated by the model in terms of concentration with depth and gradient steepness. Controls were fully oxic at the sediment surface and gradually dropped to zero a few millimeters below the interface; Disturbed cores had little or no oxygen at the sediment surface or in subsurface regions; Recovering cores showed rapid gains in oxygen concentration (generally in the vicinity of 80–120 μM) at the sediment–water interface but steep declines (i.e., sharp gradients) below the sediment surface. Note the dramatically different oxygen environments within the top 1 mm of sediment, which is the zone of exploration of burrowing individuals (Fig. 1B). Disturbed cores, on average, have little or no oxygen; Recovering cores show a

concentration differential of 30 to 100 μM and Control cores show a concentration differential 150 to 200 μM.

Although there is generally good agreement between the model and data in terms of time scales of recovery, there are discrepancies with regard to prediction of surficial concentration. In the experiments, Recovering cores did not attain the high concentrations observed in Control cores within the windows of experimentation (Figs. 1, 2A, 3A), in contrast to the model prediction. This may be related to inaccuracies in the estimation of the heterogeneous reaction rate term. It was not because of a stagnant boundary layer because, in Control cores, oxygen measurements in the water immediately above core surfaces were similar to oxygen concentrations in the surrounding water bath.

Organism behavioral responses—Arenicola: As predicted, the amount of time new *Arenicola* recruits spent on the surface prior to initiation of burrowing was inversely related to the surficial oxygen concentration, suggesting that disturbance and associated effects on surficial chemistry promoted longer exploratory times or even rejection. The order of times on the surface from fastest to slowest was Control > 2-h Recovering > Disturbed, and the differences were significant (Jonckheere–Terpstra ordered alternatives test; Fig. 2B). All individuals burrowed in the Control and 2-h Recovering cores, but only one of seven burrowed in the Disturbed cores (Fig. 2B). For those organisms that elected to burrow, total burrowing times were significantly shorter in the controls relative to the recovering sediments, suggesting that organisms were more hesitant to adopt the recovering habitat (Fig. 2C; nonparametric Jonckheere–Terpstra ordered alternatives test $P < 0.001$). Because organisms readily accepted cores after 2 h of recovery, we did not test longer recovery times for this species.

Mercenaria: The amount of time that new *Mercenaria* recruits spent on the surface prior to initiation of burrowing also generally tracked oxygen concentration (Fig. 3A,B). No organisms burrowed in the disturbed sediments, but with recovery, 33–50% of the spat burrowed within the observation period (Fig. 3B). Thus, responses of new recruits were consistent with a negative response to disturbance, and a relatively rapid return of the sediment surface to "acceptable" conditions, as indicated by exploratory and burrowing behavior. However, organism responses did not strictly follow surficial oxygen concentration because longer recovery times did not lead to shorter initiation times (4-h recovering vs. 9-h recovering, Fig 3A). Treatment differences in "time on surface" were significant, in the expected order of Control < Recovering T2 < Recovering T1 < Disturbed (nonparametric Jonckheere–Terpstra ordered alternatives test $P < 0.001$).

Discussion

We predicted that disturbance would result in dramatic changes in surface chemical properties and that recovery of these chemical properties to predisturbance conditions would obey transport–reaction processes as dictated by the general diagenetic equation. The oxygen data from our experimental cores are consistent with this prediction. In experiments with *Mercenaria* and *Arenicola,* oxygen values are relatively high in surficial sediments in Control cores, dramatically lower in Disturbed cores, and increasingly oxic in Recovering cores (Figs. 2A, 3A). Although small-scale variation in surface chemical properties is rampant and there was high variability in oxygen concentrations of surficial sediments over short spatial scales, the overall trend of oxygen concentration with disturbance/recovery was significant. The time scales of recovery generally were consistent with model predictions and on the order of minutes to hours. Although complete recovery to predisturbance oxygen conditions was not observed, a return to relatively oxic conditions occurred well within the window of time predicted by the model (Fig. 1A vs. Figs. 2A, 3A). This time period is significantly shorter than that required for re-establishment of bacterial communities subsequent to disturbance (hours to days, *see* Craven and Karl 1984) or microalgal mats (days, Marinelli unpubl. data) and supports our contention that transport–reaction processes govern the changes in surface chemistry to which recruits respond.

The behavior of new recruits generally followed changes in surficial oxygen concentrations and, in several cases, reflected the steepness of oxygen gradients in the upper 1 mm of sediment. In the *Arenicola* experiments, organisms readily accepted sediments that were undisturbed by burrowing immediately and rejected newly disturbed sediments by refusing to burrow (Fig. 2B). In recovering sediments, organisms burrowed (Fig. 2B) but took longer to commit to the habitat, as indicated by the longer burrowing times (Fig. 2C). In several cases involving the Recovering cores, organisms began to burrow, paused, backed out, and then renewed burrowing behavior. Thus, there appeared to be a hesitance associated with selecting the sediments in recovery stages. It is possible that organisms may have sensed the lower oxygen concentrations associated with steeper gradients (Fig. 1A,B) in subsurface sediments in Recovering cores. These steeper gradients are predicted by the model and were observed in the profiles. The chemical and behavioral data, and the model results, suggest that organisms may be sensing a gradient as they burrow and respond as a function of both surface and subsurface chemical conditions.

Similar behaviors were observed with *Mercenaria,* although the data are more variable. While oxygen conditions in Disturbed, Control, and Recovering cores were consistent with model predictions, behaviors of organisms were not strictly in accordance with the oxygen data. As with *Arenicola,* organisms readily burrowed into undisturbed sediments and rejected newly disturbed sediment (Fig. 3B). However, the behavior of organisms in recovering sediments was more variable. We are uncertain as to the cause of this variance because oxygen concentrations showed similar variability among all treatments. Regardless, the behavior of *Mercenaria* was consistent with predictions of rejection of newly disturbed environments and increasing acceptance with recovery.

We chose to evaluate oxygen because it is physiologically important, has strong gradients in surficial sediments, and can be measured on small length scales using microelectrodes. Our ability to gain fine-scale information allowed us

to assess the significance of gradients, as well as surficial concentrations, and provided insight into the conditions under which sediments become acceptable to recruiting organisms. For both the bivalve and the polychaete, we began to see acceptance when surface oxygen concentrations attained 75–100 μM oxygen. However, we are wary of specifying a threshold concentration of acceptance, in part because of the small number of species tested and in part because of high variation in surface chemical properties (Figs. 2A, 3A). We also recognize that many constituents covary with oxygen, according to the stoichiometry of deposited organic material and general diagenetic relationships, and that substances can serve as both positive and negative cues. Our prior experiments with ammonium demonstrate this point. In these experiments, new arenicolid recruits accepted surficial sediments containing comparatively low levels of ammonium (similar to undisturbed conditions), and rejected surficial sediments with higher levels of ammonium (similar to disturbed conditions) (Woodin et al. 1998). However, elevated ammonium has been reported to serve as a stimulus for settlement at very high concentrations (millimolar concentrations of NH_4^+) in certain environments (e.g., Coon et al. 1990). Although we did not measure sulfide, it is possible that sulfide concentrations in surficial sediments also provided a recruitment signal. The role of sulfides as recruitment cues (in the positive sense) has been debated (e.g., Pearson and Rosenberg 1978; Cuomo 1985), and its significance as a recruitment cue remains uncertain (Dubilier 1988). Careful experimentation is needed to evaluate, and perhaps separate, the relative importance of these compounds in natural systems and the extent to which the attractiveness of some porewater cues is related to selective settlement or differential mortality (Woodin 1986). Such experiments should consider variation in organism behavior and physiology because the direction of recruitment signals (positive or negative) is likely a function of both organism sensitivity and environmental context. Finally, we note that fluid dynamic conditions vary in the field and, therefore, so may recovery times. This is particularly true for sands and some muddy sands, where porosities are low, permeabilities are high, and advective flows may hasten solute exchange (Marinelli and Woodin unpubl. data).

We conclude that (1) sediment biogeochemical properties are significant determinants of recruitment on local as well as broad scales and (2) the relationship between chemistry and recruitment is dynamic, reflecting the activities of residents, the behaviors of recruits, and the properties of the habitat. Given the broad availability of diagenetic signals in a range of sedimentary habitats and the existence of such signals over evolutionary time, we suggest that sediment biogeochemical processes form a significant component of the selective regime for new recruits.

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