

Effects of abiotic stressors on infaunal burrowing and associated sediment characteristics

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ABSTRACT: Infauna play key roles in nutrient cycling and bioturbation by facilitating exchange across the sediment–water interface, but the effects of environmental stressors on the behavior of infauna are poorly studied compared to epifauna. Here we used laboratory experiments to examine the effects of temperature (15, 21, and 32°C), salinity (16, 22, 28, and 34), and food availability (low, moderate, high) on the burrowing activity of the opportunistic deposit-feeding polychaete *Capitella* sp. 1. We also used pH and O₂ fluorosensors to investigate the effects of burrowing on marine sediment chemistry. Worms buried significantly deeper at 21 than at 15°C, and they died at 32°C. Salinity only marginally affected the area of burrowing activity, with greater area at 35 than at 22. Burrows in highly enriched treatments were significantly more shallow than those in moderate and low food treatments. The fluorosensors showed that the exchange of solutes between the sediment and overlying water was associated with burrowing activity. These results show that changes in environmental conditions affect infaunal burrowing activity, which in turn affects sediment characteristics. We discuss the need to consider infaunal responses to abiotic stress in order to understand community and ecosystem responses to environmental changes associated with climate change, pollution, and eutrophication.

KEY WORDS: Annelid · Geochemistry · Mudflat · Multiple stressors

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INTRODUCTION

Infaunal invertebrates are crucial to the health of marine soft sediment ecosystems, playing key roles in nutrient cycling and bioturbation (Aller 1982, 2001, Thibodeaux & Bierman 2003). As they feed and move through the sediment, they release regenerated nutrients including ammonia, which increases primary productivity in the water column (Biles et al. 2002). By facilitating exchange across the sediment–water interface, bioturbators also regulate oxygen within the sediment (Kristensen 2000, Zorn et al. 2006) and determine the bacterial composition of the infaunal community (Kogure & Wada 2005). Bioturbators can also hasten the remediation of contaminated sediments, either directly through feeding or indirectly through the proliferation of associated bacteria (Cunningham et al.

1999, Kogure & Wada 2005). Infaunal biogenic structures interact with bacteria in sediments to form complex, 3-dimensional redox and protonic reaction patterns that are reflected in the microscale distributions of biogeochemical properties such as oxygen and pH (Wenzhofer & Glud 2004, Zhu et al. 2006).

Many animals actively or passively irrigate their burrows in order to respire, obtain food, or excrete waste products (reviewed by Kristensen & Kostka 2005). Irrigation facilitates solute exchange within the sediment and between the sediment and water (Mermillod-Blondin et al. 2005), thereby increasing nutrient regeneration rates (Heilskov et al. 2006), degradation of pollutants (Hansen et al. 1999), and oxygen penetration in sediments (Luther et al. 1998). Irrigation rates are associated with feeding and burrow types (Kristensen & Kostka 2005). For example, head-down, or conveyor-

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belt feeders have been shown to have stronger irrigation effects than surface deposit feeders (Quintana et al. 2007).

Due to the importance of bioturbators in ecosystem health and functioning, knowledge of how environmental stressors may affect the behavior of infauna is crucial for impact assessments and predictive modeling. The effects of temperature on the metabolism of marine invertebrates have been well studied, with warmer waters associated with higher metabolic rates, up to a species-specific maximal threshold (Przeslawski et al. 2008). Higher temperature can accelerate infaunal feeding and burrowing activity (Hymel & Plante 2000, Ouellette et al. 2004) and therefore irrigation (Kristensen & Kostka 2005), while extremely high temperatures can reduce activity (Sobral & Widdows 1997). Similarly, salinity deviating from conditions normally found in a given habitat can negatively affect the physiology of marine invertebrates (Roberts et al. 2006). Low salinity due to freshwater input has been shown to decrease infaunal abundance of some species (Zipperle & Reise 2005, Rutger & Wing 2006, McLeod & Wing 2008, but see Ford et al. 2007), while high salinity due to evaporation or industrial effluent can alter infaunal communities (Del Pilar Ruso et al. 2007). Food availability can vary according to temperature, salinity, and other abiotic factors (Cheng et al. 1993) and has been shown to affect bioturbation. Increasing nutrient levels promote higher infaunal abundance (Webb 1996, Reiss & Kroncke 2005) and burrowing rates (Hymel & Plante 2000), but excessive nutrient enrichment can negatively affect infauna due to associated anoxia from proliferation of microorganisms and metabolites (Pearson & Rosenberg 1978, Kelaher & Levinton 2003).

Capitella sp. 1 is an opportunistic deposit-feeding polychaete, a member of the *Capitella* species complex (Grassle & Grassle 1976). Capitellids feed by ingesting sediment and digesting organic nutrients from any associated particulate (Hu et al. 2003), thereby creating 'conveyor belt' sediment profiles in which sediment is transported from depths to the surface (Hansen et al. 1999). These species are often used as model organisms in environmental impact (Hu et al. 2003, Mendez 2006) and developmental (Qian & Chia 1991, 1993, Pechenik et al. 2001) studies due to their tolerance for pollutants and the ease with which they are cultured. Although less than 2 cm long, *Capitella* sp. 1 has been found in densities up to 200 000 ind. m⁻² in organically-enriched sediments (Grassle & Grassle 1974), and its population peaks during periods of high food availability (Kelaher & Levinton 2003) where it feeds in the upper layer of sediment (Linton & Taghon 2000).

Our objective was to determine the effects of changing environmental conditions on the burrowing activ-

ity of *Capitella* sp. 1 and the associated effects on sediment chemistry and irrigation. We used 3 factorial laboratory experiments to expose worms to salinity, temperature, and food availability treatments, and we recorded burrowing activity and associated biogeochemical gradients. We predicted that burrowing activity would be greatest in moderate conditions and that oxygen and pH gradients in the sediment would be strongly affected by burrowing activity, reflecting greater irrigation. Previous studies have examined the effects of multiple abiotic factors on marine bioturbation rates (Levinton & Stewart 1988, Hymel & Plante 2000, Lardies et al. 2001, Kristensen & Kostka 2005), but to our knowledge, this is the first time that such effects have been directly linked to sediment characteristics. Results from this study will contribute to future research examining the effects of environmental change on infaunal communities and related ecosystem processes, including effects due to pollution, eutrophication, and climate change.

MATERIALS AND METHODS

Culture of worms. *Capitella* sp. 1 were obtained from established cultures at Rutgers University, New York. Worms were cultured at 15°C in 0.45 µm filtered seawater with salinity of 28. Sediment was collected from Flax Pond (Long Island, NY, USA), filtered through a 200 µm sieve, and frozen until use. Seawater and sediment were changed fortnightly by filtering cultures through a 200 µm sieve as per culture protocols from Rutgers University, and a small amount of ground organic spinach was added to each culture. Worms with egg cases were placed into a separate container that was not touched for 4 wk. This allowed larvae to grow until they were large enough not to be lost during sieving.

For each experiment, adult non-brooding worms were randomly selected from cultures. The lengths of each stationary worm were recorded to ensure that worm size was similar across all treatments. There was no difference in initial worm size across salinity ($F = 1.0658$, $p = 0.3958$), temperature ($F = 2.5842$, $p = 0.0817$), and food availability ($F = 0.8274$, $p = 0.4411$) treatments, as confirmed by 1-way ANOVAs.

Sediment and animals were introduced into plastic microcosm chambers with exterior dimensions 10 × 10.5 × 1.4 cm (height × width × depth) and wall thickness 0.2 cm, allowing imaging of sedimentary properties through the transparent sides. For each experiment, all chambers were fitted along the larger interior walls with O₂ fluorosensors on 1 side and pH fluorosensors on the other, with the exception of the food availability experiment, in which only O₂ fluorosensors

were used. Due to reactions observed on the polystyrene O₂ sensor during the salinity experiment, O₂ membranes were coated with a protective gas-permeable silicon layer for the remaining experiments. Each chamber was then filled partially with sediment and submerged in a larger water bath with gently flowing 2 µm filtered seawater to ensure some water flow into chambers during the experiments. Water flow in each larger container was approximately 0.57 cm s⁻¹, confirmed by a neutrally buoyant bead. For each experiment, 10 worms were added to each chamber. Light was excluded from the chambers for the duration of the experiment, as diurnal fluctuations in solute exchange rates may occur due to variations in macrofaunal and meiofaunal activity (Karlson 2007).

Sediment was added to each chamber and allowed to settle for at least 4 h. For all experiments, photographs were taken of each chamber at the beginning (0 h) and end of the experiment (48 h). For each chamber, visible images were taken of both sides, and fluorescent images were taken of the pH and O₂ sensors on alternate sides. Visible images and oxygen gradients were recorded in all experiments, and pH gradients were recorded for the salinity and temperature treatments only. Visible images were used to measure depth of the individual burrows (Fig. 1A) and the area of burrowing activity within each chamber (Fig. 1B) using the image analysis software Image J v.1.38. The depth of a burrow was the maximum depth reached by a single burrow, including branches and sealed burrows (Fig. 1A). The area of burrowing activity was determined by using high-contrast images with burrows reduced to lines from which image analysis software calculated the total area (Fig. 1B). Both oxygen and pH patterns were imaged using planar optodes. The oxygen fluorosensor measured phosphorescence quenching by oxygen of

the luminescence of platinum (II) mesotetra(pentafluorophenyl)porphyrin (Pt-PFPP), which was embedded in a transparent polystyrene membrane backed by a polyester sheet (Precht et al. 2004). Oxygen quenching was quantified using steady fluorescence response and a modified form of the Stern-Volmer equation (Klimant et al. 1995). pH fluorosensors were made as described by Zhu et al. (2005). pH was quantified using the pH dependent ratiometric fluorescence response of 8-hydroxy pyrenetrisulfonic acid (HPTS) covalently bonded to a transparent polyvinylalcohol membrane backed by a polyester sheet. The image analysis programs Image Pro Plus and Maxim DL were used for fluorescence image manipulations and pseudocolor conversions as described by Zhu et al. (2005).

Effects of temperatures. Worms were exposed to cool (15.4 ± 0.3°C, mean ± SD), moderate (21.1 ± 0.3°C), and extreme (31.5 ± 0.1°C) temperatures in filtered seawater (salinity of 28) for 48 h. Treatments were chosen based on 1984 records from Flax Pond, in which summer temperatures on the sediment surface reached 34°C and temperatures at 5 cm sediment depth reached 26°C (J. Levinton unpubl.). Thus, our chosen high temperature was an ecologically realistic extreme. Three replicate chambers were used in each treatment, as well as one control chamber without worms in each treatment. A temperature-controlled room was used for the cool treatment; an aquarium heater in the water bath was used for the hot treatment; and the moderate treatment was left at room temperature. All water baths and chambers were subjected to the treatment for at least 4 h before the worms were added, thus ensuring homogenous temperatures in both water and sediment. Chambers in each treatment were monitored with thermal microchips (ACR Smart Button) for the duration of the experiment.

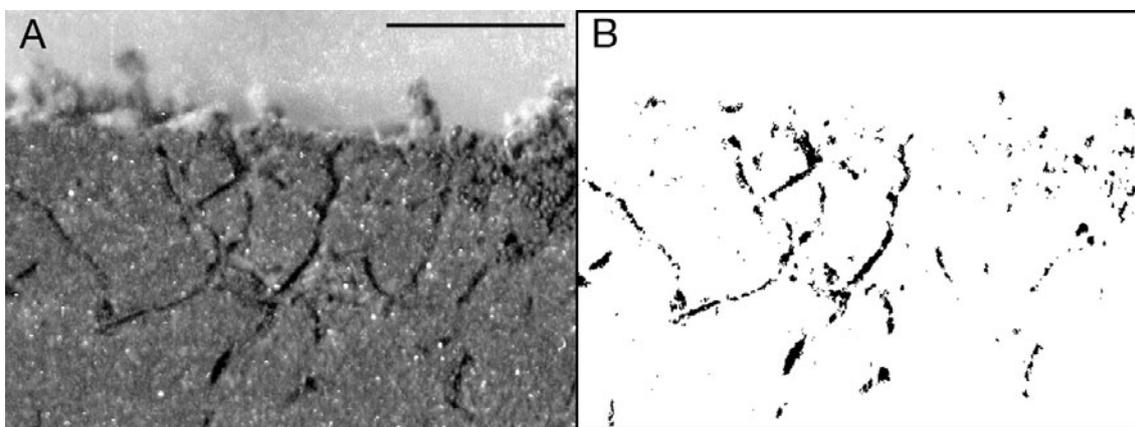


Fig. 1. *Capitella* sp. 1. Burrows 48 h after temperature treatment of 21°C: (A) image with enhanced contrast, used for quantification of burrow depth, and (B) binary image created using the threshold function in Image J software, used for quantification of the area of burrowing activity. Scale bar = 1 cm

Effects of salinity. Worms were exposed to salinities of 16, 22, 28, and 34 for 48 h at 15°C. Three replicate chambers were used in each treatment. Salinity treatments were achieved by adding distilled water to filtered seawater of salinity 28 that had been previously evaporated by boiling to a salinity of 40. Salinity was confirmed with a refractometer. Treatments were chosen based on records from Flax Pond, in which *Capitella* sp. is found (J. Levinton unpubl.), as well as previous records of salinity tolerance for this genus (Pechenik et al. 2001).

Effects of food availability. Worms were exposed to low, moderate, and high food availability for 48 h in a salinity of 28 at 15°C. Three replicate chambers were used in each treatment, as well as 1 control chamber without worms in each treatment. Food availability was achieved by adding varying amounts of desiccated ground *Ulva rotundata* to sediment: (1) Low: no *Ulva* added; (2) Moderate: 1.35 g *Ulva* per 63 cm³ sediment; and (3) High: 4.99 g *Ulva* per 63 cm³ sediment. These quantities have been recorded in the field (Levinton & Stewart 1988) and have been previously used in field-based experiments with *Capitella* spp. (Kela-her & Levinton 2003).

Statistical analyses. ANOVAs were performed on burrow area, using an arcsine transformation due to binomial distribution (Zar 1998). Nested unbalanced ANOVAs (REML) were performed on burrow depth. Tukey's HSD tests were used to identify significant relationships between treatments. Statistical analyses were conducted using the R statistical platform (v.2.5.1).

RESULTS

Effects of temperature, salinity, and food availability

No burrows were detected in the 32°C treatment. Subsequent examination revealed that most worms in this treatment died during the experiment, and this treatment was therefore excluded from statistical analyses. Temperature did not affect burrow area ($df = 1$, $F = 0.5383$, $p = 0.5038$; Fig. 2A), but it did significantly affect burrow depth ($df = 1$, $F = 7.1521$, $p = 0.0080$). Burrows in the 21°C treatment were deeper than burrows at 15°C (Fig. 2B).

Salinity significantly affected burrow area ($df = 3$, $F = 4.2194$, $p = 0.04593$); burrow area in the 35 salinity treatments was greater than that in the 22 salinity treatments (Fig. 3A). Salinity did not affect burrow depth ($df = 3$, $F = 1.4145$, $p = 0.2375$), although there was a significant difference among chambers within treatments ($df = 8$, $F = 5.2450$, $p < 0.0001$; Fig. 3B).

Food availability did not affect burrow area ($df = 2$, $F = 2.0032$, $p = 0.2156$; Fig. 4A), but it did affect burrow

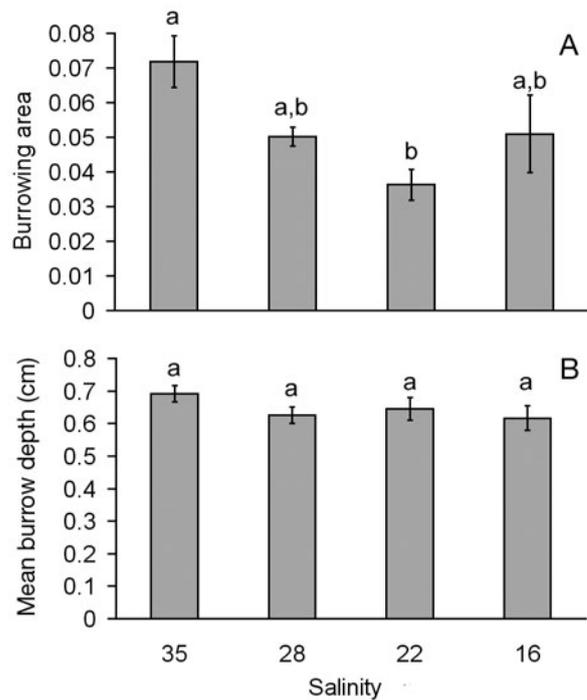


Fig. 2. *Capitella* sp. 1. Effects of temperature on (A) burrowing area and (B) burrow depth. Burrowing area represents cm² of burrows per 1 cm of sediment surface. No burrows were detected in the 32°C treatment, and this treatment was excluded from statistical analyses. Error bars are SEM. Different letters indicate significant relationships at $\alpha = 0.05$

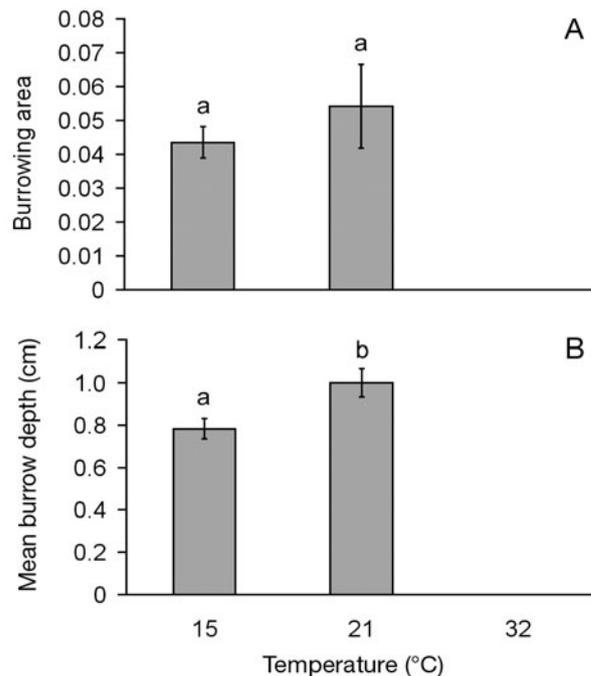


Fig. 3. *Capitella* sp. 1. Effects of salinity on (A) burrowing area and (B) burrow depth. Burrowing area represents cm² of burrows per 1 cm of sediment surface. Error bars are SEM. Different letters indicate significant relationships at $\alpha = 0.05$

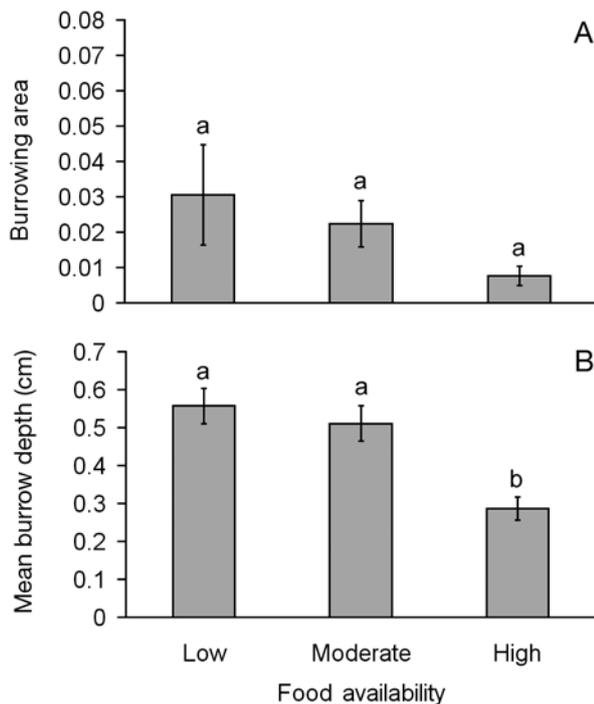


Fig. 4. *Capitella* sp. 1. Effects of food availability on (A) burrowing area and (B) burrow depth. Burrowing area represents cm² of burrows per 1 cm of sediment surface. Error bars are SEM. Different letters indicate significant relationships at $\alpha = 0.05$

depth (df = 2, $F = 9.0192$, $p = 0.0002$); burrows in high food availability treatments were significantly shallower than burrows in the low and moderate treatments (Fig. 4B).

Effects of burrowing on oxygen and pH

Burrowing activity of *Capitella* sp. 1 affected sediment oxygen and pH. Sediment in which burrowing occurred showed increased oxygen penetration depth, pH gradients, and complex distribution patterns associated with irrigated burrows (Figs. 5A,B, 6A,B, and Figs. S1–S3 in the online Supplement, available at: www.int-res.com/articles/suppl/m392p033_app.pdf). In contrast, chambers in which no worms burrowed (controls and 32°C) revealed horizontally stratified oxygen and pH distributions with depth (e.g. 32°C chambers in Figs. 5C, 6C).

Most burrows showed small or no oxygen differences with the surrounding sediment (Fig. 5A,B, Fig. S1). However, some burrows had increased oxygen levels similar to the surface, at approximately 50% oxygen relative to the surrounding water, and these effects radiated 1 to 2 mm from the burrow (Fig. 5A,B). Oxygenated burrows usually extended from the burrow base up to the surface (Fig. 5A,B), but occasionally

the burrows would be sealed (Fig. S1B). Tubes that protruded above the sediment surface showed similar oxygen concentrations throughout the entire burrow, with approximately 50% oxygen relative to the surrounding water (Fig. 5B). Within a treatment, chambers showed high variability of oxygen gradients, but there was no obvious difference in the ratio of oxygenated and non-oxygenated burrows across treatments for any of the experiments.

pH distributions demonstrate the most dramatic effects of irrigation, with the most pronounced and deepest alteration evident when burrowing depth was greatest at 21°C (Fig. 6B). Most bioturbated areas showed relatively homogenous gradients across several burrows, in which pH was approximately 0.4 units higher than non-bioturbated sediment (Fig. 6). Several burrows showed dramatic evidence of active irrigation, including vertical burrows (Fig. S3B) and U-shaped burrows (Fig. S3C) in which pH was up to 1.0 units higher than non-bioturbated sediment and similar to surrounding water.

DISCUSSION

The burrowing activity of *Capitella* sp. 1 was affected by temperature, salinity and food availability, and sediment chemical properties were affected by capitellid burrowing patterns. The effects of abiotic factors on bioturbation observed are likely linked to physiology and associated behavior. This study suggests that the depth of capitellid burrows increases with warmer temperatures up to a lethal threshold under 32°C. Warmer temperatures are well known to increase invertebrate metabolism and activity (Hymel & Plante 2000, Ouellette et al. 2004), and it may be that deeper capitellid burrows in warmer waters reflect increased activity. However, burrowing area was not different between 15 and 21°C treatments, suggesting there may be another reason for observed effects of temperature on burrow depth. Deeper burrowing at high temperatures may be an instinctual response of capitellids to burrow deeper, presumably to escape warm temperatures via the vertical thermal gradient that can exist in natural soft sediment environments (Tsubokura et al. 1997, Lardies et al. 2001). Alternatively, deeper burrowing may reflect an increased food requirement imposed by higher temperatures, thereby producing a relative response similar to that observed in both the low and moderate food availability treatments. Compared to temperature, the effects of salinity on burrowing activity were less pronounced, with only a single significant difference detected in burrowing area between the 22 and 35 salinity treatments. Due to the relatively consistent level of burrowing activity

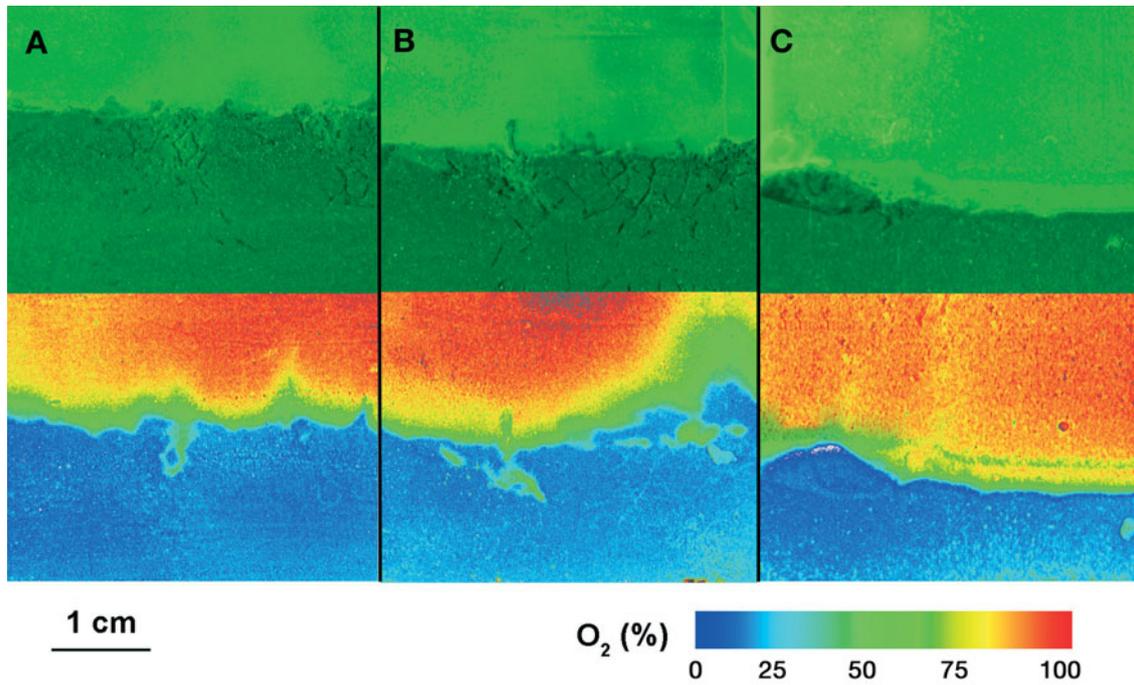


Fig. 5. *Capitella* sp. 1. Effects of capitellid burrowing on oxygen gradients across 3 temperature treatments: (A) $15.4 \pm 0.3^\circ\text{C}$, (B) $21.1 \pm 0.3^\circ\text{C}$, and (C) $31.5 \pm 0.1^\circ\text{C}$. Worms died in the hottest treatment, and no burrows were formed. Top panels represent photos taken in visible light (green band). Bottom panels represent O_2 planar optode pseudocolor images (O_2 scale key at lower right: % saturation at experiment temperature)

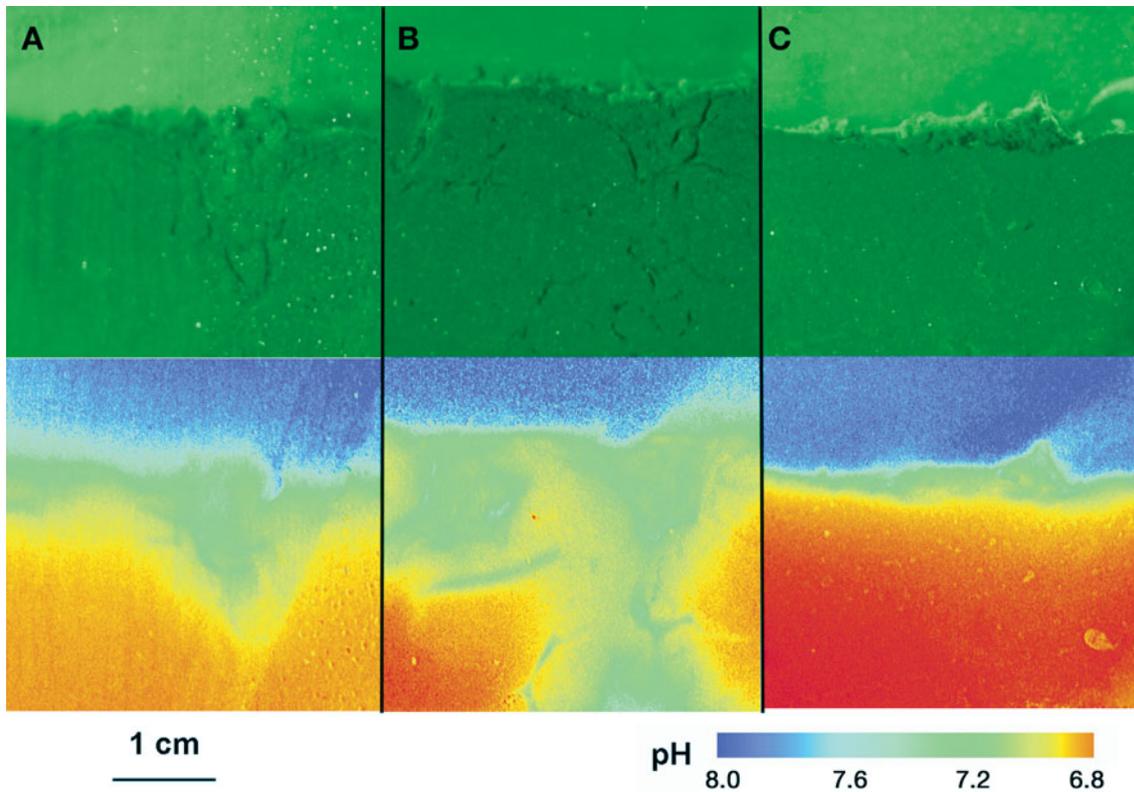


Fig. 6. *Capitella* sp. 1. Effects of capitellid burrowing on pH across 3 temperature treatments: (A) $15.4 \pm 0.3^\circ\text{C}$, (B) $21.1 \pm 0.3^\circ\text{C}$, and (C) $31.5 \pm 0.1^\circ\text{C}$. Worms died in the hottest treatment, and no burrows were formed. Top panels represent photos taken in visible light (green band). Bottom panels represent pseudocolor images of sediment pH corresponding to the overlying visible images (pH color key at lower right)

across salinity treatments, it seems likely that *Capitella* sp. 1 is tolerant to continuous exposure to low salinities for at least 2 d (the duration of the current experiments). Finally, food availability affected burrowing activity, with significantly shallower burrows occurring in high nutrient treatments compared to other treatments. The deeper burrowing that we observed in lower nutrient treatments may reflect a larger foraging area during periods of low food availability. If this is the case, the effects of bioturbation will extend into deeper sediments during periods of low food availability and warm temperatures. Alternatively, food availability may be linked to another factor that affected burrowing behavior, such as increased sulfides. Further research measuring burrowing activity, food availability, and organic sediment chemistry may help separate these potentially confounded factors.

As revealed by the fluorosensors, there is a direct correspondence among burrowing activity, biogeochemical heterogeneity and sediment–water solute exchange. In particular, pH distributions, which reflect acid–base reaction balances and proton fluxes, were sensitive measures of the increased irrigation and solute exchange that occurs as burrowing depth and activity increase (Fig. 6). Previous research has similarly shown that the other species of ‘conveyor belt-feeding’ capitellids have very strong but discontinuous irrigation effects (Quintana et al. 2007). *Capitella* sp. 1 may also passively irrigate tubes that protrude above the sediment surface (Libelo et al. 1994; Fig. 5B). Although O₂ penetration into sediment and redox reaction heterogeneity was clearly enhanced by irrigated burrows, these effects were muted relative to those observed for pH. The differences between the apparent intensity of irrigation effects on the O₂ and pH patterns as a function of variables such as temperature may reflect extremely high rates of O₂ consumption in the experimental sediments. If this were the case, high rates of oxygen consumption were likely due to the reoxidation of metabolites as sulfides or microbial respiration, as *Capitella* sp. 1 has a low rate of oxygen consumption compared to other infauna (Chareonpanich et al. 1994). In other words, metabolic activity and oxidation reaction rates may have been so dominant that O₂ was completely depleted at depth around burrow structures despite the overall increased rates of irrigation and associated solute transport and sediment–water fluxes.

Our results suggest that environmental stressors affect burrowing activity of infaunal invertebrates and associated ecosystem functioning. For example, warmer temperatures such as those predicted under climate change models (Solomon et al. 2007) may actually promote deeper burrowing of some infauna such as *Capitella* sp., thereby allowing penetration of oxy-

gen and pH further into the sediment and possibly allowing for colonization of other infauna and microbes (Wu et al. 2003, Kogure & Wada 2005). However, if the temperatures are high enough, infauna may die, which would lead to a loss of irrigation and pronounced pH and oxygen strata in the sediment, potentially causing dramatic community changes (Herringshaw & Davies 2008). Nonetheless, the current study did not allow for acclimatization of worms to the hot treatment, and it may be that capitellids can adapt to the more gradual changes of progressively warming sediment on hot days. In addition, environmental changes may alter the food availability to infauna by changing the algal or microbial communities upon which many infauna depend for nutrition. Finally, salinity changes due to freshwater runoff associated with storms, urban development, or industrial effluent (Gillanders & Kingsford 2002, Del Pilar Ruso et al. 2007) may also affect bioturbation activity and associated sediment chemistry, although likely not to the same extent as temperature and food availability.

Environmental stress may affect infauna directly by increasing mortality or reducing activity, both of which result in lowered bioturbation rates. For example, in the current study at 32°C, all capitellids died, no burrows were detected, and oxygen and pH were highly stratified. Field exposure to such temperatures for capitellids is feasible, as indicated by records from Flax Pond in 1984 (J. Levinton unpubl.). However, effects do not just depend on the stressor but also on the ability of a species to escape unfavorable conditions. Infauna live in a thermal gradient in which they can escape to cooler deeper sediments, although such gradients may not be significant in highly irrigated deposits (e.g. Johnson 1965). Indeed, the worms used in the current study burrowed deeper when exposed to warmer temperatures, despite the fact that there was no thermal gradient in our experiment. This suggests that assessments of the impacts of stressors on infauna must consider the magnitude and duration of a stressor (Rutger & Wing 2006), as well as the speed and depth to which a species can burrow (Tsubokura et al. 1997, Lardies et al. 2001).

Infaunal invertebrates are often not just exposed to a single stressor at a time; natural and anthropogenic events are often associated with multiple stressors (Fig. 2 in Przeslawski et al. 2008). For example, the increased rate of severe storms predicted under climate change models is associated with freshwater runoff, sedimentation, and physical disturbance (Solomon et al. 2007), all of which may interact to affect infaunal communities. Similarly, detrital supply is often linked to temperature. In mixed estuaries, low detrital supply can occur in summer, but invertebrate metabolic rate increases due to high temperatures, thus exposing ani-

mals to both low food availability and high thermal stress at the same time (Levinton & Stewart 1988). Indeed, Maire et al. (2007) found that sediment reworking of an infaunal clam was significantly affected by food availability in summer but not winter, revealing that food and temperature interact to affect burrowing activity. Concurrent exposure to warm conditions with low food availability may result in deeper bioturbation activity, as the current study shows that infauna burrow deeper in response to warm temperatures and low food availability. Deeper burrowing will affect the sediment characteristics and the infaunal community by facilitating the exchange of oxygen and hydrogen ions across sediment interface and deeper layers of sediment. Results from the current study examined isolated stressors and should be conservatively applied to the field, as the presence of multiple synchronous stressors may exacerbate isolated effects (e.g. Przeslawski et al. 2005). Interactions between temperature and food availability are known to significantly affect sediment reworking of other invertebrates (Maire et al. 2007) and may also apply to *Capitella* sp. Future infaunal studies should investigate interactions between stressors, particularly temperature and food availability, as these are the factors with the strongest observed effects in the current study.

The current study was conducted with a single species in a laboratory, and therefore several potential limitations must be considered regarding the applicability of these results to field populations. First of all, it is unlikely that conditions in the field would remain static as in the current study. Temperatures, salinity, and food availability vary on a daily, seasonal, or inter-annual scale, and variations in such abiotic factors may be linked to changes in feeding, irrigation, and associated sediment chemistry (Maire et al. 2007). In addition, communities in the field include mixed species, and negative interactions can occur with multiple species in which the observed irrigation effects are less than those predicted by laboratory studies of single species (Mermillod-Blondin et al. 2005). Finally, exposure to artificial conditions of the laboratory may have caused stress to the worms, thereby altering natural behavior. However, with the exception of the experimental variables, conditions during the treatments were similar to those used to culture worms over several generations and thus differences between treatments are almost certainly due to the factor considered. Technological advances in sediment profiling imagery make observations of natural infaunal populations possible (e.g. Wilson et al. 2009), and field studies using such technology are recommended to compare effects of temperature and salinity on burrowing behavior and sediment chemistry from lab and field populations.

Predicting the effects of environmental change on an infaunal community is a huge challenge for ecologists. Stressors associated with climate change, pollution, and urban development have species-specific effects, depending on physiology, mobility, habitat, and life history characteristics of a species. In addition, each infaunal species acts on the sediment in a particular manner and zone, usually linked to their feeding behavior and movement through the sediment (Biles et al. 2002). Nonetheless, results from the current study reveal that changing environmental conditions may affect the burrowing activity of a common infaunal polychaete, which will in turn affect sediment oxygen and pH gradients. Such changes have the potential to alter microbial communities (Kogure & Wada 2005) and abundances of other infaunal invertebrates (Marinelli & Woodin 2004, Volkenborn & Reise 2006). A focused effort to investigate the effects of abiotic stressors on multiple species in infaunal communities will provide more insight into potential community and ecosystem effects of changing environmental conditions.

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