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Effects of injury and nutrition on sediment reworking by *Clymenella torquata* (Annelida: Polychaeta)

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ABSTRACT

Marine infaunas influence sediment chemistry, nutrient cycling, and microbial communities as they burrow, feed, defecate, and irrigate their tubes and burrows. Nonlethal tissue loss to predators or other disturbances is frequently observed in macrofaunal communities, and previous research has reported significant effects of onetime injury on animal activity. In this study, we examined the effects of injury and nutrient enrichment on sediment reworking rates of a common deposit-feeding polychaete, *Clymenella torquata*. Individual worms in cores were monitored in a recirculating seawater system, and their defecation and sediment mixing monitored under several experimental conditions. Worms held in control (unenriched) sediment or in homogeneously diatom-enriched sediment were injured on days 0 and 7 in a 21 d experiment. Worms held in control sediment or sediment with high surface diatom enrichment were observed in a 7 d experiment following repeated injury. Posterior segments were ablated for the injury treatments, and injury and nutrient supply treatments were crossed in all experiments. Repeated injury significantly decreased surface activities and defecation, and injured worms transported significantly less surface sediment to depth than intact worms. Microalgal enrichment at the sediment surface correlated with an increase in bioturbation; intact worms in surface-enriched sediments were more active and more likely to hoe surface sediments to depth as evidenced by vertical profiles. These findings help explain how infaunal activities are modified by injury and food availability and can be used to improve models of bioturbation to further elucidate complex benthic community dynamics.

Keywords. Benthic ecology, bioturbation, cropping, deposit feeding, infauna, Maldanidae, regeneration, sublethal predation

1. Introduction

In soft-sediment habitats that make up the majority of benthic marine environments, infaunal invertebrates such as polychaetes, clams, echinoderms, and burrowing crustaceans act as ecosystem engineers as they burrow, feed, defecate, and irrigate their tubes and burrows (Berke 2010; Woodin, Wetthey, and Volkenborn 2010; Kristensen et al. 2012). Collectively

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termed bioturbation (sensu Kristensen et al. 2012), these activities alter the sediment structure and pore waters, with important ecological and biogeochemical impacts on varied spatial and temporal scales. For example, biogenic irrigation by marine polychaetes through open tubes and burrows affects diagenetic reaction rates in sediments as changing spatial patterns of pore-water solute concentrations within sediments modify oxidant availability and redox chemistry (Aller and Aller 1998). Vertical redistribution of oxidants in turn alters microbial populations (Jensen 1996; Lei et al. 2010). Maldanid polychaete tube building and irrigation modifies pore-water hydrogen sulfide concentrations (Fuller 1994), and larger-scale trends in reactive organic carbon (OC) flux in continental slope regions correlate with macrofaunal densities (Blair et al. 1994). Thus, polychaetes have important effects on sediment diagenesis, which in turn affects rates of carbon remineralization and its return to the water column. Indeed, polychaetes and other infauna act as hydraulic engineers (Woodin, Wethey, and Volkenborn 2010).

Bioturbation also influences biotic interactions of the sedimentary environment. Infaunal sediment disturbance mediates competitive interactions (Rhoads and Young 1970; Woodin 1976; Brenchley 1981), animal distribution patterns and dispersal (Wilson 1981; Günther 1992), including distribution and dispersal of resting eggs and cysts belonging to planktonic organisms (Marcus and Schmidt-Gengenbach 1986), as well as recruitment (Posey 1986; Luckenbach 1987; Flach 1992; Marinelli and Woodin 2002). The rate of bioturbation will vary according to the frequency and intensity of infaunal activity. In this study, we examine how injury and nutrition influence bioturbation rates in an abundant maldanid polychaete species, *Clymenella torquata*.

Infauna often experience nonlethal tissue loss to predators or other disturbances (reviewed by Lindsay 2010). Repeated injury is highly likely, although few studies have quantified its frequency or effects. Many members of the infauna can regenerate lost tissue, but injuries can affect growth (De Vlas 1979a; Coen and Heck 1991; Kamermans and Huitema 1994), fecundity (Zajac 1985, 1995), feeding behavior (Lindsay and Woodin 1992, 1995), and sediment disturbance rates (Woodin 1984; Lindsay and Woodin 1996). Because sediment disturbance mediates ecological interactions, changes in activity can have indirect effects on the community (Lindsay, Wethey, and Woodin 1996).

Maldanid polychaetes are head-down deposit feeders commonly found in marine benthic habitats ranging from intertidal zones to the continental slope. Conveyor-belt feeders, these worms ingest bulk sediment at depth and deposit feces on the sediment surface (Mangum 1964; Rhoads 1967). Additionally, *C. torquata* uses posterior segments to hoe surface sediment rapidly down to the feeding pocket just below the bottom opening of its mud- or sand-encrusted tube (Dobbs and Whitlatch 1982). Posterior segments are frequently injured during defecation or hoeing (Mangum 1964; Dobbs and Whitlatch 1982; Clavier 1984), and tissue loss to predators occurs frequently enough that biomass production from regeneration in maldanids can be a significant source of energy to higher trophic levels (De Vlas 1979a; Clavier 1984). *C. torquata* regenerates the number of segments lost, maintaining its original 22 segments following injury (Sayles 1932). Relatively few studies have documented

effects of injury on polychaete bioturbation. Following a single injury of posterior segments, *Axiiothella rubrocincta* defecated significantly less frequently and produced less egesta relative to intact worms but did not alter tube production (Woodin 1984). In *C. torquata*, loss of posterior segments may result in a switch between hoeing of surface sediments and subsurface feeding.

Food supply is likely to affect bioturbation by polychaetes (e.g., Hymel and Plante 2000; Michaud, Aller, and Stora 2010). Deposit feeders, such as *C. torquata*, ingest material of low bulk food value; this strategy constrains them to feed at very rapid rates (Jumars et al. 1990). In temperate regions such as the Gulf of Maine, sediment nutritive value fluctuates due to seasonal large-scale phytoplankton and phytobenthos blooms and subsequent deposition of phytodetritus (Charette et al. 2011). Such seasonality is likely to result in temporally variable food quality and quantity for subtidal *C. torquata* populations, but intertidal food supplies may be less variable due to nutrient delivery from terrestrial systems. Episodic pulses of material can be buried quickly and deeply (Levin et al. 1997).

Nutrient caching (Jumars et al. 1990) is one possible response to large seasonal fluctuations in food availability. Evidence of a long-term “food bank” of labile organic material in sedimentary habitats has been described previously for the Gulf of Maine and other high-latitude locations (Mincks, Smith, and DeMaster 2005; Smith, Mincks, and DeMaster 2006; McClintic et al. 2008; Smith and DeMaster 2008; Weissberger et al. 2008). Nutrient caching may be an advantage for regenerating maldanids because a cached high-quality food supply is available without risk of injury. A cache of labile organic matter may also increase the rate of regeneration, thereby reducing the time of increased vulnerability due to injury. However, an outcome of posterior injury may be that maldanids are less likely to hoe sediments from the surface. If hoeing is the primary mechanism to rapidly subduct nutrients, caching may be temporarily reduced while animals regenerate. If injury occurs during a seasonal phytoplankton bloom, individuals may experience long-term food limitation due to a lack of stored nutrients.

Given the significant role that maldanid polychaetes can play in sediment subduction and bioturbation (Rhoads 1967; Levin et al. 1997), the frequency at which they experience injury (see references in Lindsay 2010), and the potential for sediment nutritive quality to influence their deposit feeding, we investigated the following questions: (1) Do single or repeated injuries affect *C. torquata* bioturbation rates? (2) Does homogeneous sediment enrichment or surface sediment enrichment affect *C. torquata* bioturbation rates? (3) Is there an interaction between single or repeated injury and sediment enrichment? In particular, is hoeing of enriched surface sediment reduced following injury?

2. Methods

Two laboratory experiments were conducted. The first experiment, lasting 3 weeks, was conducted in July 2010 to evaluate effects of single and repeated injury and sediment enrichment on growth and activity in *C. torquata*. This experiment compared the effects of

single and repeated injury with concurrent low-level, homogeneous microalgal enrichment. A second laboratory experiment (2 weeks) was conducted in August 2011 to evaluate the effects of repeated injury and surface sediment enrichment on activity in *C. torquata*. Posterior segments were removed twice, and worm activity and the resulting bioturbation were monitored over a 7 d interval following the second ablation.

a. Worm collection

Adult *C. torquata* and sediment were collected in July 2010 and August 2011 from a large intertidal flat of mixed sand and mud on the northwestern side of West Quoddy Head peninsula in Lubec, Maine (44°48' N, 66°58' W), and transported in coolers to the University of Maine, Orono, Maine. *C. torquata* is patchily distributed on this tidal flat, and average densities in the area ranged from ~38 to ~2,100 individuals m⁻² depending on season and location (S. M. Lindsay, unpublished). The sedimentology of the flat is described by Walsh (1988). At the University of Maine, worms were held in their collection sediment in a 76 × 76 × 22 cm deep recirculating seawater tank, which had an average temperature of 17°C and average salinity of 33 ± 1 ppt measured daily. Twenty-four hours after collection, sediment was gently sieved through a 1 mm mesh screen, and worms were removed from tubes and evaluated for obvious injury. Worms used for these studies were considered intact if no evidence of recent injury was visible (i.e., no missing or small segments). Worms were not fed during the 24 h between collection and use in the experiments.

b. Injury treatments and handling

For both experiments, worms of similar sizes were randomly assigned to the four treatment groups: intact worm with control sediment (intact control, or IC), intact worm with enriched sediment (intact enriched, or IE), injured worm with control sediment (ablated control, or AC), and injured worm with enriched sediment (ablated enriched, or AE). To examine the effects of single or repeated injury and homogeneous sediment enrichment, a total of 72 *C. torquata* were observed ($n = 18$ for all treatments). To examine the effects of repeated injury and surface enrichment, 64 *C. torquata* were observed ($n = 16$ for all treatments). Worms were weighed using a Mettler Toledo AX205 balance, then anesthetized in a 3.5% solution of MgCl₂ in seawater and photographed using a Color Mosaic Spot camera mounted on an Olympus SZ-40 stereomicroscope. Mean starting wet weights for worms in all treatment groups were similar (grand mean ± 95% confidence interval [CI]: 2010, 97.01 mg ± 16.99 mg; 2011, 131.26 mg ± 10.10 mg).

Posterior segments of worms in injured treatment groups were ablated using a razor blade to remove the pygidium and five adjacent segments on day 0 of the homogeneous enrichment experiment, and 7 d prior to the initiation of the surface sediment enrichment experiment, which only examined effects of repeated injury on worm activity. This loss approximated that observed in field studies, where ~50% of regenerating individuals had lost four to six posterior segments (Sayles 1932). Following the initial injury, injured and

control worms were either placed in their experimental cores (homogeneous enrichment experiment) or maintained in individual cores of field sediment in the recirculating seawater system for 1 week (surface enrichment experiment). Regenerated tissue plus two posterior segments were ablated from worms assigned to injury treatments 7 d following the initial injury (i.e., day 7 of the homogeneous enrichment experiment, day 0 of the surface sediment enrichment experiment). All worms in the homogeneous enrichment experiment were handled, photographed, and weighed on days 7 and 14; wet weights were used to calculate relative growth rates (RGRs) according to the equation $RGR = [\ln(W_1) - \ln(W_0)] / t_1 - t_0$ (Fisher 1921). Following all surgeries/handling, worms recovered in seawater for ~30 min before adding them to sediment-filled cores within the experimental seawater tank. All worms burrowed within ~20 min following addition to cores.

c. Sediment preparation and tracer addition

Individual worms were held in PVC cores (depth 15 cm, inner diameter 4 cm) filled with enriched or unenriched azoic sediment. The bottom opening of each core was covered by 1 mm window screening to prevent worms from escaping. Cores were placed in the seawater tank in an alternating intact worm/injured worm pattern with control sediment cores placed “upstream” from enriched sediment cores to lessen the chances of worms responding to concentrated enrichment cues that might leach from other cores.

Azoic sediment was prepared by freezing field sediment for a minimum of 24 h (-3°C). Sediment was then thawed and sieved (half through a 0.5 mm screen, half through a 1 mm mesh screen), mixed in equal parts, washed in seawater twice, and stirred by hand to create a relatively homogeneous mixture. For the homogeneous enrichment, a microalgal concentrate (*Thalassiosira weissflogii*, Reed Mariculture, Campbell, CA) was mixed into one-half of the homogenized azoic sediment (1% by volume); the other half of the sediment was not enriched (control). This enrichment level was selected based on a study done by Levin et al. (1997) examining rapid surface subduction on the continental shelf off the coast of North Carolina. Batches of enriched and unenriched (control) sediment were stored at 3°C until use. For surface sediment enrichment, *T. weissflogii* was added to sediment “cookies” (~45% by volume, see below), and this resulted in an order of magnitude increase in bioavailable amino acids (Table 1). Analyses of bioavailable amino acids in sediments (enzymatically hydrolyzable amino acids) were performed by the Mayer Lab (University of Maine), according to methods described by Mayer et al. (1995).

Red glass microbeads were used as surface sediment tracers to track weekly vertical sediment movement. Microbeads (5 mL, 0.4–0.6 mm diameter, Blockheads Paper Arts, Portland, OR) were added to the sediment surface of each core 24 h after addition of worms. For the surface enrichment experiment, frozen surface sediment “cookies” were prepared similarly to the method for tracer delivery in the field outlined by D’Andrea, Lopez, and Aller (2004). Cookies were prepared in aluminum foil trays by thoroughly mixing the following ingredients: for control cookies, 2.5 mL sediment, 5 mL microbeads,

Table 1. Weekly mean concentrations of enzymatically hydrolyzable amino acids (EHAAs) for control field sediment and diatom-enriched field sediment in the two experiments.

Experiment	Control sediment EHAAs concentration \pm SD (μg amino acid g^{-1} dry weight sediment)	Enriched sediment EHAAs concentration \pm SD (μg amino acid g^{-1} dry weight sediment)
Single and repeated injury with homogeneous sediment enrichment		
Week 1	313.6 \pm 62.1	456.7 \pm 39.0
Week 2	471.0 \pm 21.2	517.6 \pm 28.1
Week 3	630.7 \pm 169.5	808.4 \pm 95.0
Repeated injury with surface sediment enrichment		
Week 1	229.7 \pm 51.4	2,482.3 \pm 174.6

and 2.5 mL seawater; and for enriched cookies, 2.5 mL sediment, 5 mL microbeads, and 2.5 mL microalgal concentrate (*T. weissflogii*, Reed Mariculture). Sediment cookies (8 mm thickness) were frozen at -3°C and stored in plastic bags until use, when they were added to the sediment surface of each core 24 h after addition of worms. When thawed on the surface of cores, the layer of beads was ~ 2 mm thick. Worm tubes and fecal piles were visible on the new sediment surface within 24 h of bead/cookie addition.

d. Activity observations

Cores were monitored daily for general surface features such as fecal piles, tubes, and sinkholes. Twice each week, feces produced over a 3 h time interval were collected using a plastic, flat-bottomed weighing tray. A standard hole punch was used to produce a hole in the tray to fit over the worm tube. After 3 h, trays were removed, and feces deposited on the tray were rinsed in freshwater twice before drying overnight (60°C). Dry mass of feces was determined, then samples were dried overnight a second time (60°C), and dry mass was measured again; the average of the two mass measurements was used for analysis.

In the surface enrichment experiment, we monitored worm activity on the surface of cores as a potential indicator of surface sediment relocation to depth within the 7 d following the second posterior injury. A time-lapse camera (PlantCam by Wingscapes, Alabaster, AL) was used to monitor behaviors during 3 h intervals on days 3, 4, 6, and 7, with photos taken every 30 s. Images were analyzed by eye for surface changes. Four behaviors were recorded and tallied as evidence of surface activity: posterior segments at tube opening, posterior segments extended out of tube, defecation, and hoeing (evidenced by drag marks). Not all cores were within the field of view, and behaviors were scored only for worms that were visible on all days ($n = 3$ for IC, IE, and AC; $n = 2$ for AE).

e. Bioturbation measurements

Destructive subsampling of one-third of cores occurred each week in the homogeneous enrichment experiment. On days 7, 14, and 21, these cores were carefully removed from the

experimental tank, placed upright to drain for 24 h, and sliced into 1 cm vertical sections. Worms not included in destructive subsampling were handled weekly as described previously and then returned to their respective cores in the seawater tank. In the surface enrichment experiment, all cores were placed in a -3°C walk-in freezer and frozen solid following the 7 d observation period. To section, frozen sediment cores were placed in a modified caulking gun, sediment was extruded in 1 cm intervals, and sediment was cut using a Craftsman multitool.

Sediment cross sections were dried, crushed, and sieved before counting microbeads. Specifically, sections in the homogeneous enrichment experiment were dry-sieved through a $500\ \mu\text{m}$ screen, then wet-sieved through a $500\ \mu\text{m}$ screen; sediment sections in the surface enrichment experiment were dry-sieved through a $300\ \mu\text{m}$ screen and then a $500\ \mu\text{m}$ screen. Samples with greater than ~ 30 beads were later wet-sieved through a $300\ \mu\text{m}$ screen. This combination of screen sizes best captured the microbeads, which ranged from 0.4 to 0.6 mm in diameter. Beads in subsurface sections (i.e., below 1 cm depth) were counted using an Olympus SZ-40 stereomicroscope or an Ultra Optix $2.5\times$ handheld magnifying lens.

Surface export for all samples was calculated as the proportion of beads in each vertical section relative to the average number of beads added to the surface of each core (18,089 beads). The average number of beads in 5 mL was determined by digitally photographing (Nikon D5000 camera) seven replicate 5 mL samples of beads and counting the beads using the NIH software package Image J (<http://rsbweb.nih.gov/ij/>). To compare mechanisms of bead movement, bead counts in vertical sections below 1 cm were categorized as surface mixing and subduction or nonlocal mixing due to hoeing. Beads were considered relocated by surface subduction and mixing if they were found in a layer(s) below, but continuous with, the surface bead layer. Beads were considered relocated by hoeing if they were found in a vertical layer(s) below the surface that was separated from the surface bead layer by at least a 1 cm vertical section with zero beads.

f. Statistical analyses

Statistical analyses were performed using the software program R (www.r-project.org/). Statistical comparison for most types of data included ANOVA with either Tukey's honest significant difference (HSD) or Fisher's least significant difference (LSD) multiple comparisons. Data were transformed if necessary to meet assumptions of normality and homogeneity of variance, but untransformed data are presented. When sample sizes were too small for ANOVA, differences among treatments were inferred from CI comparison (Cumming, Fidler, and Vaux 2007). Vertical section data were evaluated based on standard errors.

3. Results

These studies reveal significant effects of repeated injury (i.e., one injury per week for 2 weeks) on growth, defecation, surface behaviors, and vertical redistribution of glass microbeads by *C. torquata*; effects of single injury were less apparent. Surface sediment

enrichment influenced *C. torquata* surface behaviors and glass microbead vertical profiles, and low-level homogeneous nutrient enrichment caused slight changes in defecation by *C. torquata*. Tube production in *C. torquata* was unaffected by injury or sediment enrichment, consistent with published results from a previous study by Woodin (1984).

a. Growth

Because the primary focus of these experiments was on measures of sediment disturbance, we only monitored worm growth in the homogeneous sediment enrichment experiment. During the first week, all worms lost weight (Fig. 1) and injury had a significant impact on RGRs (Fig. 1a; two-way ANOVA: injury, degrees of freedom [df] = 1,42, Mean Square [MS] = 0.003, $F = 10.05$, $P = 0.003$), but neither sediment enrichment or the interaction terms were statistically significant. During the second week, intact worms gained weight, whereas twice-injured worms lost weight (though less than during the first week; two-way ANOVA: injury, df = 1,18, MS = 0.003, $F = 12.73$, $P = 0.002$); twice-injured worms in enriched sediment tended to have higher growth rates than those in unenriched sediment (Fig. 1a), but this result was not statistically significant. On average, RGRs over 14 d were significantly lower for injured worms (Fig. 1a; two-way ANOVA: injury, df = 1,18, MS = 0.005, $F = 79.8$, $P < 0.0001$). As a percent of initial body mass, both single and repeated injury significantly reduced worm body mass over the 2-week experiment compared with intact worms (Fig. 1b; day 7 two-way ANOVA: injury, df = 1,43, MS = 935.6, $F = 8.972$, $P = 0.004$; day 14 two-way ANOVA on log-transformed data: injury, df = 1, MS = 0.18, $F = 79.81$, $P < 0.0001$), but homogeneous sediment enrichment had no significant effect.

b. Defecation

Defecation by worms injured twice was very different than that by worms injured only once. Compared with intact worms, the proportion of worms defecating following a single ablation of five segments in *C. torquata* was reduced for worms in control sediment 3 d following ablation (Fig. 2a); however, worms recovered quickly, and the proportion defecating did not differ significantly from intact worms by 6 d postablation. Following a second ablation on day 7, only two injured worms defecated on day 10, and by 6 d after the second injury (i.e., day 13), only 58% of injured worms defecated. At the end of the second week following repeated injury, 50% fewer intact worms in low-level homogeneously enriched sediment defecated (Fig. 2a), and this trend was also observed in ablated worms, with 20% fewer worms defecating when in enriched sediment.

Injury also affected the mass of feces produced by worms (Fig. 2b). Over the first experimental week, all individuals showed a trend of increasing fecal mass indicating recovery from initial handling. Three days following a single ablation, average fecal mass from injured worms was statistically less than from intact worms (two-way ANOVA on log-transformed data: injury, df = 1,46, MS = 2.94, $F = 20.68$, $P < 0.0001$).

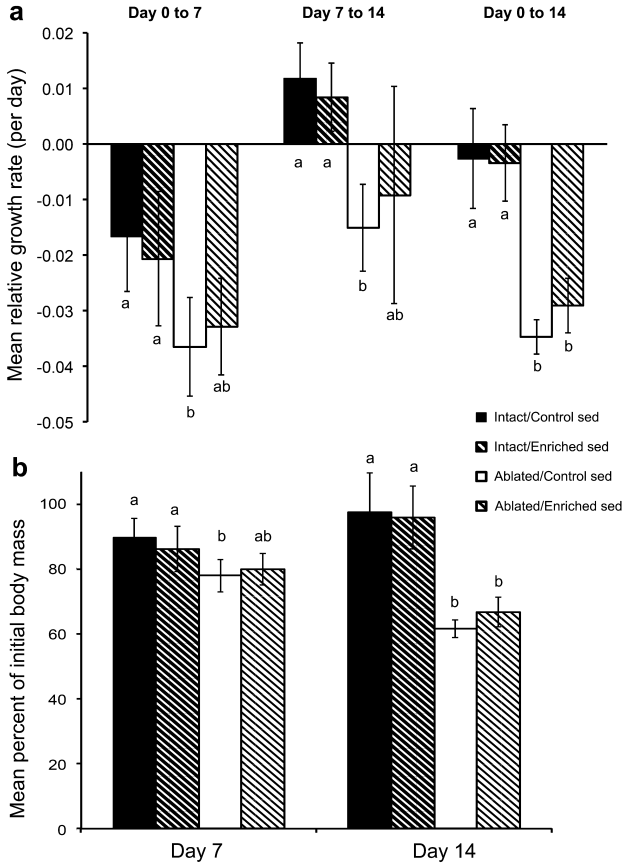


Figure 1. Effects of injury and homogeneous sediment enrichment on *Clymenella torquata* growth; injured worms were ablated on day 0 and again on day 7. (a) Weekly and cumulative relative growth rate: $\ln(\text{mg}) \text{d}^{-1}$, mean \pm 95% confidence interval (CI). Within each time period, lowercase letters indicate results of Fisher's least significant difference (LSD) multiple comparisons of means; means with different letters are significantly different ($P \leq 0.05$). Sample sizes varied: $n = 11$ or 12 worms per treatment days 0 to 7; $n = 5$ or 6 per treatment days 7 to 14 and days 0 to 14. (b) Percent of initial body mass (mean \pm 95% CI; $n = 11$ or 12 worms per treatment day 7; $n = 5$ or 6 worms per treatment day 14). Within each day, means with different lowercase letters are significantly different at $\alpha = 0.05$ level (Fisher's LSD multiple comparisons, $P \leq 0.05$).

By day 6, no statistically significant differences were observed among treatments (two-way ANOVA, $P > 0.05$). Three days following repeated injury, feces produced by the only two injured worms that defecated weighed < 10 mg. Fecal mass produced by injured individuals remained significantly lower than that produced by intact worms during the week following the second injury (day 13, two-way ANOVA on square-root-transformed data: injury, $df = 1,31$, $MS = 295.78$, $F = 49.93$, $P < 0.0001$;

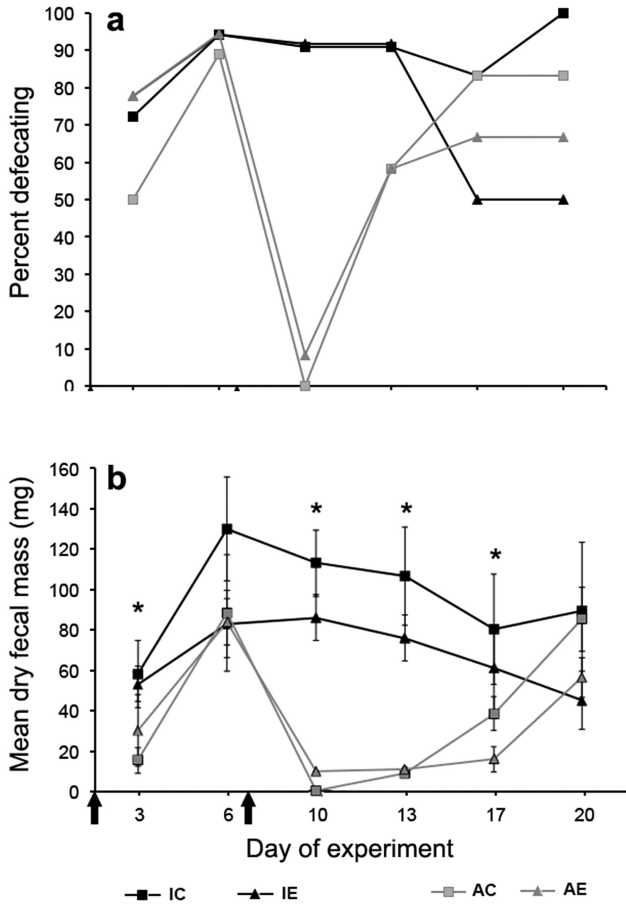


Figure 2. Effects of injury and homogeneous sediment enrichment on defecation by *Clymenella torquata*. (a) Proportion of individuals defecating; AE and IE proportions were identical on day 3. Sample sizes varied due to destructive sampling: $n = 18$ worms per treatment in week 1; $n = 12$ per treatment week 2; $n = 6$ per treatment week 3. (b) Mean (± 1 SE) mass of feces produced in 3 h by individuals that defecated. Treatments: IC (intact worm in control sediment), IE (intact worm in enriched sediment), AC (ablated worm in control sediment), and AE (ablated worm in enriched sediment). Arrows indicate posterior ablation on days 0 and 7 for injured worms; intact worms were not ablated. The number of defecating worms in each treatment varied due to destructive sampling and worm activity, ranging from $n = 9$ to 17 during week 1, $n = 1$ (AE and AC day 10) to 11 during week 2, and $n = 3$ to 6 during week 3. Stars indicate statistically significant differences (two-way ANOVA for injury, $P < 0.05$) between intact and ablated treatments. Day 10 significance inferred from 95% confidence interval due to low sample sizes.

day 17 two-way ANOVA on square-root-transformed data: injury, $df = 1, 13$, $MS = 36.27$, $F = 4.67$, $P = 0.05$). Worms in control sediment tended to defecate more than worms in enriched sediment relative to their respective intact or injured treatment groups; however, this trend was not statistically significant, and by day 20, fecal mass for all treatment groups was similar (two-way ANOVA on log-transformed data, $P > 0.05$; Fig. 2b).

We observed similar patterns and magnitude of defecation frequency and fecal mass for worms in the repeated injury with high-level surface enrichment treatments. At 3 d following the second injury, no injured worms in control sediment defecated, and only 6% of injured worms in surface-enriched sediment defecated (producing an average of 4.5 mg of feces). In contrast, 94% of intact worms in control sediment and 88% of intact worms in surface-enriched sediment defecated, producing on average 74 mg and 86 mg of feces, respectively. On day 6, only 44% of injured worms defecated in either the control or surface-enriched sediments, whereas 94% and 100% of intact worms in control and enriched sediments, respectively, defecated. Again, the average fecal mass produced by injured worms was significantly less than that produced by intact worms (AC = 8.2 mg, AE = 9.4 mg, IC = 99 mg, IE = 84 mg). Although injury significantly reduced defecation measures, no differences were observed due to surface enrichment or interaction (two-way ANOVA on square-root-transformed data, $P > 0.05$).

c. *Surface activity*

Surface activity by *C. torquata* changed in response to both repeated injury and surface sediment enrichment. The percent of time worms were engaged in surface behaviors (defecation, posterior segments extended out of tube, posterior segments at mouth of tube, and probable hoeing as evidenced by drag marks on the surface) varied among treatment groups (Fig. 3a). Small sample size in the AE treatment precluded ANOVA, but a Kruskal-Wallis test indicated a significant effect of treatment on total surface activity (adjusted $H = 8.08$, $df = 3$, $P = 0.04$). Overall, injured worms exhibited less frequent surface behaviors than intact worms, and worms with surface enrichment had more frequent surface behaviors than worms in control sediment (Fig. 3a). Intact worms with surface enrichment were observed at the surface approximately three times more frequently than intact worms in control sediment and injured worms in enriched sediment (Fig. 3a). Intact worms with surface enrichment engaged in probable hoeing more frequently (by an order of magnitude) than worms in the other three treatments (Fig. 3b).

d. *Sediment mixing vertical profiles*

Vertical profiles constructed from 1 cm interval microbead counts reveal some interesting features of worm bioturbation occurring over 7 d. In cores from the surface sediment enrichment experiment, microbead proportions declined sharply over the top few centimeters for all treatments, indicative of surface subduction from feeding at depth in addition to diffusive mixing; however, intact worms in control sediment subducted a greater proportion of beads

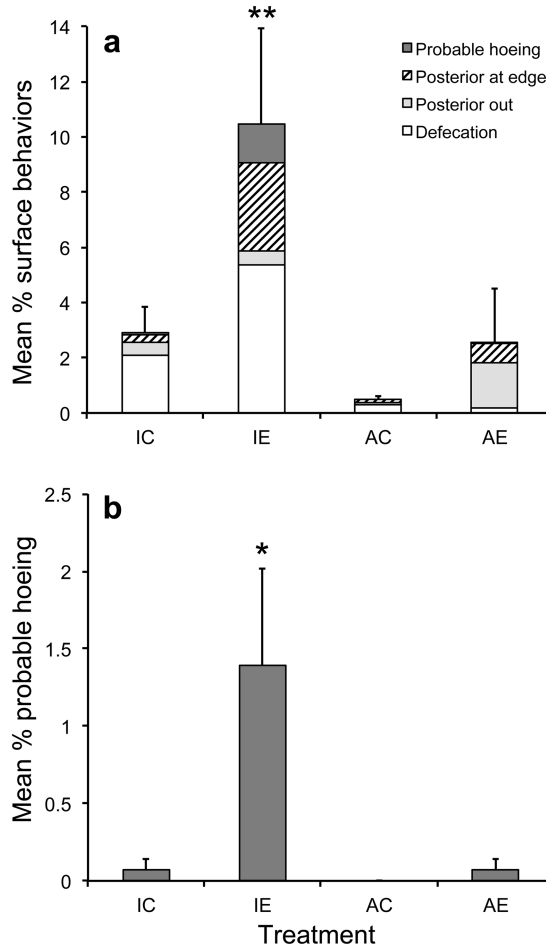


Figure 3. Percent of time worms engaged in behaviors linked to types of sediment subduction during the surface enrichment experiment. (a) Mean (± 1 SE) percent of photos showing surface activity (entire column), with columns subdivided to indicate proportion of photos showing defecation, posterior segments extended out of tube, posterior segments at the edge of tube, and probable hoeing evidenced by drag marks. (b) Mean (± 1 SE) percent of photos showing drag marks due to probable hoeing. Treatments: IC (intact worm in control sediment), IE (intact worm in enriched sediment), AC (ablated worm in control sediment), and AE (ablated worm in enriched sediment). $n = 3$ worms (IC, IE, AC) or 2 worms (AE). Asterisks in panel (a) indicate significant difference between IE and AC for total surface activity determined by 95% confidence interval (CI) comparison. Asterisk in panel (b) indicates percent of probable hoeing behavior in IE is significantly different from IC, AC, and AE (90% CI comparison). Total of 1,440 photos scored for each worm.

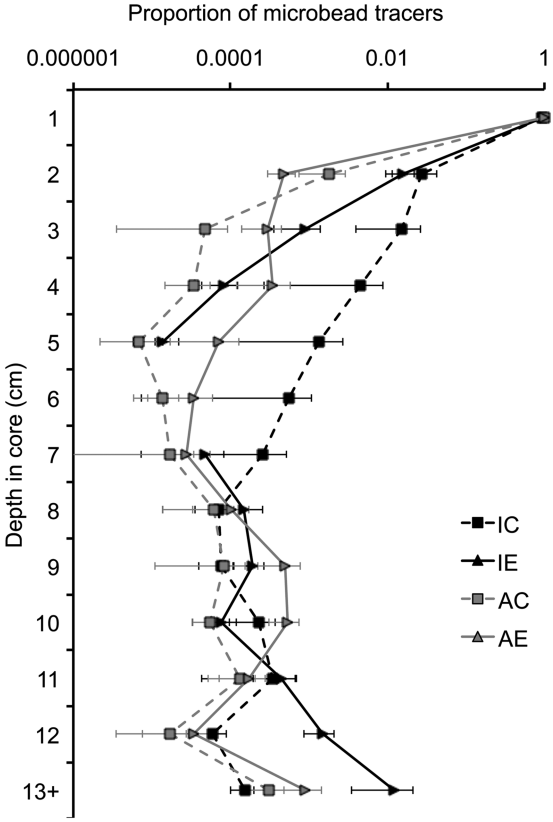


Figure 4. Vertical profile of microbeads transported by *Clymenella torquata* over 7 d following repeated injury with surface-enriched sediment. Treatments: IC (intact worm in control sediment), IE (intact worm in enriched sediment), AC (injured worm in control sediment), and AE (injured worm in enriched sediment). Segments were ablated 1 week prior to the start of the experiment and again at day 0 for injured worms or not at all for intact worms. Bars represent ± 1 SE; $n = 16$ worms per treatment.

down to 7 cm, illustrated by the gradual slope of the profile (Fig. 4). Also, the shape of the profiles in the top few centimeters revealed two patterns: (1) a log-linear pattern for intact worms in both control sediment and enriched sediment; and (2) a steeply sloped pattern over the top 2 or 3 cm, and then a dramatic shift to an overall vertical pattern in the centimeters below for injured worms in both control and enriched sediment. At depths below 7 cm, we observed subsurface microbead maxima in all treatments, suggesting rapid drawdown of surface material via hoeing, but the greatest proportion of microbeads at depth occurred with intact worms in enriched sediment. Vertical profiles constructed for treatments comparing single and repeated injury with homogeneous sediment enrichment ($n = 6$) showed no

significant differences among treatments but did show evidence of subduction and hoeing (data not shown; see Campbell 2012).

e. Hoeing and surface subduction

Methods of feeding by *C. torquata* appear to be modified by injury and surface sediment enrichment, based on a comparison of total subsurface glass microbead tracers attributed to hoeing and surface subduction mechanisms (Fig. 5). The only treatment with a significant difference between surface subduction and hoeing was IC, both in terms of percentage and number of microbeads. In this treatment group, ~74% of microbead tracers were moved to depth via surface subduction (Fig. 5a), and the mean number of microbead tracers attributed to surface subduction was significantly greater than hoeing (90% CI comparison; Fig. 5b). Interestingly, the number of microbeads relocated by hoeing increased for intact worms in enriched sediment, consistent with the photographic evidence that these worms had the most probable hoeing events recorded. As a percentage of the total beads exported from the surface, relocation of microbeads by hoeing by injured worms also tended to be greater than that for intact worms in control sediment (Fig. 5b). However, the mean number of microbeads relocated via surface subduction for intact worms in control sediment (average 866 microbeads) was significantly greater than either surface subduction or hoeing in all injured worm treatments (90% CI comparison).

A significant injury \times transport mechanism effect was observed for percentage of microbeads below 1 cm (three-way ANOVA with Tukey's HSD: injury \times behavior interaction, $df = 1, 18$, $MS = 21, 086$, $F = 15.24$, $P < 0.01$). Trends indicate that intact worms in either sediment type showed a greater proportion of microbeads relocated by surface subduction relative to hoeing (>50% bead export attributed to surface subduction; Fig. 5). Injured worm treatments in both sediment types appeared to have the opposite pattern, with more microbeads relocated due to hoeing relative to subduction (>50% bead export attributed to hoeing; Fig. 5). On average, intact worms in either sediment type moved significantly more microbeads than injured worms (three-way ANOVA: injury, $df = 1, 18$, $MS = 3, 702, 601$, $F = 5.89$, $P = 0.02$). Because tube building by maldanids appears not to be affected by injury (this study; Woodin 1984), the impact of injury on transport is primarily due to such feeding activities.

Overall, injured worms in both sediment types moved relatively few beads over the 7 d interval following repeated injury (injured worms in control sediment: on average 47 microbeads; injured worms in enriched sediment: average 63 microbeads). On average, injured worms in enriched sediment did hoe more than three times more microbeads than injured worms in control sediment, but this difference was not statistically significant (three-way ANOVA, $P > 0.05$).

4. Discussion

Based on preliminary studies, we expected repeated injury to cause greater reductions in bioturbation than single injury. This study provides evidence that bioturbation resulting

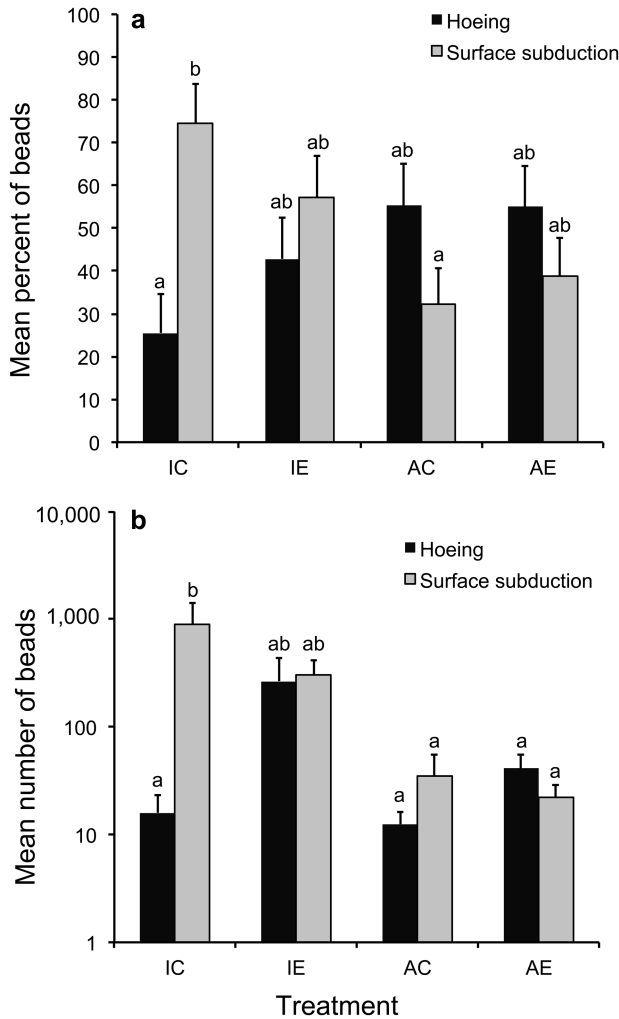


Figure 5. Movement of surface glass bead tracers below 1 cm by *Clymenella torquata* via surface subduction or hoeing during the surface enrichment experiment. (a) Mean (± 1 SE) percent of beads below 1 cm depth attributed to subduction or hoeing; $n = 16$ worms per treatment. (b) Mean (± 1 SE) number of beads below 1 cm depth attributed to subduction or hoeing; $n = 16$ worms per treatment. Treatments: IC (intact worm in control sediment), IE (intact worm in enriched sediment), AC (ablated worm in control sediment), and AE (ablated worm in enriched sediment). Segments were ablated 1 week prior to the start of the experiment and again at day 0 for injured worms and not at all for intact worms. For each graph, bars sharing a letter were not significantly different by 95% confidence interval (CI) comparison (a) or 90% CI comparison (b).

from feeding and defecation by *C. torquata* is significantly reduced following a repeated posterior injury. Removal of posterior segments once in 2 weeks significantly reduced defecation only in the 3 d following injury. In contrast, defecation data strongly suggest that feeding is drastically reduced relative to controls for several days following a second injury in 2 weeks (Fig. 2). Tissue regeneration, both in terms of structure (e.g., sphincter) and function, plays a key role in feeding behavior of injured worms; these data suggest differences in regeneration that depend on the frequency of injury. Alternatively, following a second injury, these head-down deposit feeders may become risk averse and temporarily modify their behavior to avoid yet another immediate injury; if worms do not eat, they will not be exposing their posterior segments at the surface during defecation. Risk averse foraging has been documented for some surface deposit feeders following injury but not others (Lindsay and Woodin 1995). In the current study, defecation data suggest that worms recovered during the second week following repeated injury.

The presence of a layer of fresh algal material deposited on the seafloor may increase rapid surface sediment drawdown by head-down deposit feeders that exhibit hoeing, such as *C. torquata* (Levin et al. 1997). Temporary OC storage at depths of even 10 cm allows modification and processing of food molecules by macrofauna, meiofauna, and bacteria. Indicators of hoeing by twice-injured *C. torquata* were greatly reduced compared with intact worms (i.e., percent of surface activity attributed to hoeing, Fig. 3b; and number of microbead tracers relocated due to hoeing, Fig. 5b). These data suggest that potential risks and perhaps associated physiological costs outweigh the potential gain from hoeing. Depending on the frequency and its occurrence, repeated injury in a population could significantly reduce the amount of fresh OC stored, at least temporarily, below the sediment surface.

The results of this study suggest that repeated injury does alter the relative frequency of feeding mechanisms, as predicted. In the week following injury, we observed reductions in both surface subduction and hoeing by worms, as indicated by tracers. Interestingly, we also observed changes in the apparent method by which worms relocated microbeads, suggesting that changes in feeding mechanism also occurred following repeated injury. Subsurface feeding appears to be the dominant method of surface sediment transport in intact worms; however, following repeated injury, hoeing was more frequent (Fig. 5a), although the absolute number of microbead tracers relocated due to hoeing was not significantly different from that relocated by intact worms. This result contradicts a conclusion that twice-injured worms showed risk-averse behaviors. Perhaps, without predators present, the worms had no cue other than experienced injury to indicate whether continued exposure of posterior segments during hoeing might be risky. Certainly, risk-averse responses to injury are not always observed. Lindsay and Woodin (1995) found that *Rhynchospio gluatensis*, a surface-deposit-feeding spionid polychaete, continued to expose anterior segments on the surface to feed following loss of its feeding palps; however, another species, *Pseudopolydora kempji japonica*, did not.

Differences in microbead abundance versus depth in the few centimeters below the sediment surface also indicate a difference in subsurface feeding patterns between intact and injured *C. torquata* (Fig. 4). Log-linear profiles for intact worms in both control and enriched surface sediment are signatures of near-surface vertical mixing, in this case resulting from noticeable subsurface feeding at depth. The mechanism appears to be vertically diffusive for two reasons. First, sinkholes of varying diameters and depths result from variation in feeding rates and sediment properties. Second, slicing the cores for sampling averages horizontally. When worms are injured, this pattern disappears, and relatively little surface sediment is transported past 2 cm depth. This dampened effect of local mixing, despite the presence of bioturbators, is likely due to behavioral modifications in response to repeated injury. These results suggest using caution when estimating sediment reworking based on worm population densities without taking into account their injury status, as injury appears to greatly decrease bioturbative signals at the frequencies examined, and probably even more so at higher frequencies. Thus, it would be helpful to know not just the proportion of individuals injured in a population, but also how frequently they are injured. Also, a comparison of bioturbation results for cumulative vertical sediment transport and snapshot measurements of defecation suggests that caution is warranted in making conclusions based on a single data collection method. Defecation data convey valuable information regarding worm activity, but they do not include the role of gravity in subduction. Sediment profiles provide useful context to interpret behaviors on longer temporal scales, and subtle changes may become evident.

a. Homogeneous sediment enrichment

As expected from previous studies, injury had a significant impact on worm growth immediately following injury (Fig. 1). However, RGR data collected in the homogeneous enrichment experiment indicated faster growth rates for 7 d following repeated injury compared with single injury (Fig. 1a), and injured worms in enriched sediment tended to have faster RGRs than injured worms in control sediment (Fig. 1a), although this latter pattern was not statistically significant. No significant differences in the surface area of regenerated tissue were observed between injured worms in control sediment and injured worms in enriched field sediment over the 3-week time frame of this experiment (data not shown; see Campbell 2012). However, worms in control sediment regenerated more tissue overall (18.5%, day 7; 21.5%, day 14) than worms in enriched sediment (Campbell 2012). Perhaps energy-reserve molecules, such as lipids, provided a buffer to mass loss after the first injury. However, at the time of the second injury, energy reserves may not have been restored. Worms in control sediment may have utilized a greater amount of energy stores, and this visibly resulted in a greater relative weight loss compared with injured individuals that were consuming more nutrient-rich material. Taken together, these observations of growth suggest that a compensatory response might be possible following repeated injury and that sediment enrichment might “rescue” worms from the impact of injury on growth. An

interesting note in this experiment was that half of the worms in control sediment autotomized one segment within the week following second injury, whereas no autotomy was observed for worms in homogeneous enriched sediment. The lack of autotomy by worms in enriched sediment may indicate that enrichment effectively reduced physiological stress.

Although homogeneous nutrient enrichment may have enhanced regeneration rate, it appeared to have little effect on sediment processing (i.e., defecation; Fig. 2) or vertical patterns of downward sediment movement (Campbell 2012). However, this level of enrichment may have been too low for worms to detect and respond to, and given the observed variances, tests would have benefited from larger sample sizes. Bioturbation (sensu Kristensen et al. 2012) includes tube ventilation (bioirrigation), which we did not monitor in this experiment, but which also may have been reduced due to injury. Defecation and tube irrigation by *C. torquata* occur cyclically but not simultaneously (Mangum 1964), and both move water in the tube. Irrigation by *C. torquata* may be subsidized by water movement that produces pressure gradients around the tube (e.g., Vogel and Bretz 1972; Huettel and Gust 1992). So in our experimental system, with low flow rates, and reduced feeding due to injury, homogeneous enrichment of the sediment might have resulted in changes in the redox conditions of the sediment, especially at depth. This is relevant because Fuller (1994) found that elevated hydrogen sulfide levels can decrease fecal production by *C. torquata*. We did not monitor pore-water chemistry in this experiment, except to note whether sediments were relatively oxygenated or black or smelled of sulfur when we sectioned them. In this experiment, we only observed five cores that smelled of sulfur, and these were sectioned on day 21. All of these cores contained enriched sediment; however, in two cores, there was no worm, and in a third, the worm had died. Thus, it seems unlikely that the low-level homogeneous enrichment was sufficient to depress feeding via changes in redox chemistry of the sediments, especially in the first 2 weeks of the experiment. However, as with any laboratory experiment, our estimates of feeding rates may not be directly comparable to field activities.

C. torquata likely utilizes some particle selectivity during feeding, based on the principle of lost opportunity described by Jumars et al. (1990). If there is a change in the bulk sediment nutrient content, the rate at which sediment passes through the gut may be modified. Longer gut residence times allow greater digestion and absorption (Penry and Jumars 1986). If the ratio of nutritional organic material in sediment increases, and sediment continues to pass through the gut at the same rate as when organic content is low, some usable food molecules may not be absorbed. A maximum rate of absorption must exist, but until this rate is reached, it would seem likely that worms may slow the passage of food through their guts to increase residence time of food molecule uptake prior to defecation, assuming linear or hyperbolic kinetics. Alternatively, if the rate of sediment processing is not altered due to nutritional content, it could be assumed either that food quantity and quality do not vary enough to be limiting or that the energetic costs of “digestive rate adjustment” are not worth the increased food uptake. The trend observed in both the rate and amount of defecation observed at day 20 of this study suggests retention of food in the gut of worms when sediment is even slightly enriched (Fig. 2).

b. Surface sediment enrichment

Subsurface maxima reported in deep-sea systems (Smith and Schafer 1984; Smith, Jumars, and DeMaster 1986; Graf 1989; Jumars et al. 1990) and the North Carolina continental slope (Blair et al. 1996) have been attributed to nonlocal transport and possibly caching. In this study, surface enrichment was designed to be at a high level to stand out from background field sediment levels, modeling the deposition of fresh algal material to the benthos in subtidal populations. Observations of subsurface maxima in sediment tracers at depth, indicative of hoeing, appeared in all treatments, but the largest peaks occurred at 9 to 10 cm (injured worms in enriched sediment) and at 12 to 13 cm (intact worms in enriched sediment; Fig. 4). These data suggest that enriched surface sediment leads to an increase in surface material moved to depth by both intact and injured worms. This study provides evidence that *C. torquata* shows selectivity for high levels of surface enrichment, especially intact worms, which is contrary to conclusions drawn by Levin et al. (1997) that *C. torquata* may be nonselective in its feeding.

Previous studies have not evaluated effects of injury on surface behavior and hoeing in *C. torquata*. Trends over 7 d indicate that intact worms with an enriched surface layer spent greater time at or above the surface relative to intact worms without this sediment enrichment or injured worms in either sediment type (Fig. 3). Statistically significant differences ($P \leq 0.05$) were observed between intact worms with enriched surface sediment and injured worms in control sediment, but not for injured worms in enriched sediment. The combination of repeated injury and control sediment produced lower worm surface activity. Repeated injury or enrichment alone did not produce the same significant result. Although the observations of probable hoeing were not suitable for testing by ANOVA and are highly variable, observations of greater hoeing by intact worms in enriched sediment suggest a positive correlation between surface sediment enrichment and worm activity.

C. torquata populations occur from the intertidal to the continental shelf and experience differing food supply patterns in such habitats, which may modify responses to increases in food quantity and quality. *C. torquata* specimens in this study were collected from an intertidal location, and background control field sediment was collected at an adjacent site. Typically, worms living in intertidal and shallow subtidal locations have a more consistently nutrient-rich food source due to shallow depths and the predominance of benthic diatom populations, relative to deep subtidal worm populations that experience short, semiannual bursts of pelagic phytoplankton feasts delivered to the benthos, interspersed with longer periods of relative famine. Subtidal benthic populations experience surface changes in surface sediment nutrient levels on timescales similar to this study following the spring and fall phytoplankton blooms. Intertidal worm populations also experience variation in surface nutrition, as is evident with the growth of thick diatom mats in the spring that lessen by midsummer.

Based on the results in this study, we can predict that behavioral patterns of time spent at the surface will differ between intertidal and deeper subtidal populations. Subtidal populations may significantly increase their surface time following the major bloom events,

with rapid bursts of intense activity. Intertidal populations may also increase their surface time, but over an extended nutritionally rich season of months rather than days or weeks, depending on the rate of the bloom collapse. Injury in *C. torquata* is frequent over this depth range (Sayles 1932, 1934; Moment 1951; Mangum 1964), often attributed to predation (De Vlas 1979a, 1979b) and human activities (intertidal digging and subtidal trawling; Lindsay 2010). Injury likely dampens the expected increase in surface behavior signal during periods of surface enrichment.

Surface sediment enrichment does appear to alter some surface behaviors and may impact worm physiological state. Perhaps even modest increases in surrounding sediment nutrition can lessen the impacts of injury on the individual. For populations, this could mean increased survival and greater reproductive potential over time. Phytoplankton supply may directly alter these effects, and changes in phytoplankton bloom dynamics and species composition due to climate change or other factors may have unanticipated impacts on the benthos.

In summary, sedimentary habitats are ubiquitous in oceans and organisms that live within these habitats modify them. Such bioturbation (*sensu* Kristensen et al. 2012) has profound effects on the biology, geology, chemistry and physics of the habitat and on ecological interactions. Thus, factors that influence bioturbation rates can have cascading effects. As this study demonstrates, both food availability and injury by themselves can alter sediment disturbance rates by infauna, and food availability may modify infaunal responses to injury. Both factors are likely to influence temporal and spatial distribution of sediment mixing, and this should be considered in models of sediment reworking.

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