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Biotic disturbance mitigates effects of multiple stressors in a marine benthic community

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Abstract. Predicting how communities respond to multiple stressors is challenging because community dynamics, stressors, and animal–stressor interactions can vary with environmental conditions, including the intensity of natural disturbance. Nevertheless, environmental laws stipulate that we predict, measure, and mitigate the ecological effects of some human-induced stressors in the environment, including chemical contaminants in aquatic ecosystems. We conducted an experiment in Antarctica to test how a marine soft-sediment benthic community responded to multiple chemical contaminants and biotic disturbance by manipulating organic carbon enrichment, copper metal contamination, access by large epibenthic animals, and their interaction. Biotic disturbance caused mainly by large echinoderms was manipulated with exclusion cages and cage-control treatments. Colonization patterns in sediment trays revealed that total infaunal abundance and arthropods decreased with toxic Cu (0, 100, and 500 ppm) and total organic carbon (TOC; 0%, 1%, and 2% by wt), as enrichment produced increasing levels of sediment hypoxia/anoxia. Annelids and echinoderms decreased with Cu but increased with TOC because many colonizing polychaete worms, seastars, and epifaunal sea urchins were deposit feeders. Bioturbation by echinoderms disturbed sediments, leading to a substantial decline in total infaunal abundance in uncontaminated sediments, but also an increase in the relative abundance in contaminated sediments, as bioturbation mitigated the effect of both chemical stressors. Biotic disturbance also caused substantial shifts in the species composition of the invertebrate assemblages and an overall increase in species diversity. Prior predictions about the response of benthic marine phyla to the separate and combined effects of Cu and carbon enrichment appear robust to variation in natural biotic disturbance.

Key words: Antarctica; biotic disturbance; community response; copper; marine invertebrates; multiple stressors; organic enrichment.

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Introduction

A major challenge in ecology is predicting community dynamics. Ecologists meet this challenge mainly because they want to know how communities respond to disturbance (Godfray and May 2014). Disturbance kills individuals or exerts physiological stress, both of which can reduce ecological fitness, thereby decreasing the abundance and altering the distribution of populations. Impacts to populations can lead to complex ecological outcomes, including non-linear community dynamics, disruption of ecosystem functioning, and suppression of ecosystem services (Vitousek et al. 1997). As the human population grows so do the intensity and diversity of disturbances and environmental stressors. Accordingly, many ecologists are focused

on identifying cause-and-effect relationships between multiple human-induced stressors and deleterious ecological outcomes (Breitburg et al. 1998, 1999). Understanding the community effects of anthropogenic chemical contaminants, or stressors, has proven especially challenging because the number of toxic contaminants is constantly growing, chemicals interact in complex ways in the environment, and our ability to predict outcomes of multiple stressors at the level of community is nascent (Adams 2005, Bernhardt et al. 2010).

Ecotoxicologists have made headway in predicting the impacts of chemical stressors by developing conceptual adverse outcome pathways (AOPs) that link chemical properties to macro-molecular interactions, which are then matched with cellular responses and eventually to potential population responses considered relevant to ecological risk assessment (Kooijman et al. 2008, Ankley et al. 2010). The utility of AOPs and ecological risk assessments for managing multiple stressors has improved with better integration of information gleaned from empirical work (e.g., surveys and experiments) conducted in the natural environment (Schmitt and Osenberg 1996, Godwin et al. 2009, Groh et al. 2015). For example, work in terrestrial plant communities indicates that limitations of water and nutrients are common co-occurring stressors, often combining synergistically to reduce productivity, species diversity, and resilience to disturbance (Chapin et al. 1987). Likewise, sedimentation, nutrient loading, toxins, introduced predators, and water temperature combine in different ways to impact freshwater ecosystems (Carpenter et al. 1987, Folt et al. 1999, Townsend et al. 2008). Many stressors interact to degrade estuarine and marine communities, including habitat destruction, overfishing, climate change, and pollution, to name but a few (Lenihan and Peterson 1998, Lenihan et al. 1999, Sala et al. 2000, Halpern et al. 2008). Progress is being made to predict the ecological effects of multiple stressors, but identifying robust generalities has proven difficult. For example, a meta-analysis conducted by Crain et al. (2008) found that similar combinations of stressors in marine ecosystems interacted synergistically (in 36% of cases), additively (26%), or antagonistically (38%) depending on response level (population vs. community), trophic level, and environmental conditions.

The discharge of anthropogenic chemicals into the ocean has profound impacts on ecological processes (Clarke et al. 1997, Peterson et al. 2012). Various combinations of chemical compounds including biotic wastes, pharmaceuticals, synthetic organic compounds (e.g., polychlorinated biphenyls [PCBs] and pesticides), metals, hydrocarbons, and nanomaterials are released into coastal regions from municipal and industrial outfalls, atmospheric deposition, rivers, spills, and non-point discharges. These materials accumulate at different rates in the sediments of bays, estuaries, and nearshore coastal zones. Some headway has been made in identifying, understanding, and predicting the effects of multiple chemical stressors in marine ecosystems, especially in cases where various but similar types of contaminants are lumped together. For example, Lenihan et al. (2003) developed predictions of the community response of marine benthic, soft-sediment organisms when exposed to the separate and combined effects of two broad forms of coastal marine pollutants, organic enrichment and toxic metals (e.g., Cu). Their predictions were based on the life history characteristics and tolerance to contaminants displayed by the most commonly found benthic phyla (see also Warwick 1988). The basic prediction was that marine annelid worms increase in abundance in response to organic enrichment (Pearson and Rosenberg 1978), which provides food (but see Diaz and Rosenberg 1995), but that annelids show no clear response to metals contamination because many species can detoxify metals (Wallace et al. 1998, but see Steichen et al. 1996). By contrast, arthropods and echinoderms show no clear response to organic enrichment yet usually decrease in abundance when exposed to metals, primarily because many species are relatively sensitive to metal toxicity (Warwick 1986, Bryan and Langston 1992). Results from a large field experiment conducted in McMurdo Sound, Antarctica, confirmed these predictions (Lenihan et al. 2003). Assessing community response to multiple stressors at high taxonomic levels may help streamline marine pollution monitoring efforts that now cost >$1 billion per year in the United States (NRC 1990, Lovett et al. 2007).

Here, we examine whether natural biotic disturbance influences the separate and combined effects of chemical contaminants in a marine benthic community. Specifically, we tested whether sediment disturbance by large epibenthic and infaunal echinoderms modifies the response of an invertebrate assemblage to increasing levels of total organic carbon (TOC) and copper (Cu) in a large-scale field experiment. We used a benthic community located in McMurdo Sound, Antarctica, as a model system because the local soft-sediment fauna are species rich, well described, and consist of taxa generally found elsewhere in temperate latitude locations and the deep sea (Dayton and Oliver 1977). The impacts of natural and anthropogenic disturbances in McMurdo Sound are also well known (Lenihan and Oliver 1995). We hypothesized that biotic disturbance reduces abundance and species diversity in invertebrate communities but does not modify the general pattern of response to multiple stressors predicted by Lenihan et al. (2003). Models to predict responses to multiple stressors should be robust to chronic forms of natural disturbance, and in soft-sediment communities, this includes bioturbation, foraging by epibenthic and demersal predators, input of detritus, and other biotic disturbances (Lenihan and Micheli 2001). Our study was executed to better understand how multiple anthropogenic stressors interact with natural disturbance in increasingly human-dominated marine ecosystems.

Methods

Experimental design

We tested our hypothesis near McMurdo Station (77°50′ S, 166°40′ E; Ross Island, McMurdo Sound), the major U.S. research station in Antarctica. Prior to the turn of the century, when this study was conducted, McMurdo Sound was an ideal location to conduct long-term benthic colonization experiments because wave- and surge-related disturbances were dramatically minimized by a thick (2–3 m) cover of sea ice, temperature variation and riverine sedimentation were nonexistent, and benthic invertebrate communities were very abundant, well described, and species rich (Dayton and Oliver 1977, Lenihan and Oliver 1995). The nearshore marine habitats near McMurdo Station were continuously loaded with raw sewage and food refuse from 1957 to 2003, causing organic enrichment (Lenihan 1992). Similar organic materials, including paper and brewery distillates and agricultural organic wastes, are deposited on the seafloor worldwide. Benthic habitats at McMurdo Station were also contaminated with PAHs, PCBs, and heavy metals, especially Cu, due to shipping activities and the dumping of industrial and scientific wastes (Lenihan et al. 1990, 1995, Risebrough et al. 1990). We conducted our study in 1998–2000 before an accumulation of massive icebergs dramatically altered McMurdo Sound's regional hydrography, sea ice regime, patterns of primary production, and benthic marine communities (Thrush and Cummings 2011).

We used a field experiment with soft-sediment invertebrate colonization trays to assess whether TOC, Cu, and their interaction cause specific responses in community assemblages under natural environmental conditions. Our factorial experimental design allowed us to control contaminant levels and sediment conditions, control most biotic disturbances, and quantify the impact of chemicals on the recolonization of sediment and community structure after a 1-yr period. Sediment (~750 L total) collected by divers at a pristine site (Cinder Cones, north of Knob Pt.; 9 km from McMurdo Station) was returned to the McMurdo Station laboratory, sieved through 1-mm mesh to remove debris and large fauna, and then defaunated by drying over a 7-d period at 42°C. Subsamples of sediment were then spiked with either a solution of $CuSO_4$, an organic carbon mixture (homogenized wheat flour, beans, and peas), or both, to create an orthogonal combination of three Cu concentrations (0, 100, and 500 ppm [i.e., μg Cu/g sediment]) at each of three levels of TOC (0, 1, and 2% by weight), thereby creating nine total sediment treatments. The 0 ppm Cu and % TOC treatment contained a low ambient range of Cu concentrations (~53 ppm) and TOC (~0.30%), which is normally present in sediments at the two sites (Lenihan et al. 1990). Our organic carbon mix was used to mimic the two major organic enrichment sources at McMurdo Station, food refuse from the local galley and human sewage waste (Lenihan et al. 2003).

Spiked sediments were placed into plastic colonization trays (440 cm^2; ~9 cm deep; Rubbermaid) that were capped, moved, and subsequently

uncapped after placement onto the seafloor. Divers buried the trays in the seafloor at 18 m water depth at Cinder Cones such that the tops of the sidewalls sat flush with the sediment surface. To test the influence of biotic disturbance on patterns of community response, one-third of the sediment trays were fitted with predator exclusion cages made of plastic mesh (Vexar, 1-cm mesh; 10 cm high; covering the entire contents of the sediment trays). Another third of the sediment trays were procedural controls (partial cages) consisting of the mesh cage without 75% of the lid section. The remaining full control trays had no caging material. Our experiment was designed to test the influence of Cu and organic enrichment on infauna and epifauna. Use of the three cage types also allowed for a comparison of the subsequent influence of epifauna and biotic disturbance on infauna recolonization, as the cage designs controlled epifaunal colonization across all levels of contaminants. Seven replicate recolonization trays were used for each treatment (N = 189 trays total).

The predator exclusion cages were designed specifically to exclude benthic predatory fishes, mainly dragonfish *Gymnodraco acuticeps* and notothens (*Trematomus* spp.), which prey on benthic annelids and arthropods (Oliver and Slattery 1985); the giant Antarctic isopod *Glyptonotus antarcticus*; the epibenthic seastar *Odontaster validus* and sea urchin *Sterechinus neumayeri*, both of which disturb surface sediments (Dayton et al. 1974); and the infaunal heart urchin (*Abatus* spp.), which burrows in subsurface sediments (McClintock 1994). The fish were observed to visit several partial cages and no cage treatment replicates over the course of the experiment, but echinoderms were the only animals present and counted in trays. Divers counted the number of epibenthic animals in partial cage, and no cage treatments twice before trays were collected in November 1999: once in November 1998, and again in January 1999. Therefore, counts reported here provide only an index of the actual number of echinoderms that visited the trays, as all the species were highly mobile. Weddell seals were never observed disturbing open sediment trays, but this may have occurred.

After 1 yr, caging material was carefully removed underwater, and sediment trays were recapped and brought back to the laboratory. Each replicate tray was sampled for % TOC, Cu concentration, and grain size using an acid-washed (trace-metal clean), 4 cm diameter polyethylene core that was inserted to 5 cm depth, providing 63 cm^3 of sediment sample. Remaining sediments were sieved for organisms through 0.25-mm mesh, fixed with buffered 10% formalin, and animals later identified and counted under a dissecting microscope. Appropriate trace-metal clean procedures were used throughout the experiment. Chemical analyses and sediment grain size were analyzed by the Moss Landing Marine Pollution Laboratory: Percentage TOC was analyzed with a Control Equipment elemental analyzer (Hunt et al. 2001); bulk Cu levels were analyzed with inductively coupled plasma mass spectrometry (McLaren et al. 1987); and grain size analysis was conducted using a combination of sieve and hydrometer analysis (Loveland and Whalley 2001).

Statistical analyses

Separate three-way ANOVAs were used to test whether the mean total abundance of colonists and mean species diversity responded to TOC, Cu, biotic disturbance (i.e., caging) treatments, and their interaction. Species diversity was assessed as diversity order 1, calculated as the exponential of Shannon-Weiner diversity entropy index (*H*) (sensu Jost 2006). A three-way MANOVA was used to test whether the mean abundances of annelids, arthropods, and echinoderms varied together in response to the experimental treatments. MANOVA was used because changes in one phylum may have influenced the response of the other phyla through multiple direct (e.g., predation and competition) and indirect (e.g., attracting and repelling colonists) ways. When significant differences were found in MANOVA, three-way ANOVAs as described above were used to test for differences in the mean abundance of each phylum. Prior to ANOVA and MANOVA, all data were square root transformed and tested for heterogeneity of variances using Cochran's test. Transformed data passed subsequent Cochran's tests for homogeneity of variances ($\alpha = 0.05$). Differences between specific treatments were determined with Student-Newman-Keuls (SNK) post hoc tests ($\alpha = 0.05$). The percent of total variation in the ANOVA model explained by each treatment was estimated with partial r^2 values. The adjusted r^2 value of the ANOVA

models is presented to indicate how well the model described patterns in the data. Finally, multiple linear regression was used to detect the influence of echinoderms on total infaunal abundance and species diversity. The influence of echinoderms was examined while controlling for the influence of percentage TOC, Cu, and caging type. All statistical analyses were conducted in STATA (College Station, Texas, USA).

Results

Sediment characteristics

Sediment characteristics in the colonization trays after 1 yr of exposure on the seafloor were very similar to the targeted chemical combinations across all three cage treatments (Table 1). The percentage TOC in sediments ranged from 0.28 to 0.32 in the 0% TOC treatment; 0.92–1.07 in the 1% TOC treatments; and 1.95–2.12 in the 2% TOC treatment. Concentrations of Cu were 58–62, 123–134, and 479–519 ppm in the 0 ppm (i.e., control), 100, and 500 ppm treatments, respectively. Sediment grain size was also very consistent across treatments (Table 1). Hypoxia/anoxia and hydrogen sulfide were detected qualitatively in all replicates of the 2% TOC treatment, as subsurface sediments smelled like sulfide, changed color from gray to black rapidly with depth (indicative of reducing conditions), and sediment surfaces supported colonies of a white bacterium, probably *Beggiatoa*, which thrives on sulfide flux (Fenchel and Bernard 1995). Most 1% TOC replicates also released a faint sulfide odor but did not support *Beggiatoa* growth. Evidence of hypoxia/anoxia was faint or absent in the no cage and

Table 1. Mean (± 95% C.I.) values for sediment chemistry and grain size in colonization trays for all treatment types after 1 yr of exposure on the seafloor.

			Realized sediment treatments		
Treatments	% TOC	Cu ppm	% TOC (% by wt sediment)	Cu (ppm in sediment)	Grain size (% silt and clay)
No cage	0	0	0.28 ± 0.04	62.60 ± 2.88	5.83 ± 0.24
	0	100	0.30 ± 0.04	126.00 ± 11.40	6.19 ± 0.89
	0	500	0.30 ± 0.05	491.00 ± 22.28	5.78 ± 0.40
	1	0	0.98 ± 0.01	61.50 ± 2.55	6.48 ± 0.97
	1	100	0.92 ± 0.08	121.50 ± 6.86	6.66 ± 0.82
	1	500	0.96 ± 0.21	506.50 ± 18.35	6.09 ± 0.50
	2	0	1.97 ± 0.20	59.10 ± 3.53	6.88 ± 0.23
	2	100	2.10 ± 0.09	124.50 ± 2.94	6.69 ± 0.33
	2	500	2.05 ± 0.05	485.45 ± 15.68	7.02 ± 0.25
Cage control	0	0	0.29 ± 0.00	63.25 ± 3.04	5.91 ± 0.18
	0	100	0.30 ± 0.01	134.00 ± 19.60	6.00 ± 0.57
	0	500	0.29 ± 0.03	485.00 ± 35.28	5.60 ± 0.30
	1	0	1.01 ± 0.12	62.80 ± 2.55	6.89 ± 0.07
	1	100	0.95 ± 0.06	124.70 ± 3.92	6.34 ± 1.17
	1	500	0.97 ± 0.15	511.50 ± 11.83	6.64 ± 0.40
	2	0	2.06 ± 0.10	57.70 ± 4.11	7.08 ± 0.18
	2	100	2.08 ± 0.11	123.50 ± 2.94	6.98 ± 0.21
	2	500	1.95 ± 0.22	475.45 ± 12.32	7.17 ± 0.23
Cage	0	0	0.32 ± 0.03	63.20 ± 1.02	6.17 ± 0.27
	0	100	0.29 ± 0.10	141.00 ± 13.33	6.25 ± 0.62
	0	500	0.31 ± 0.00	507.50 ± 38.22	6.27 ± 0.45
	1	0	1.00 ± 0.16	58.85 ± 11.07	6.88 ± 0.81
	1	100	0.94 ± 0.05	122.50 ± 0.98	7.18 ± 0.43
	1	500	1.07 ± 0.03	519.50 ± 173.46	6.92 ± 1.07
	2	0	1.95 ± 0.28	62.25 ± 3.63	7.25 ± 0.09
	2	100	2.05 ± 0.29	125.00 ± 11.76	7.26 ± 0.51
	2	500	2.12 ± 0.05	477.50 ± 83.20	7.48 ± 0.70

Note: N = 4 per treatment.
TOC, total organic carbon.

partial cage treatment replicates that were colonized by large invertebrates.

Community composition and abundance

Experimental trays were colonized by relatively high densities of arthropods (crustaceans: amphipods, tanaids, isopods, ostracods, cumaceans, and harpacticoid copepods), annelid worms (polychaetes and oligochaetes), and echinoderms (epifaunal asteroids, and epifaunal and infaunal echinoids). The small infaunal anemone *Edwardsia meridionalis* (Cnidaria) was another common colonist. Except for relatively few and large echinoderms and nemerteans, most colonists were small (0.3–1 mm) deposit-feeding, suspension-feeding, or predatory infaunal species that colonized either by larval settlement or immigration. Trays were also colonized by a few gastropods, bivalves, and the large protist *Gromia oviformis*. Other rarely observed species were the isopod *Munna* sp., the archiannelid *Polygordius* sp., and several unidentified mites. The general species composition and size structure of communities found in trays resembled those of the surrounding benthos (Lenihan and Oliver 1995).

Mean total abundance of infauna varied with percentage TOC, Cu, and cage treatment (full cage vs. partial cage vs. no cage), as signified by a significant three-way interaction in the ANOVA ($F_{8,162}$ = 11.06; TOC × Cu × Caging; P < 0.0001). The model explained a majority of the variation among treatments (adjusted model r^2 = 0.89), but the three-way interaction explained only 5% of the total variation in the experiment. Total infaunal abundance declined rapidly with increasing Cu concentration across all three levels of percentage TOC (Fig. 1). Total abundance also generally declined with increasing percentage TOC, but this factor explained only ~1% of the total variation among treatments. In contrast, Cu explained 57% of response among treatments.

The significant three-way interaction was due in large part to differences between the cage treatments as the intensity of the two stressors increased. Mean total abundance was much higher in the fully caged trays (i.e., no biotic disturbance) with no contaminants (i.e., 0% TOC–0 ppm Cu) than all other treatments, due mainly to very large numbers of arthropods (Fig. 1; and see below for details). Abundance was also

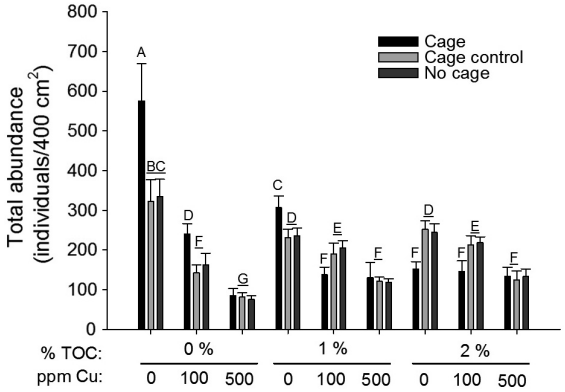

Fig. 1. Mean (± 95% C.I.) density of all infaunal invertebrates in fully caged (caged), partially caged (cage control), and uncaged (no cage) colonization trays containing contaminant-treated sediments at Cinder Cones in McMurdo Sound, Antarctica. N = 7 replicate colonization trays per treatment. Results of a Student-Newman-Keuls post hoc test are provided above each bar (a > b > c, etc., at P < 0.05).

higher in trays with cages than exposed trays (i.e., partial cages and no cages) for the 0% TOC–100 ppm Cu and 1% TOC–0 ppm Cu treatments (SNK test, P < 0.05). That pattern was reversed in trays with 1% TOC–100 ppm Cu, 2% TOC–0 ppm Cu, and 2% TOC–100 ppm Cu, where abundance in the exposed trays was higher than in full cages (SNK, P < 0.05; Fig. 1). There was no difference among cage treatments in trays with 500 ppm Cu, in which abundance was relatively low. This pattern was observed repeatedly for the other infaunal responses (see *Arthropods, Annelids, and Echinoderms*).

Arthropods

There was a significant three-way interaction in the MANOVA comparing the mean abundance of arthropods, annelids, and echinoderms across treatments (three-way MANOVA; TOC × Cu × Caging; Wilk's lambda = 0.6193; $F_{8,162}$ = 3.48; P < 0.0001), thereby justifying the examination of each phylum separately using univariate three-way ANOVAs. The most abundant organisms in colonization trays were arthropods (Fig. 2), which showed a pattern similar to that observed for total infaunal abundance (Fig. 1). Especially, numerous in the trays were the tube-dwelling tanaid crustacean *Nototanias dimorphus*, the ostracod

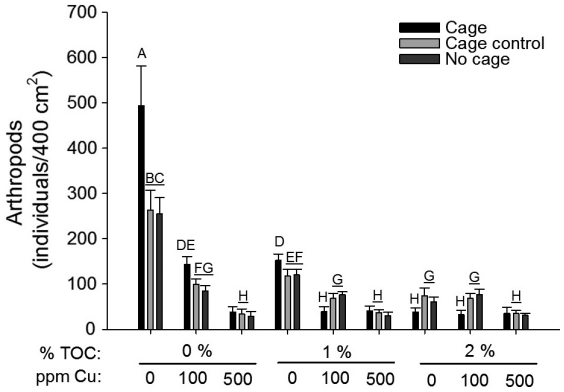

Fig. 2. Mean (± 95% C.I.) densities of arthropods in caged, cage control, and no cage colonization trays containing contaminant-treated sediments at Cinder Cones in McMurdo Sound, Antarctica. N = 7 replicate colonization trays per treatment. Results of a Student-Newman-Keuls post hoc test are provided above each bar (a > b > c, etc., at $P < 0.05$).

Philomedes spp., the cumacean *Eudorella splendida*, the isopod *Austrosignum grande*, the predatory heterophoxid amphipod *Heterophoxus videns*, and a deposit-feeding oedicerotid amphipod *Monoculodes scabruculosus*. Found rarely were large unidentified harpacticoid copepods and the scavenging lysianassid amphipod *Orchomene penguides*.

The ANOVA model explained most of the total variation in arthropods (adjusted $r^2 = 0.92$), and Cu explained the greatest amount of variation among treatments (38%). A significant three-way interaction of TOC, Cu, and cage treatment (three-way ANOVA; $F_{8,162} = 5.83$; TOC × Cu × Caging; $P < 0.0001$) explained only 2% of the variation while TOC explained 25%. The mean density of arthropods was highest in uncontaminated sediments in full cages (Fig. 2; SNK, $P < 0.05$), and decreased consistently with increasing Cu concentration at all three levels of percentage TOC, although less rapidly in the exposed trays than full cages (SNK, $P < 0.05$). Arthropod abundance was also generally lower in the 1% and 2% TOC treatments than the 0% TOC, but there was no difference as function of percentage TOC at the 500 ppm Cu level (SNK, $P > 0.05$). As observed for total infauna, arthropod numbers increased in exposed tray treatments relative to full cage treatments in the 1% TOC–100 ppm Cu, 2% TOC–0 ppm Cu, and 2% TOC–100 ppm Cu (SNK, $P < 0.05$). They also did not differ as a function of caging in trays with 500 ppm Cu (SNK, $P > 0.05$). The most abundant arthropod in uncontaminated sediments within full cages was by far the tube-building *Tanais* (mean ± 95% C.I.: 263 ± 59 per tray), yet in exposed trays this arthropod declined (99 ± 28) while amphipods, cumaceans, ostracods, and isopods increased substantially. The abundance of tanaids dropped dramatically as levels of the two stressors increased, especially in the exposed trays.

Annelids

The second most numerous group of organisms colonizing the trays were annelid worms, including *Spiophanes tcherniai*, a polychaete worm that, like *Tanais*, builds a dense biogenic tune mat inhabited by other species. *Spiophane*s were most abundant in sediments with 1% TOC. The annelid assemblage also had a relatively large number of errant polychaete species from the families Capitellidae, Dorvilleidae, Hesionidae, Cirratulidae, Ophelidae, Phyllodocidae, and Terebellidae. Species of Capitellids (*Capitella capitata*) and Dorvillids (*Ophryotrocha claperedii*), considered opportunistic species with relatively high tolerances of hypoxia and chemical stress, dominated the annelid abundance in highly contaminated sediments.

The three-way ANOVA model explained 83% of the total variation in annelid abundance among treatments (adjusted $r^2 = 0.83$). The significant three-way interaction of percentage TOC, Cu, and cage treatment (three-way ANOVA; $F_{8,162} = 5.74$; TOC × Cu × Caging; $P < 0.0001$) explained only 4% of the total variation, while much of the variation (46%) was explained by differences in percentage TOC. Mean annelids density was significantly higher in 1% and 2% TOC sediments than 0% TOC sediment (Fig. 3; SNK, $P < 0.05$). There were no differences between the caging treatments in trays with 500 ppm Cu (SNK, $P > 0.05$), but there were striking differences between cage treatments in all other Cu–% TOC combinations (SNK, $P < 0.05$). More annelids, and especially *Spiophanes*, colonized fully caged trays than exposed trays with 0% and 1% TOC-ladened sediment. These patterns were reversed in 2% TOC, a treatment also colonized by relatively

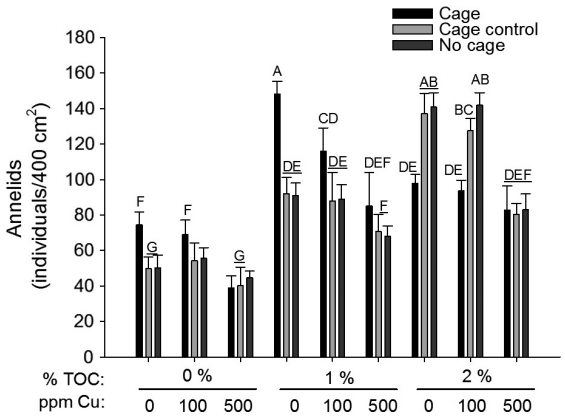

Fig. 3. Mean (± 95% C.I.) densities of annelids in caged, cage control, and no cage colonization trays containing contaminant-treated sediments at Cinder Cones in McMurdo Sound, Antarctica. N = 7 replicate colonization trays per treatment. Results of a Student-Newman-Keuls post hoc test are provided above each bar (a > b > c, etc., at $P < 0.05$).

many errant polychaetes. Cu contamination explained 20% of the variation in annelids among treatments, and in general, their abundance declined with Cu concentration. As the levels of percentage TOC and Cu increased so did the relative abundance of *Capitella* and *Ophryotrocha*.

Echinoderms

The largest organisms found in colonization trays were echinoderms, especially the seastar *Odontaster validus* (deposit feeder), the epibenthic urchin *Sterechinus neumayeri* (omnivorous scavenger), and the infaunal heart urchin *Abatus* spp. (deposit feeder). The large predatory-scavenging nemertean worm *Parborlasia corrugatus,* not an echinoderm, was also found in some organically enriched trays, mostly those without full cages. Echinoderms were recorded almost exclusively in exposed trays, as the full cages effectively excluded them except for some juveniles that were found in Cu-free treatments. The juveniles probably colonized the trays as larvae. The only echinoderm found in uncontaminated sediments (0% TOC–0 ppm Cu) was *Abatus,* which intensively excavated sediments through subsurface burrowing activity in exposed trays. In contaminated sediments, *Odontaster* and *Sterechinus* found in exposed trays appeared highly attracted to organic enrichment (sensu Kim et al. 2007). These surface-deposit feeders disrupt the top several millimeters of sediment and sometimes leave mucous trails on sediment surfaces related to their feeding activity. *Parborlasia* may have also caused a small degree of sediment disturbance in enriched sediments but appeared mainly interested in preying on the few clams present.

The three-way ANOVA explained much of the variation in mean echinoderm abundance in the experiment (adjusted $r^2 = 0.78$), while most of variation among treatments was explained by Cu (47%) and caging (25%). There was a significant two-way interaction of Cu and cage treatment (two-way ANOVA; $F_{4,162} = 26.49$; Cu × Caging; $P < 0.0001$; 8% of variation) that was driven by (1) a decrease in echinoderms with Cu (SNK, $P < 0.05$), (2) the absence of echinoderms in any treatments with 500 ppm Cu, and (3) higher densities in exposed trays than those with full cages (Fig. 4A). There was also a significant two-way interaction of percentage TOC and Cu (two-way ANOVA; $F_{4,162} = 4.21$; TOC × Cu; $P < 0.003$; 1% of variation; Fig. 4B). *Odontaster* generally increased with percentage TOC but that trend was tempered by Cu. *Sterechinus* was not found in treatments with 100–500 ppm Cu. Counts of echinoderms reported here from December 1999 were not significantly different than counts made in November 1998 and January 1999 (one-way ANOVA; $F_{2,162} = 0.24$; $P = 0.55$). In addition to large echinoderms, we infrequently observed dragonfish (*Gymnodraco acuticeps*) and notothens (*Trematomus* spp.) visiting the exposed trays. Overall, we detected no obvious signs that predation by fish, nemertean worms, or other organisms significantly influenced our results.

Species diversity

Mean Shannon-Weiner diversity (*H*) entropy (order 1) varied among treatments as a three-way interaction of percentage TOC, Cu, and cage treatment (three-way ANOVA; $F_{8,162} = 2.56$; TOC × Cu × Caging; $P = 0.01$; 4% of total variation). The three-way interaction was driven by a complex pattern of responses highlighted by a general decline in diversity with increasing percentage TOC, and higher diversity in the exposed trays than fully cages trays (Fig. 5). Differences in percentage TOC explained more of the variation (44%) than any other treatment

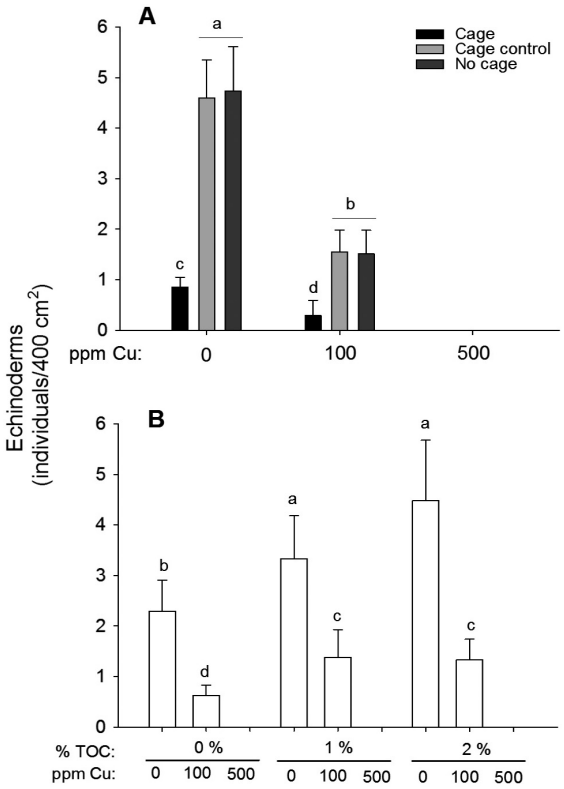

Fig. 4. Mean (± 95% C.I.) densities of echinoderms in caged, cage control, and no cage colonization trays containing contaminant-treated sediments at Cinder Cones in McMurdo Sound, Antarctica. A. Results of a significant two-way interaction of cage treatment and Cu concentration in the ANOVA. B. Results of a significant two-way interaction of % total organic carbon (TOC) and Cu concentration. N = 21 replicate colonization trays per treatment. Results of Student-Newman-Keuls post hoc tests are provided above each bar (a > b > c, etc., at $P < 0.05$).

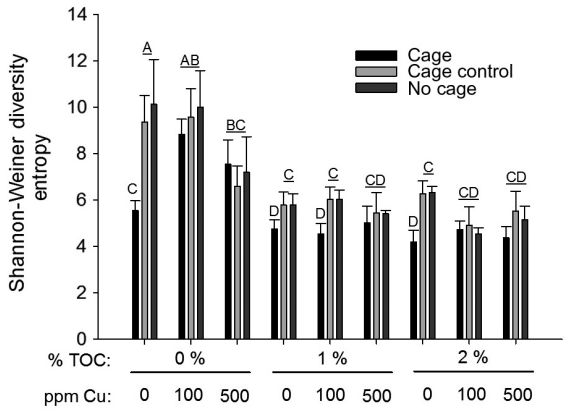

Fig. 5. Mean (± 95% C.I.) of the Shannon-Weiner Diversity (H) entropy (order 1) of invertebrates assemblages in caged, cage control, and no cage colonization trays containing contaminant-treated sediments at Cinder Cones in McMurdo Sound, Antarctica. N = 7 replicate trays per treatment. Results of a Student-Newman-Keuls post hoc test are provided above each bar (a > b > c, etc., at $P < 0.05$).

combination, and in general, diversity declined as the relative abundance of annelids increased (see Fig. 3).

Effects of biotic disturbance

To test the influence of biotic disturbance on community patterns, we examined how total infaunal abundance and Shannon-Weiner (H) entropy varied as function of echinoderm density across all treatment types. All three cage treatments were used in the analyses because we found echinoderms in all treatments after one year. Our multiple regression models examined the influence of echinoderms on abundance and species diversity while also controlling for the effects of Cu, percentage TOC, and the cage treatment. Results of the regression for total abundance showed that infaunal density tended to decrease with the density of echinoderms but that the relationship was not statistically significantly (Multiple regression; Echinoderm effect, Correlation coefficient = −5.56, $t = -1.25$, $P = 0.21$). When re-analyzing the data after removing the 0 Cu–0% TOC treatment (i.e., all three cage types) from the analysis, a test we executed to detect the effect of biotic disturbance in contaminated sediment only, we found the same basic result: no statistically significant influence of echinoderms on total infaunal abundance (Multiple regression; Echinoderm effect, Correlation coefficient = −5.82, $t = -1.28$, $P = 0.20$).

Results from the regression testing the influence of echinoderms on Shannon-Weiner (H) entropy showed that species diversity tended to increase with echinoderm density, but the effect was not statistically significant (Multiple regression; Echinoderm effect, Correlation coefficient = 0.150, $t = 1.53$, $P = 0.13$). However, when we removed the uncontaminated sediment treatment (0 Cu–0% TOC; all three cage types) from the analyses, we found that H entropy increased significantly

as a function of echinoderm density in contaminated sediments (Multiple regression; Echinoderm effect, Correlation coefficient = 0.197, t = 2.06, P = 0.04). To illustrate the effect of echinoderms on species diversity, we calculated the difference in H entropy between the no cage and full cage treatments (i.e., no cage–full cage) and plotted the values as a function of echinoderm density (Fig. 6). Results showed that species diversity difference in contaminated sediments increased with echinoderm abundance (e.g., simple least-squares linear regression; adjusted r^2 = 0.57, P = 0.03). There was also relatively high species diversity in the uncontaminated sediment treatment: Thus, the difference in diversity between no cages and full cages containing 0 Cu–0% TOC sediment was quite high where there where moderately high numbers of echinoderms (See data point in Fig. 6T1). A similar positive relationship between species diversity and echinoderms was observed when we used the cage controls to calculate the difference (i.e., cage controls–full cages).

The positive influence of echinoderms and species diversity emerged because (1) the *Abatus* burrowing that excluded *Tanais* in uncontaminated sediment apparently opened up space for many other species; and (2) disturbance by *Odontaster* and *Sterechinus* in contaminated sediments shifted communities from those composed of only a few opportunistic and/or stress-tolerant species (mainly *Capitella*, *Ophryotrocha*, oligochaetes, and harpacticoid copepods) to those composed of relatively many species of polychaetes and arthropods. A greater variety and abundance of infauna living deeper in sediments were found in trays that had evidence of bioturbation than in fully caged trays without bioturbation. This pattern held for trays with 100 ppm of Cu but not in trays with 500 ppm Cu, which were devoid of echinoderms and biotic disturbance.

Discussion

Physical disturbance caused by large deposit-feeding and scavenging echinoderms helped to mitigate the impact of multiple stressors on a benthic soft-sediment community in our experiment. As the level of organic enrichment

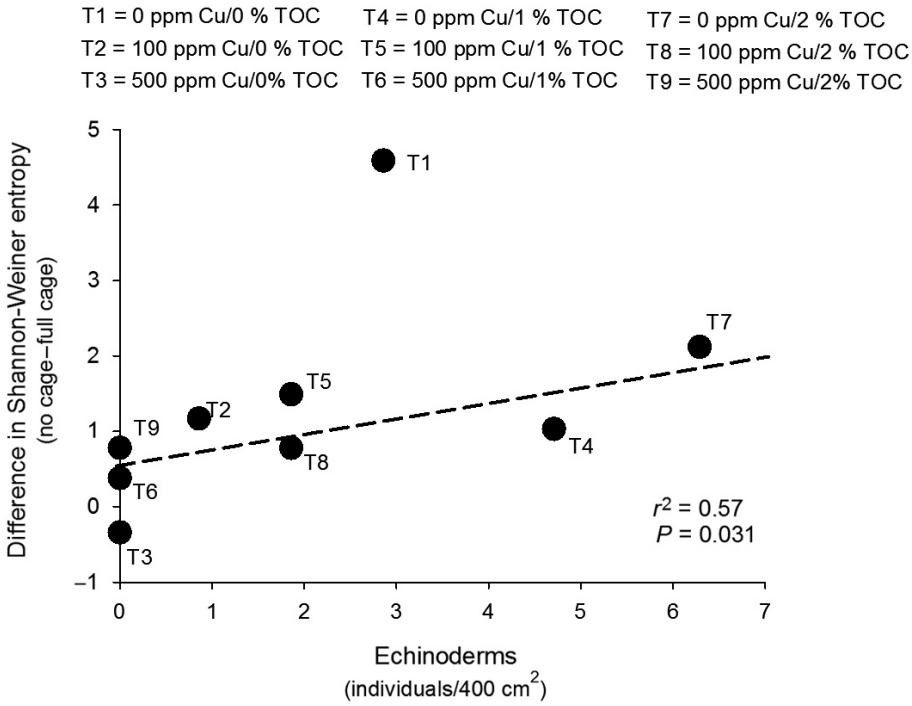

Fig. 6. Difference in mean Shannon-Weiner Diversity (H) entropy (order 1) between no cage and caged treatments as a function of the mean echinoderm density measured in the same sediment trays. Results of a simple least-squares linear regression are displayed for all contaminated sediment treatments (i.e., T2–T9).

increased so did the abundance of echinoderms and intensity of bioturbation, even in sediments with moderate levels (100 ppm) of Cu. In turn, bioturbation enhanced the abundance and species diversity of the invertebrate assemblage relative to contaminated sediments that experienced little to no bioturbation. In their study of benthic communities in McMurdo Sound, Kim et al. (2007) reported that *Sterechinus* avoided highly enriched, hypoxic sediments with *Beggiatoa* bacterial mats, reportedly because the bacteria indicated the presence of toxic sulfides. Bioturbation by epibenthic organisms in our experiment probably prevented hypoxia and production of sulfides in organically enriched trays by excavating and aerating surficial sediments. Biotic disturbance thus facilitated the colonization by infaunal species in sediments with 1% TOC and 2% TOC, even those with 100 ppm Cu. The combined effect of enrichment and bioturbation may have also reduced the toxic effect of 100 ppm Cu by (1) enhancing levels of negatively charged organic carbon-rich molecules that bound free Cu ions, making them less toxic; and/or (2) by burying, remineralizing, or otherwise reducing the bioavailability of sediment-bound Cu (Klinkhammer et al. 1982, Shaw et al. 1990, Aller and Aller 1998, Ciutat and Boudou 2003). By contrast, we never observed epibenthic organisms or signs of bioturbation in heavily Cu-contaminated sediments, which in the presence of organic carbon enrichment had bacterial growth, clear signs of hypoxia, and very few infauna. These patterns indicate that biotic disturbance had an antagonistic effect on the multiple stressors.

Biotic disturbance had an overall positive effect on the species diversity of communities subjected to multiple stressors. Communities inhabiting sediments with both enrichment and Cu contamination that also experienced bioturbation had higher species diversity than sediments in full cages with little or no bioturbation. This pattern probably emerged because bioturbation created spatial refuges for some species that were sensitive to hypoxia or Cu. In uncontaminated sediments, biotic disturbance may have enhanced species diversity by preventing competitive dominance for space by a few species, especially the arthropod *Tanais* and annelid *Spiophanes* (Gibson et al. 2001). Both species form dense tube mats that can exclude some polychaetes, infaunal arthropods, and the anemone *Edwardsia* (Lenihan and Oliver 1995). Similar effects of biotic disturbance on species diversity have been observed in communities in the rocky intertidal (Dayton 1971), estuarine soft sediments (Ambrose 1984), the deep sea (Dayton and Hessler 1972), grasslands (Maalouf et al. 2012), forests (Hicke et al. 2012), and on oyster reefs (Kimbro and Grosholz 2006) and sand dunes (Forey et al. 2008). We know of no other example where biotic disturbance enhanced the diversity of a community impacted by multiple chemical stressors.

Surprisingly, biotic disturbance did not alter the predicted response of the communities to the multiple stressors observed at a high taxonomic level, specifically phyla (sensu Lenihan et al. 2003). Arthropods, annelids, and echinoderms responded in a manner very similar to that reported by Lenihan et al., even when impacted by bioturbation. Thus, separate and combined effects of organic enrichment and toxic metals on the most common benthic marine fauna appear robust to chronic, low levels of biotic disturbance commonly experienced by marine soft-sediment communities. We suggest that Lenihan et al.'s conceptual model be tested elsewhere as a means of streamlining the difficult and expensive process of assessing the effects of chemical stressors released together into the marine environment (e.g., from industrial and metropolitan outfalls). We also predict that adding a small amount of organic enrichment to areas with metal-contaminated sediment would attract epibenthic deposit feeders that could act to mitigate toxicity through bioturbation (e.g., Kupryianchyk et al. 2013).

As ecologists increase their reliance on syntheses of existing data, an increasing number of ecological models are being produced to explain global-scale phenomena, including the effects of multiple stressors (e.g., Halpern et al. 2008). Such syntheses increase public awareness, stimulate the formation of new policy, and benefit conservation efforts, mainly by helping to prevent or reduce anthropogenic disturbances. Whether the proliferation of ecological syntheses also benefits the management of perturbed ecosystems is uncertain in many cases, in large part because detecting the cause and specific ecological effects of multiple anthropogenic and natural disturbances remains challenging. Ecological risk assessment remains an exercise in prediction

generation, and managing ecological impacts frequently requires field assessments or experiments designed to rigorously test specific predictions (Schmitt and Osenberg 1996). When ecologists have collaborated with managers to conduct field-based management experiments, new ecological insights and management strategies have emerged (e.g., McAllister and Peterman 1992, Lenihan and Micheli 2000, Lenihan and Peterson 2004). Our study is an example of how information from large-scale field experiments can be used to improve the management of marine ecosystems, in this case by developing well-tested predictions that may preclude the need for expensive chemical and taxonomically detailed surveys.

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