Deep-sea faunal communities associated with a lost intermodal shipping container in the Monterey Bay National Marine Sanctuary, CA

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ABSTRACT

Carrying assorted cargo and covered with paints of varying toxicity, lost intermodal containers may take centuries to degrade on the deep seafloor. In June 2004, scientists from Monterey Bay Aquarium Research Institute (MBARI) discovered a recently lost container during a Remotely Operated Vehicle (ROV) dive on a sediment-covered seabed at 1281 m depth in Monterey Bay National Marine Sanctuary (MBNMS). The site was revisited by ROV in March 2011. Analyses of sediment samples and high-definition video indicate that faunal assemblages on the container's exterior and the seabed within 10 m of the container differed significantly from those up to 500 m. The container surface provides hard substratum for colonization by taxa typically found in rocky habitats. However, some key taxa that dominate rocky areas were absent or rare on the container, perhaps related to its potential toxicity or limited time for colonization and growth. Ecological effects appear to be restricted to the container surface and the benthos within ~10 m.

1. Introduction

The Monterey Bay is characterized by a submarine canyon beginning just offshore of Moss Landing, California, along the central CA coast. The main channel of the submarine canyon meanders over 400 km into the Pacific Ocean, and reaches depths over 4000 m (Paull et al., 2011). Monterey Canyon and the waters above it provide diverse habitats, from the rocky outcroppings and soft seafloor that comprise the benthos, to the vast midwater habitat, and surface waters that undergo the dramatic seasonal changes characteristic of an upwelling ecosystem. These characteristics led the National Oceanographic and Atmospheric Administration (NOAA) to establish the Monterey Bay National Marine Sanctuary (MBNMS) in 1992. As the Monterey submarine canyon system meanders into the Pacific Ocean, major shipping routes cross directly overhead (Fig. 1), within the MBNMS.

The estimated 10,000 shipping containers lost at sea each year along international shipping routes (Podsada 2001; IMO 2004; Frey and DeVogelaere, 2014) may take centuries to degrade on the seafloor, and have varied and often-unknown levels of toxicity

associated with their contents and exterior coatings. Incidents of catastrophic grounding of container ships on shallow reefs (e.g., M/V *Rena*; Bateman 2011) and beaching/salvaging of lost cargo (e.g., global beaching of rubber ducks from a container lost in 1992 in the North Pacific (Ebbesmeyer and Scigliano 2009; Nagel and Beauboeuf 2012)) are often reported widely. However, the vast majority of shipping container losses are presumed to occur in deep water during inclement weather. Because lost containers are rarely located and deep-sea research is costly and challenging, their effects on deep-sea benthic communities have not been investigated.

During a winter storm in February 2004, 24 standard metal intermodal containers (12.2 × 2.4 × 2.6 m, empty weight 4 t, maximum gross mass over 30 t) fell off the Chinese M/V *Med Taipei* along the central coast of California en route to the Port of Los Angeles, CA. Of these, 15 were lost within the MBNMS. Four months later, scientists from the Monterey Bay Aquarium Research Institute (MBARI) discovered one of these containers (numbered TGHU7712262) at 1281 m depth off central California during a research dive using the remotely operated vehicle (ROV) *Ventana* (Fig. 1). Upon discovery, a limited amount (<1 h) of video observations (inset image, Fig. 1) were collected. Subsequent inquiry of the shipping company by NOAA revealed the container's cargo to be 1159 steel-belted automobile tires. In January 2005, the NOAA

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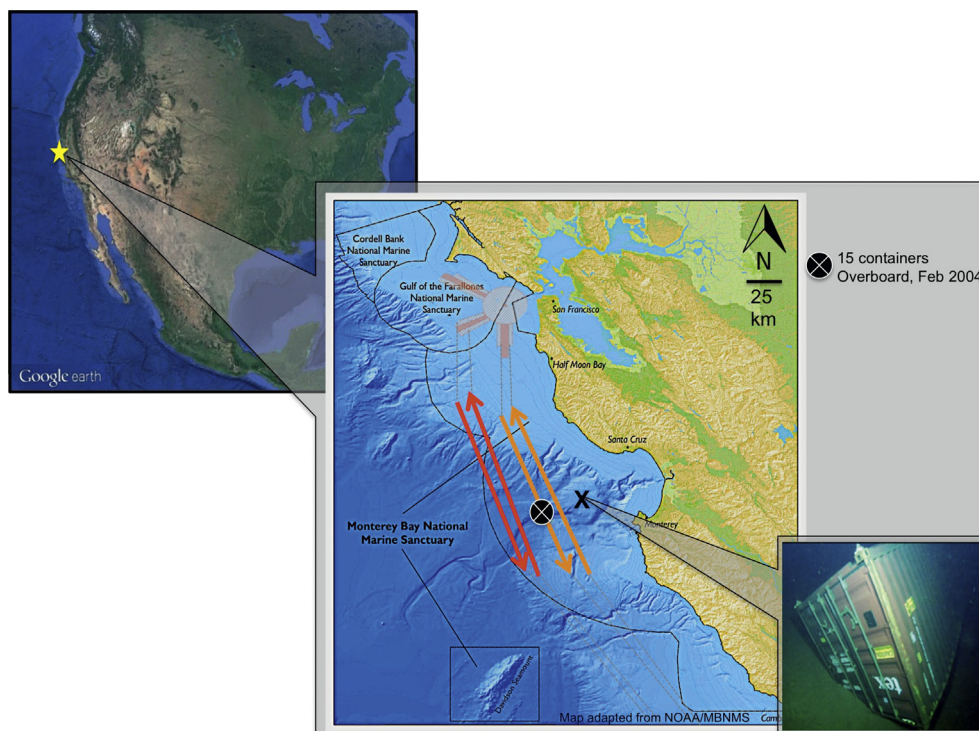E-mail address: josi@mbari.org (J.R. Taylor).

Fig. 1. Location of intermodal container lost by the M/V *Med Taipei* (crosshair) in February 2004, and found in the Monterey Bay National Marine Sanctuary (MBNMS) in June 2004 (**X**). International Maritime Organization shipping routes for large vessels (orange arrows) and HAZMAT vessels (red arrows). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Damage Assessment Center (DAC) assessed the prospective financial impact of the deposition and deterioration of the 15 containers lost in the MBNMS. With consideration of NOAA-DAC's evaluation, as well as potential fines, legal fees and costs to date, etc., the shipping company paid the MBNMS reparation of $3.25 million. The Compensatory Restoration Plan implemented by the MBNMS includes assessment and monitoring of the deep-sea benthos at the container site. The site was revisited for this purpose during a March 2011 research cruise as a collaborative venture between MBNMS and MBARI scientists. The aim of this cruise was to produce a detailed assessment of the diversity, abundance, and assemblages of benthic mega- and macrofauna on and around this intermodal container, seven years after its deposition in the MBNMS.

Habitat heterogeneity increases biodiversity (Buhl-Mortensen et al., 2010; Levin et al., 2010; Ramirez-Llodra et al., 2011), with natural and artificial structures typically attracting high densities and a wide variety of marine taxa; so long as structures are not made from materials acutely toxic to prospective inhabitants (Bohnsack and Sutherland 1985; Baine 2001; Collins et al., 2002). Indeed, artificial reefs are frequently installed in coastal regions at depths <100 m to enhance the diversity and abundance of ecologically and commercially important marine species (Bohnsack and Sutherland 1985; Baine 2001). Artificial reefs have been shown to affect biological productivity and ecological connectivity; however, the types of organisms and their persistence on and around a newly introduced structure depend largely on their shape, composition, and location (Bohnsack and Sutherland 1985; Baine 2001; Macreadie et al., 2011). Although there is general scientific agreement that artificial reefs accumulate fish and other organisms (Bohnsack and Sutherland 1985), less is known about the effects of artificial reefs on living resource production, their ability to act as stepping-stones that facilitate the dispersal of native and non-native species, how they affect disease frequency in fish and invertebrates, toxicological impacts, their long-term structural integrity, and changes to socioeconomic conditions of adjacent coastal communities (Broughton 2012). Structures crafted to promote recreational fishing and diving sites are typically created by intentionally sinking dilapidated ships, airplanes, bridges, and concrete (Bohnsack and Sutherland 1985; Baine 2001; Broughton 2012). Less common and more controversial artificial habitats include worn tires, coal-power waste, and other components (Woodhead et al., 1982; Collins et al., 2002). The potential toxicity of such structures is as variable as the materials used in their construction. Such installations are also known to affect the surrounding benthos in soft sediments, due to changes in predator forays around the new refugium (Broughton 2012).

Little is known about the effects of artificial reefs and other structures installed at depths >100 m (Macreadie et al., 2011). Once considered to be constant, spatially homogeneous, and isolated, deep-sea sediments are now recognized as a dynamic, diverse habitat that is intricately linked to the global biosphere (Levin et al., 2001). Deep-sea biodiversity has been shown to correlate positively with ecosystem function (Danovaro et al., 2008), and therefore is an important consideration when evaluating the impact of an introduced structure. Potential negative impacts of human-introduced structures in marine ecosystems include physical damage to the seabed, undesirable changes in marine food webs, colonization of invasive species, and release of contaminants (Macreadie et al., 2011). Furthermore, efficiently dispersing, fast-growing, highly fecund (i.e., "weedy", typically non-native) species can create additional oxygen demand in marine ecosystems. In already hypoxic environments such as those in and adjacent to the Oxygen Minimum Zone (a layer of oxygen-deplete water ranging from approx. 500–1000 m depth), additional oxygen demand may promote declines in ecosystem richness and evenness due to physiological stress (Levin et al., 2001).
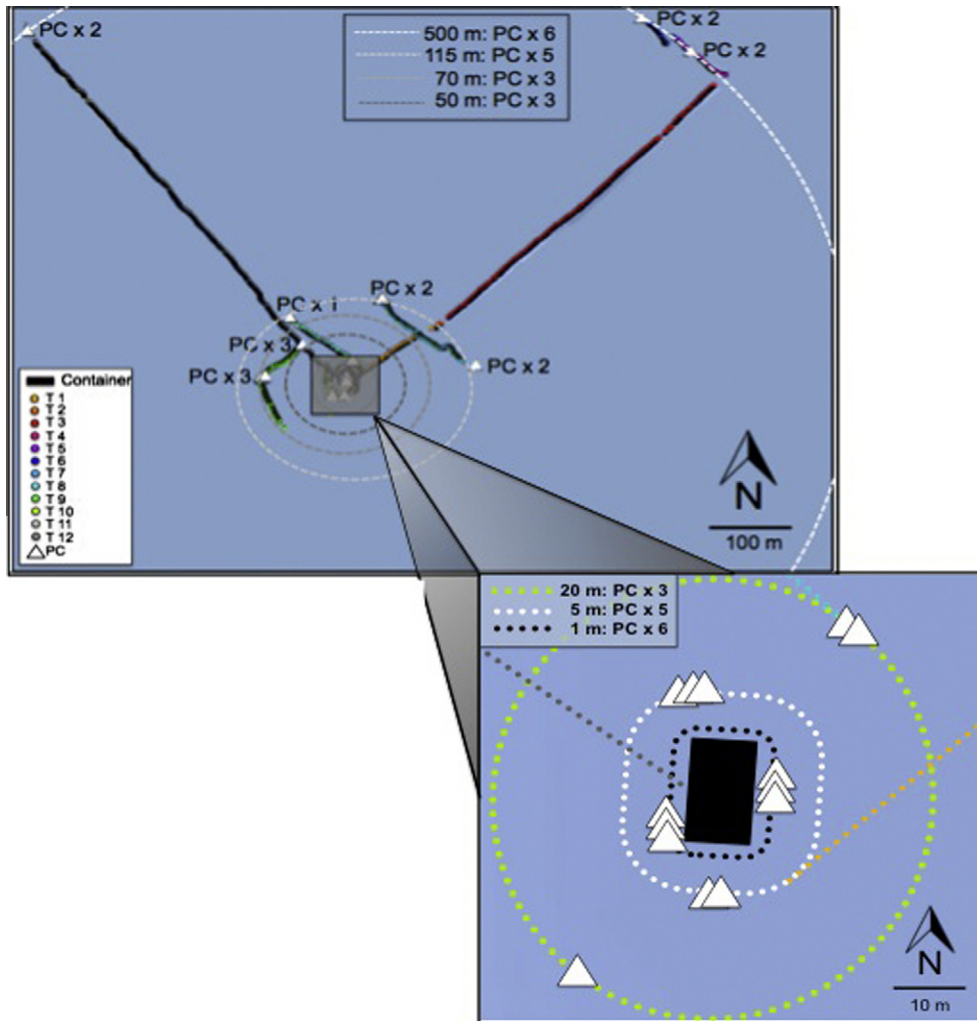
Fig. 2. Location of video transects (T1-T12) and 31 sediment samples (PC) around the container.

In this study we evaluate the hypothesis that the diversity, distribution, and abundance of benthic organisms near the lost intermodal container vary spatially in association with the container.

2. Methods

2.1. Study area

The shipping container is located on a mildly sloping, sediment-covered seabed (1281 m depth) on the upper continental slope in the MBNMS (Fig. 1). A megafaunal assemblage of soft corals, crustaceans, and echinoderms dominates the sea floor in this location, while benthic macrofauna (infauna) is comprised largely of polychaete worms, nematodes, and harpactacoid copepods. Scientists from the MBNMS and MBARI inspected and sampled the container and nearby benthic faunal assemblages during March 2011 using the ROV *Doc Ricketts* (dive D219), operated by MBARI from the R/V *Western Flyer*. ROV pilots flew the vehicle up to a 500 m radius from the intermodal container to record high resolution video along 12 transects up to 480 m long (with total video survey area in excess of 3000 m^2). In addition, benthic macrofaunal organisms were analyzed from sediments collected in 31 sediment cores (7 cm diameter, 192.4 cm^3 of sediment in the top 5 cm analyzed; Fig. 2).

Video data collection- A studio-quality Ikegami HDL-40 1920 × 1080i video camera was used to survey the container via ROV *Doc Ricketts*, with two parallel red laser beams (640 nm) posi-

tioned 29 cm apart for scale. Over 10 h of video observations were recorded to digital video tape, and were later annotated in detail using MBARI's Video Annotation and Reference System (VARS; Schlining and Jacobsen Stout 2006). All benthic and demersal megafauna were annotated to the lowest possible taxonomic unit. For organisms that could not be identified to species (i.e., undescribed or unidentified organisms), a unique name was applied within the VARS database (e.g., *Actiniaria* sp. 1).

Sediment core collection and processing- Several sediment push-core samples were taken from each push-core sampling location (Fig. 2); one or two push-cores were allocated for CHN (Carbon, Hydrogen, Nitrogen) and grain size analysis, and two to four for macrofauna analysis. Upon recovery of the ROV, push-core samples were maintained at 5 °C until processed (within 2 h). The top 3 cm of 11 push-cores was subsampled (by syringe) for grain size and CHN analyses. Sediment from the remaining 20 cores was sieved to remove organisms by gently washing the top 5 cm (of up to 20 cm core depth) from each core through a 0.3 mm mesh sieve using chilled (5 °C) seawater. Organisms were preserved in a 4% formaldehyde (10% formalin) solution for 1–3 days, and then stored in 70% ethanol. Qualified experts subsequently identified macrofauna to the lowest practical taxonomic unit.

2.2. Data analysis

Megafauna observations were binned into nine survey zones, the first being the container surface. The remaining eight zones

Table 1
A complete record of megafauna taxa observations, organized as individuals per taxon per survey location.

Common	Phylum	Taxon	Container	0–10 (m)	11–25 (m)	26–50 (m)	51–100 (m)	101–200 (m)	201–300 (m)	301–400 (m)	401–500 (m)
Annelid worm	Annelida	*Polychaeta*	0	2	4	0	10	15	4	5	10
Fan (tube) worm	Annelida	*Sabellidae*	1314	0	0	0	0	0	0	0	0
Tube worm	Annelida	*Serpulidae*	1416	0	0	0	0	0	0	0	0
Tanner crab	Arthropoda	*Chionoecetes*	0	2	1	2	12	5	3	9	0
Crab	Arthropoda	*Decapoda*	0	0	0	0	1	0	0	0	0
Squat lobster	Arthropoda	*Galatheidae*	0	0	0	0	1	0	2	0	0
Crab	Arthropoda	*Lithodidae*	0	1	0	0	7	3	1	3	3
Lithodid crab	Arthropoda	*Neolithodes diomedae*	0	0	0	0	0	0	0	0	1
Hermit crab	Arthropoda	*Paguroidea*	0	3	1	1	3	2	3	1	13
Bigeye shrimp	Arthropoda	*Pandalopsis ampla*	2	3	2	0	1	0	0	0	0
Oregon hair crab	Arthropoda	*Paralomis*	0	0	0	0	1	0	0	0	0
Lobster	Arthropoda	*Stereomastus*	0	1	0	0	1	0	0	0	0
Sablefish	Chordata	*Anoplopoma fimbria*	0	0	0	0	0	0	1	0	0
Cod	Chordata	*Antimora microlepis*	0	0	0	0	0	1	1	0	1
Rattail	Chordata	*Coryphaenoides*	0	0	1	0	1	0	0	1	3
Sole	Chordata	*Embassichthys bathybius*	0	0	0	0	1	0	0	0	1
Snailfish	Chordata	*Liparidae*	0	0	0	1	0	0	0	0	0
Eelpout	Chordata	*Lycenchelys*	0	7	14	5	26	16	12	17	31
Eelpout	Chordata	*Lycodapus*	0	1	0	0	2	0	1	3	8
Rattail	Chordata	*Macrouridae*	0	0	0	0	0	0	1	0	1
Bony fish	Chordata	*Osteichthyes*	0	0	0	0	1	0	0	0	0
Thornyhead rockfish	Chordata	*Sebastolobus*	0	8	8	0	5	5	2	1	3
Anemone	Cnidaria	*Actiniaria sp. 1*	16	5	3	5	21	10	9	15	24
Anemone	Cnidaria	*Actiniaria sp. 2*	2	0	0	0	0	0	1	0	0
Anemone	Cnidaria	*Actiniaria sp. 3*	1	0	0	0	1	2	2	4	1
Anemone	Cnidaria	*Actiniaria sp. 4*	0	0	0	0	1	0	0	0	0
Feather star	Cnidaria	*Antedonidae*	2	0	0	0	0	0	0	0	0
Sea pen	Cnidaria	*Anthoptilum grandiflorum*	0	1	2	0	0	0	0	2	1
Tube anemone	Cnidaria	*Cerianthidae*	0	1	2	0	7	2	4	3	8
Soft coral	Cnidaria	*Clavularia*	17	0	0	0	0	0	0	0	0
Soft coral	Cnidaria	*Gersemia juliepackardae*	0	0	0	0	3	0	0	0	0
Sea fan	Cnidaria	*Gorgonacea*	1	0	0	0	0	0	0	0	0
Sea whip	Cnidaria	*Halipteris*	0	20	42	11	66	57	42	33	52
Fly trap anemone	Cnidaria	*Hormathiidae*	3	1	0	0	0	0	0	0	0
Pom-pom anemone	Cnidaria	*Liponema brevicorne*	0	8	12	8	16	12	12	5	9
Sea pen	Cnidaria	*Pennatula*	0	215	652	255	1141	808	730	773	960
Sea pen	Cnidaria	*Pennatulacea*	0	23	52	29	110	45	51	67	74
Jelly	Cnidaria	*Siphonophora*	0	0	0	1	21	2	2	8	7
Droopy sea pen	Cnidaria	*Umbellula*	0	2	3	1	7	5	4	1	7
Amphipod	Crustacea	*Amphipoda*	32	0	0	0	0	0	0	0	0
Sea star	Echinodermata	*Asteroidea*	0	6	7	6	7	2	5	3	9
Sea star	Echinodermata	*Lophaster*	1	5	9	9	20	12	18	20	5
Brittle star	Echinodermata	*Ophiuroidea*	7	5	12	5	29	8	5	5	5
Sea star	Echinodermata	*Peribolaster*	5	0	0	0	0	0	0	0	0
Cushion star	Echinodermata	*Pterasteridae*	0	0	0	0	2	0	0	0	1
Sea pig	Echinodermata	*Scotoplanes*	0	80	130	42	242	135	118	146	177
Sun star	Echinodermata	*Solaster*	0	0	0	0	2	2	2	1	1
Pink urchin	Echinodermata	*Strongylocentrotus fragilis*	0	0	0	0	2	2	0	2	3
Spoon worm	Echiura	*Echiura*	0	0	1	1	0	1	2	0	0
Octopus	Mollusca	*Benthoctopus*	0	0	1	0	2	3	1	0	1
Topsnail	Mollusca	*Calliostoma*	108	0	0	0	0	0	0	0	0
Gastropod eggcase	Mollusca	*Eggcase (gastropod)*	53	0	1	0	0	0	0	0	1
Neptune snail eggcase	Mollusca	*Eggcase (neptunea)*	2	0	0	0	0	0	0	0	0
Snail	Mollusca	*Gastropoda*	1	0	0	0	0	0	0	0	0
Octopus	Mollusca	*Graneledone*	0	0	0	1	1	0	0	0	0

Table 1 (continued)

Common	Phylum	Taxon	Container	0–10 (m)	11–25 (m)	26–50 (m)	51–100 (m)	101–200 (m)	201–300 (m)	301–400 (m)	401–500 (m)
Neptune snail	Mollusca	*Neptunea*	12	18	7	1	11	6	3	5	12
Limpet	Mollusca	*Patellacea*	2	0	0	0	0	0	0	0	0
Scallop	Mollusca	*Pectinidae*	285	0	0	0	0	0	0	0	0
Giant nudibranch	Mollusca	*Tritonia diomedea*	0	0	0	0	2	1	0	0	2
Foram tube	Sarcomastigophora	*Bathysiphon*	0	4	3	0	4	2	1	1	1
Tunicate	Urochordata	*Urochordata*	100	0	0	0	0	0	0	0	0
Total megafauna			3382	422	970	384	1791	1164	1043	1134	1436
Total Taxa Observed			22	24	24	18	38	27	30	26	33
Area sampled (m²)			15.7	214.6	376.4	157.1	569.9	424.1	380	380	524.5

were incrementally farther from the container's base: 0–10 m; 11–25 m; 26–50 m; 51–100 m; 101–200 m; 201–300 m; 301–400 m; and 401–500 m.

Analyses of mega- and macrofauna data were performed using Primer and Permanova + software (Primer-E Ltd, Plymouth Marine Laboratory, UK), after applying a square root transformation to raw counts to down-weight frequently observed taxa. Statistical significance of trends in megafaunal abundance derived from video surveys (comprising 384–3382 individuals observed at each of nine distance ranges, covering areas of 16–570 m^2) was determined using Monte Carlo methods in a permutational MANOVA test. Similarly, macrofauna data were assessed by permutational MANOVA with Monte Carlo methods, using 9999 unrestricted permutations of raw data.

Distance-based redundancy analysis (*db*RDA) was used to assess resemblance (based on Bray-Curtis Similarity) of mega- and macrofauna assemblages among their respective survey locations and to determine the taxa with the highest correlation to each sampling location. Bray Curtis similarity was used on standardized, down-weighted data to quantify the resemblance of megafauna communities on the container *vs* the benthos ⩽10 m vs. >10 m from the container's base. *db*RDA was performed in Primer/ PERMANOVA+, with vector overlays of taxa having a correlation >0.2 with their habitat. Similarity contours were calculated for levels of 30%, 40%, 50%, and 60% similarity.

Univariate diversity indices were calculated for mega- and macrofauna data using the Primer function DIVERSE. Additional statistical calculations were made using StatPlus (AnalystSoft Inc.) software. Normality was assessed using the Shapiro–Wilk test, and measures among survey zones were compared using two-tailed *T*-tests or Mann Whitney *U* tests, as appropriate. For most statistical analyses, data from 26 to 500 m were pooled, as described in the text, after finding no significant differences in data collected among these distances. *F*-tests were used to determine differences in sample variance between sites. Throughout, $P < 0.05$ was considered statistically significant.

3. Results

3.1. Megafauna

A total of 11,184 megafaunal individuals from 10 phyla and 61 taxa (Table 1) were observed from video transects covering an area of 3089 m^2 (Fig. 2).

As expected, the megafaunal assemblage on the container surface differed greatly (Permutational MANOVA, Monte Carlo $P = 0.0001$) from the assemblages found on sediment-covered survey zones around the container (Fig. 3). Container megafauna was dominated by serpulid and sabellid worms, pectinid scallops, *Calliostoma* sp. top snails, and attached tunicates (Fig. 4). These taxa were only associated with the container's surface and not observed on sediment habitats. Megafauna on the container were present in higher density (two-tailed *T*-test of individuals m^{-2}, $P < 0.001$), lower taxa richness (two-tailed *T*-test of Margalef's *d*, $P < 0.001$), and lower diversity (two-tailed *T*-test of H'Log$_e$, $P < 0.001$) than observed for the sediment-dwelling assemblage pooled from 26 to 500 m (Fig. 5). Furthermore, the variance in density of individuals (*F*-test of individuals m^{-2}, $F \geqslant 9.0$, $P \leqslant 0.048$), diversity (*F*-test of H'Log$_e$, $F \geqslant 11.6$, $P \leqslant 0.032$), and dominance (*F*-test of 1-λ', $F \geqslant 51.6$, $P \leqslant 0.002$), of megafauna on the container was higher than measured for the sediment assemblage (26–500 m; Fig. 5). Overall, the container surface houses a megafauna assemblage approximately 40% similar to the benthos within 10 m of its base and 30% similar to the benthos >10 m, based on distance-based redundancy analysis (*db*RDA) with standardized densities of individuals per survey location (Fig. 6).
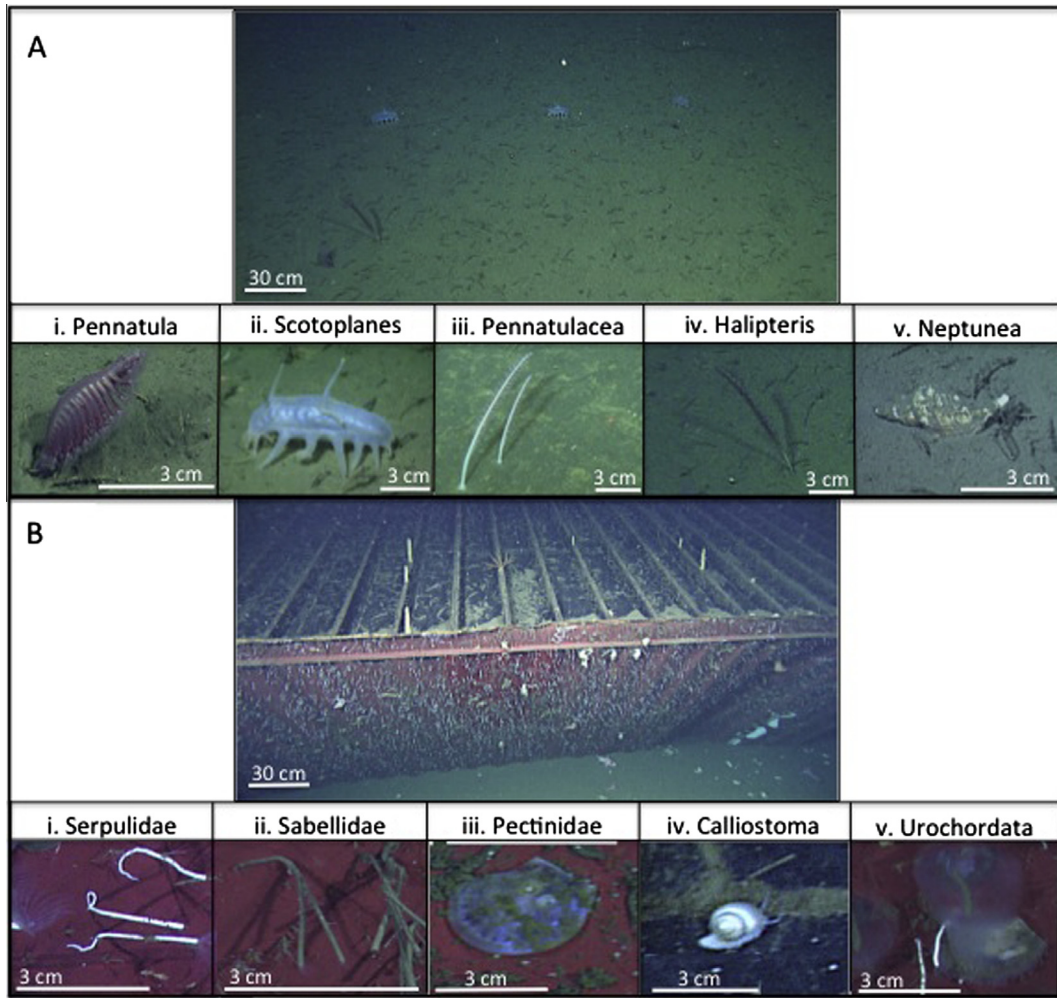
Fig. 3. Megafauna assemblages off (A) and on (B) the container. Representative images of abundant megafauna taxa off (Ai-v) and on (Bi-v) the container are shown.

Sediment-dwelling megafauna varied in abundance according to their distance from the container. Within 10 m of the container, the megafaunal assemblage was distinctive from all more distant areas (Permutational MANOVA, Monte Carlo $P < 0.05$). The megafauna dominating the benthos (Fig. 7a–d) were not observed on the container and were present in lower densities within 10 m of the container compared to all more distant locations (two-tailed T-tests, $P < 0.05$). The principal difference in megabenthos near the container was the decreased abundance of the sea pen *Pennatula* sp. and other filter feeders (Fig. 7). Mobile taxa were more abundant within 10 m of the container (ca. 35% of total abundance overall) compared with more distant areas (21%) due mainly to the increased abundance of *Neptunea* sp. (Fig. 7e), *Sebastolobus* sp. (Fig. 7f), the prawn *Pandalopsis* sp., and the pom pom anemone *Liponema brevicorne*. In the survey zone 0–10 m from the container's base, the neogastropod *Neptunea* sp., for example (Fig. 7e), was present in significantly greater (Mann–Whitney U test, $U = 41$, $P = 0.014$) abundance and with greater variability (Equality of variance test; $F_{5,9}=8670.295$, $P < 0.001$) than at survey locations farther from the container. Benthic megafauna within 10 m of the container showed a lower density (two-tailed T-test of individuals m^{-2}, $P = 0.009$), lower taxa richness (two-tailed
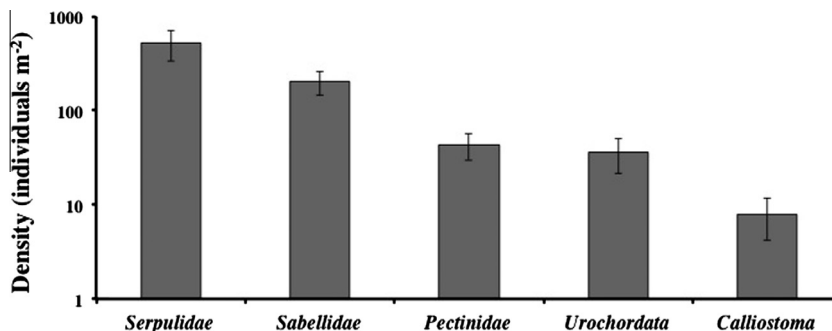

Fig. 4. Mean densities (95% CI) of dominant megafauna taxa on the container are shown on a log scale. None of these taxa were observed at any location off the container surface.
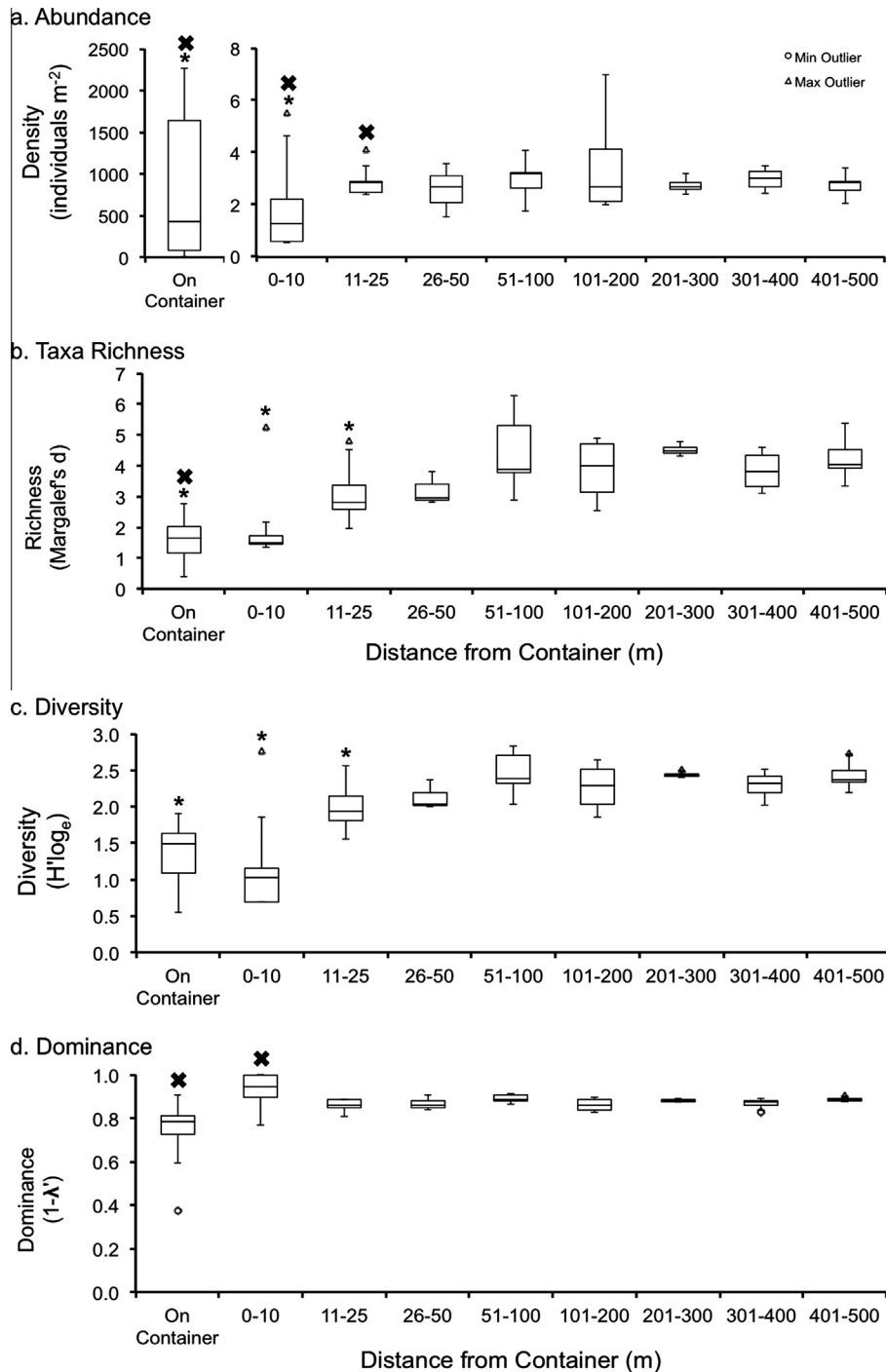
Fig. 5. Box plots for measures describing the megafauna assemblage at nine survey zones on and 0–500 m away from the container: (a) abundance; (b) taxa richness; (c) H' diversity; and (d) dominance. Box defines boundaries for the 25th and 75th percentiles, median indicated by line across box. Whiskers show the lowest and highest data within 1.5 IQR of the lower and higher quartile; min and max outliers are shown as open circles and triangles, respectively. Statistically significant differences from the collective data for 26–500 m, as described in the text, were calculated using a two-tailed *T*-test or Mann–Whitney U Test as appropriate, and are represented by ∗ for *P* < 0.05. The *F*-test was used to determine significant differences in variance from the most distant survey zone (500 m), represented by × when *P* < 0.05.

T-test of Margalef's *d*, *P* < 0.001), and lower diversity (two-tailed *T*-test of H'Log$_e$, *P* < 0.001) compared with the collective data from 26 to 500 m (Fig. 5). Lower taxa richness (two-tailed *T*-test of Margalef's *d*, *P* = 0.0461) and diversity (two-tailed *T*-test of H'Log$_e$, *P* = 0.0130) were also found in the survey zone 11–25 m from the container when compared with the collective data from 26 to 500 m. Among survey zones >25 m from the container, the relative abundances and univariate diversity indices of megabenthos varied insignificantly.

3.2. Macrofauna

A total of 941 macrofaunal individuals were found in sediment cores taken at distances 1–500 m from the container (Fig. 2, Table 2). Macrofauna represent 12 phyla and 117 distinct taxa (Table 2). Sediment samples contained 18 to 78 individuals per core, with 2–6 cores per distance (Table 2).

Using a permutational MANOVA, we found no significant correlation between the composition and relative abundance of the
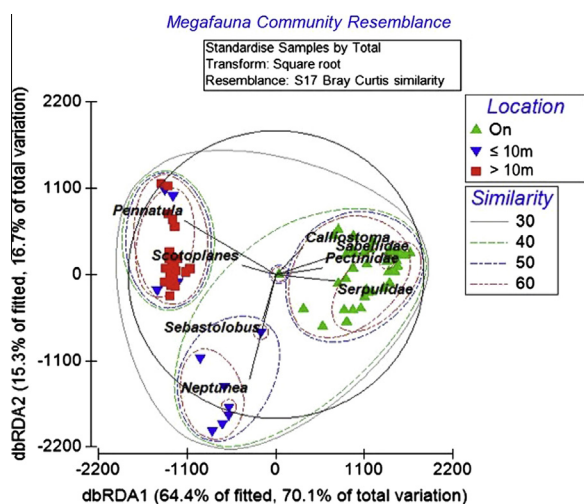
Fig. 6. Megafauna community resemblance was analyzed for data collected on the container, within 10 m, and >10 m from the container, and similarity contours are shown for levels of 30%, 40%, 50%, and 60% similarity. Data collected on the container are shown in green upward-facing triangles; benthos within 10 m of the container are shown with blue downward-facing triangles; and benthos >10 m from the container are shown with red squares. Defining taxa are labeled for each grouping.

macrofaunal community versus distance from the container. Analysis of relative abundance at each location revealed fine-scale differences in macrofauna assemblages. Significantly fewer harpactacoid copepods were observed in sediment sampled 1 m (two-tailed *T*-test, $P = 0.002$) and 5 m (two-tailed *T*-test, $P = 0.044$) from the base of the container, compared with 500 m from the container (Fig. 8); however, this difference was not significant when compared with the collective data from 20 to 500 m (two-tailed *T*-test, $P = 0.058$ at 1 m and $P = 0.693$ at 5 m).

Univariate diversity indices calculated using the Primer function DIVERSE indicated that the taxa richness of infaunal assemblages 1 m from the base of the container were significantly lower (two-tailed *T*-test, $P = 0.019$) than assemblages 500 m from the container (Fig. 9), or from the pooled data from 20 to 500 m (two-tailed *T*-test, $P = 0.026$). Furthermore, the density of individuals was more variable in sediment samples taken 1 m from the container (Equality of variance test; $F_{4,4} = 20.179$, $P = 0.034$) than at any other location. Other univariate measures of macrofauna diversity showed no significant correlation with distance from the container (Fig. 9).

3.3. Sediment

Sediment analyzed from the top 3 cm of push-core samples had larger grain size and lower total organic carbon (TOC) than sediments collected nearest the container (Table 3), such that grain size $G = -0.005$ (distance in meters) + 17.735. Assuming a single explanatory variable, this relationship accounts for 29.5% of the observed variation in grain size among stations (distances). Similarly, the TOC (% by weight) content of sediment increased slightly, but significantly, with distance from the container such that TOC = 0.001 (distance in meters) + 2.1211 ($R^2 = 0.84$).

4. Discussion

Deep-sea sedimentary ecosystems are one of the most extensive, but least studied systems on Earth. Consequently, the impacts of litter in these systems are rarely understood (Ramirez-Llodra et al., 2011; Schlining et al., 2013). Our results indicate that faunal assemblages on or very near an intermodal container on the deep seafloor in the Monterey Bay National Marine Sanctuary are anom-

alous compared to the surrounding benthos. Owing to the nature of this study, the effects of the container on the nearby deep-sea benthos cannot be identified unambiguously. However, observations of the faunal colonization on the container and the pattern of macrofaunal and megafaunal assemblages in soft sediments surrounding the container offer strong clues concerning the local ecological effects of the container.

One of the most compelling results of our evaluation of the container site is that the dominant megafauna associated with the container's surface are markedly dissimilar from those reportedly associated with natural hard substrata at similar depths along the central California coast. Rocky canyon walls within 10 km of the study site in Monterey Canyon support an abundance of phyla Chordata, Cnidaria, Porifera, and Echinodermata (McClain et al., 2009; McClain and Barry 2010). Similarly, megafauna surveys of Davidson Seamount, Pioneer Seamount (approx. 125 km SSW and NW of the study site, respectively), and Rodriguez Seamount (over 300 km SSE of the study site) show dominance at these sites by the phyla Cnidaria, Porifera, and Echinodermata (Lundsten et al., 2009; McClain et al., 2010). Long-lived crinoids, sponges, and soft corals are the predominant taxa found along these canyon walls and seamounts, while our survey of the container's hard substratum shows a lack of these taxa, and dominance by taxa from the Annelida and Mollusca. This faunal contrast is due in part to the different emphasis of the seamount studies. Smaller megafauna such as the annelids and mollusks observed on the container are common at seamounts and other rocky habitats in the region (JPB, pers. obs.), but were not included in the seamount surveys cited above. However, why were corals, crinoids, and sponges that dominated the seamount reports largely absent from the container? Our working hypothesis is that the faunal assemblage on the container after seven years is still at an early successional stage, particularly considering the generally slow rates of colonization and growth for deep-sea megafauna; for example, deep-sea corals live up to several thousand years (Andrews et al., 2002). Alternatively, does the existing species assemblage on the container represent the suite of species tolerant of its potentially toxic surface? This alternative hypothesis may explain the lack of even small recruits of corals, sponges, and other later successional dominants more common on seamounts.

The high density of individuals and taxa observed on the container suggests this habitat is highly amenable to colonization by taxa not normally associated with deep-sea soft sedimentary habitats (Lundholm and Larson 2004; Kogan et al., 2006; Crooks et al., 2010). The variation in the composition and abundance of megafaunal taxa among our survey sites is largely associated with a few key taxa. Taxa most closely associated with the container include fast-growing serpulid and sabellid polychaete tubeworms. These dominant annelids are common on other rocky habitats outside our survey area, including seamounts (Lundsten et al., 2009; McClain et al., 2010); however, their small size relative to other megafauna means they are rarely reported (JPB et al., personal obs.). While these tube worms are expected to colonize any hard substrate their larvae reach, it is notable that disturbance – including metal pollution – has been found to increase the densities of some serpulid species in shallower habitats through their enhanced ability (as successful early colonizers) to sequester new space when hard substrate is limited (Johnston et al., 2003; Piola and Johnston 2007). Serpulid polychaetes are known to be a common "fouling invertebrate" in shallow water, able to colonize relatively quickly even in the presence of anti-fouling marine paints (Wisely 1964; Johnston and Keough 2000; Crooks et al., 2010). Although not tested here, the coatings used to make intermodal containers durable for ocean transport typically contain a number of potentially toxic compounds and metals, such as zinc, chromate, phosphorous, copper, nickel, and lead-based paints (Pagnotta 2011).
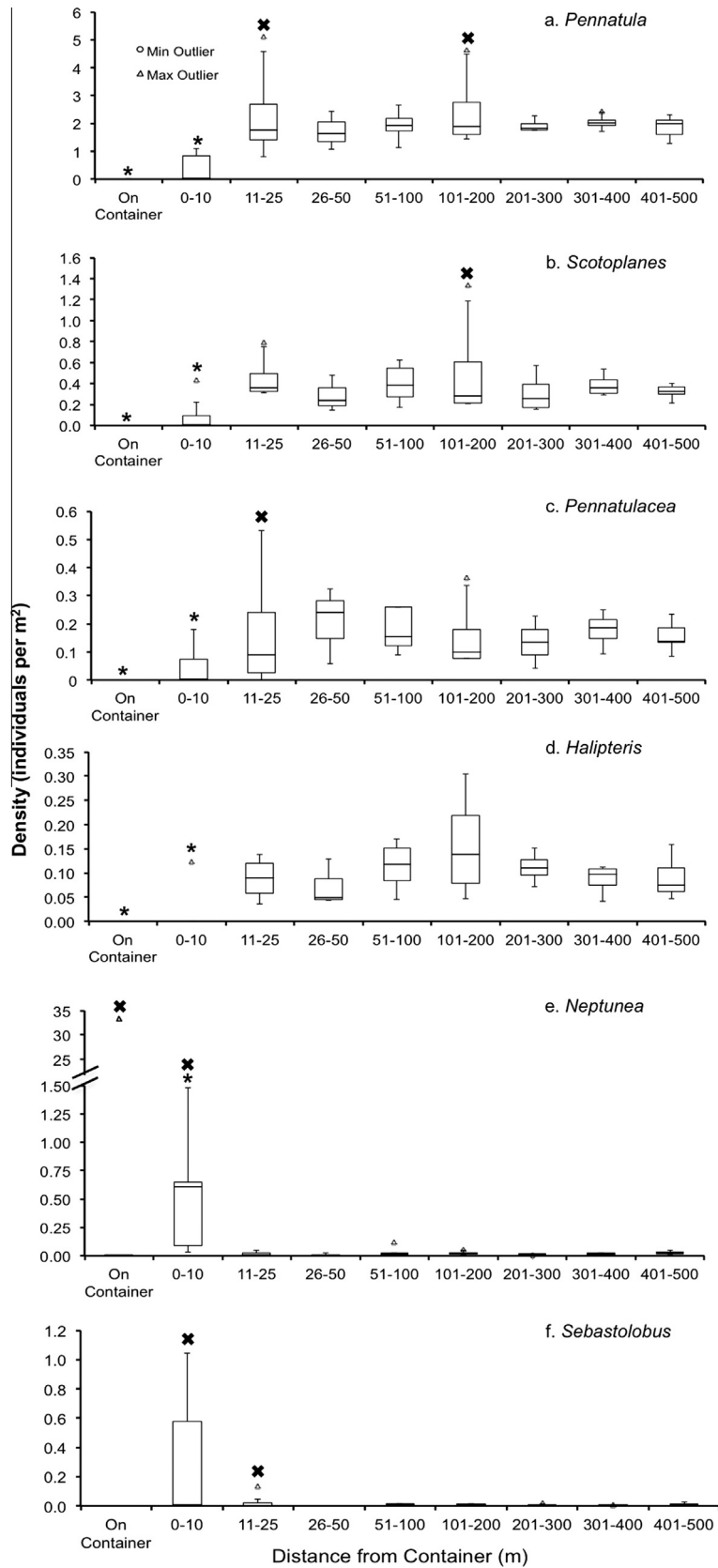
Fig. 7. Boxplots representing densities of abundant megafauna taxa in sediment habitats near the container. Symbols and indicators of statistical significance as in Fig. 5.

Anomalous megafaunal and macrofaunal assemblages within 10 m of the container's base are very likely due to both direct and indirect effects of the container on the seabed and faunal assemblage. In particular, the snail *Neptunea* sp., and a number of teleost fish taxa including the thornyhead rockfish, *Sebastolobus* sp., are typically attracted to any type of habitat heterogeneity

Table 2
A complete record of macrofauna taxa observations, organized as total individuals per survey location. Number of cores contributing to counts is given in the last row.

Phylum	Taxon	1 m	5 m	20 m	50 m	70 m	115 m	500 m
Annelida	Aglaophamus paucilamellata	0	0	1	0	0	0	0
Annelida	Ampharetidae	1	1	0	0	2	0	0
Annelida	Ampharetidae genus 1	0	0	0	0	0	0	1
Annelida	Ampharetidae genus 2	1	0	0	0	0	0	0
Annelida	Ampharetidae genus 3	1	0	0	0	0	0	0
Annelida	Ampharetidae sp 4	0	0	0	0	0	1	0
Annelida	Anobothrus mancus	0	0	0	0	0	1	0
Annelida	Anobothrus sp 2	0	0	0	0	0	0	1
Annelida	Anobothrus sp 3	0	0	1	0	0	0	0
Annelida	Aphelochaeta	0	0	1	0	0	0	0
Annelida	Aphelochaeta bullata	1	0	0	0	0	0	0
Annelida	Aphelochaeta sp 1	1	0	0	0	0	0	0
Annelida	Aphelochaeta sp 2	0	1	0	0	0	0	0
Annelida	Apistobranchus ornatus	0	0	1	0	0	2	0
Annelida	Aricidea (Acmira) simplex	1	0	0	0	0	0	0
Annelida	Aricidea (Acmira) sp 1	0	1	1	2	4	0	1
Annelida	Aricidea (Allia) antennata	0	0	0	0	0	1	0
Annelida	Aricidea (Allia) sp 1	1	0	0	0	0	0	1
Annelida	Aricidea (Allia) sp A	0	0	1	0	0	0	0
Annelida	Aricidea (Aricidea) wassi	0	1	0	0	0	0	0
Annelida	Capitellidae	0	1	0	0	0	0	1
Annelida	Capitellidae genus A	0	0	0	1	0	0	1
Annelida	Ceratocephale loveni	0	0	0	1	0	0	0
Annelida	Chaetozone sp 1	0	0	2	0	0	1	0
Annelida	Chaetozone sp 2	0	0	0	0	1	0	0
Annelida	Chaetozone spinosa	0	0	0	0	0	1	1
Annelida	Cirratulidae	0	1	0	0	0	0	0
Annelida	Cossura sp 2	4	2	1	0	0	2	6
Annelida	Cossura sp 3	8	2	0	4	3	2	0
Annelida	Dorvilleidae	0	1	0	0	0	0	0
Annelida	Dorvilleidae genus 1	0	0	0	0	0	1	0
Annelida	Ephesiella brevicapitis	0	1	1	0	0	1	2
Annelida	Euclymeninae	0	0	1	0	0	0	0
Annelida	Flabelligeridae sp 1	0	0	0	0	0	0	1
Annelida	Goniada	0	1	0	0	0	0	0
Annelida	Gyptis hians	0	0	0	1	0	0	0
Annelida	Heteromastus sp 1	1	1	1	0	0	1	2
Annelida	Levinsenia gracilis	1	2	1	2	1	2	1
Annelida	Lumbrineridae	0	1	0	0	0	0	0
Annelida	Lumbrineris sp 1	1	0	1	1	1	1	0
Annelida	Lysippe sp 1	0	0	1	0	2	0	1
Annelida	Maldanidae	0	1	2	1	0	0	0
Annelida	Mediomastus	0	0	0	0	0	1	0
Annelida	Mugga wahrbergi	1	3	1	3	0	0	1
Annelida	Neoheteromastus lineus	0	0	0	0	0	1	0
Annelida	Neomediomastus glabrus	1	2	1	1	0	1	1
Annelida	Nephtys cornuta	1	1	1	1	1	1	4
Annelida	Nephtys sp 1	0	2	0	3	1	0	1
Annelida	Ninoe sp 1	0	0	0	0	0	0	1
Annelida	Notomastus precocis	0	1	0	0	0	0	0
Annelida	Octobranchus	0	0	0	0	0	0	1
Annelida	Octobranchus sp 1	1	0	0	0	0	0	0
Annelida	Oligochaeta	16	1	0	0	0	0	0
Annelida	Paraonidae	0	0	0	0	0	1	0
Annelida	Paraonidae sp 1	1	0	0	0	0	0	0
Annelida	Parougia Sp 1	0	0	0	0	0	0	1
Annelida	Pholoe courtneyae	0	0	0	0	0	0	1
Annelida	Phyllochaetopterus limicolus	0	1	2	0	0	1	1
Annelida	Phyllodocidae	0	1	0	0	0	0	0
Annelida	Phylo nudus	0	0	0	0	0	0	1
Annelida	Polychaete (juvenile)	0	1	4	0	4	0	3
Annelida	Polychaete (unidentified)	0	0	0	0	0	0	1
Annelida	Polycirrus	0	1	0	0	0	0	0
Annelida	Polynoidae	0	0	0	0	0	1	0
Annelida	Prionospio	0	0	0	0	0	1	0
Annelida	Sphaerodoropsis sp 1	0	0	0	0	0	0	1
Annelida	Terebellidae	0	0	0	1	0	0	0
Annelida	Terebellides	0	0	0	0	0	1	2
Annelida	Tharyx sp 1	45	48	36	40	33	40	46
Annelida	Tharyx sp 2	0	4	3	0	0	0	1
Aplacophora	Aplacophora (juvenile)	0	1	0	0	1	0	0
Aplacophora	Falcidens longus	0	0	0	0	0	1	0
Aplacophora	Neomeniomorpha	0	1	0	0	0	0	0
Aplacophora	Spathoderma californica	0	1	0	0	0	0	1

Table 2 (continued)

Phylum	Taxon	1 m	5 m	20 m	50 m	70 m	115 m	500 m
Bivalvia	*Bivalvia* (juvenile)	1	0	1	0	0	0	3
Bivalvia	*Bivalvia sp. (mature adult)*	1	0	0	0	0	1	1
Bivalvia	*Cardiomya planetica*	0	1	0	0	0	0	0
Bivalvia	*Enucula tenuis*	1	0	0	1	0	0	0
Bivalvia	*Nucula carlottensis*	0	1	1	0	0	0	0
Bivalvia	*Nuculana conceptionis*	2	0	0	0	0	1	1
Bivalvia	*Yoldiella nana*	0	0	0	0	1	2	1
Cnidaria	*Hydroida*	0	2	0	0	0	0	0
Cnidaria	*Hydrozoa B*	0	0	0	0	0	0	1
Crustacea	*Aceroides*	1	0	0	0	0	0	0
Crustacea	*Amathillopsis sp.*	0	0	0	0	0	1	0
Crustacea	*Ampelisca amblyopsoides*	1	0	0	0	0	0	0
Crustacea	*Araphura cuspirostris*	0	1	0	0	0	0	0
Crustacea	*Bathymedon sp.*	0	0	1	0	0	0	0
Crustacea	*Campylaspis sp.*	0	1	1	0	0	0	0
Crustacea	*Dulichia sp.*	0	0	0	1	0	0	1
Crustacea	*Eudorella pacifica*	0	0	0	0	0	0	1
Crustacea	*Eudorella sp.*	0	0	0	0	0	0	1
Crustacea	*Harpactacoida*	3	8	2	5	4	8	23
Crustacea	*Ilyarachna profunda*	2	0	0	1	0	0	0
Crustacea	*Ilyarachna sp.*	0	0	1	0	0	0	0
Crustacea	*Isaeidae*	0	1	0	0	0	0	0
Crustacea	*Lepechinella arctica*	0	1	0	0	0	0	0
Crustacea	*Leptostylis sp.*	0	1	1	0	0	0	0
Crustacea	*Mypocopida*	0	0	1	0	0	0	0
Crustacea	*Paramunnidae*	0	0	0	1	0	0	0
Crustacea	*Pardaliscidae*	0	0	0	0	0	0	1
Crustacea	*Photis typhlops*	0	1	0	0	0	0	0
Crustacea	*Podicopida*	0	1	0	0	0	0	0
Crustacea	*Protomedeia sp.*	0	0	0	0	0	0	1
Crustacea	*Synopidae*	0	0	0	0	1	0	0
Crustacea	*Syrrhoe longifrons*	0	1	0	0	0	0	0
Crustacea	*Tanaopsis*	0	0	1	0	0	1	0
Crustacea	*Tritella tenuissima*	0	0	0	0	0	0	1
Gastropoda	*Gastropoda* (juvenile)	0	1	0	0	0	0	0
Loricifera	*Loricifera*	0	0	1	0	0	2	0
Nematoda	*Nematoda*	42	44	20	60	27	40	59
Nemertea	*Nemertea*	3	2	0	1	6	0	4
Ophiuroidea	*Ophiura leptoctenia*	0	1	0	1	1	0	0
Scaphopoda	*Gadila sp.*	1	0	0	0	0	1	1
Scaphopoda	*Scaphopoda*	0	0	0	0	2	0	0
Sipuncula	*Sipuncula*	0	0	0	0	0	1	1
Sipuncula	*Spinucula B*	0	0	0	0	0	0	1
	Total Macrofauna	146	155	96	133	96	125	190
	Total Taxa Observed	30	46	33	22	19	34	47
	Number of Cores Sampled	4	3	2	2	2	3	4

(Buhl-Mortensen et al., 2010; Levin et al., 2010). Predatory fish and large crabs aggregating around the container may have responded to the presence of the container, but led to indirect impacts on nearby prey and competitors. Furthermore, the high prevalence of the semelparous gastropod mollusk *Neptunea* sp. and their empty shells suggests the container provides hard substrate for egg case attachment.

In contrast to the benthos surrounding the container, megafauna assemblages >25 m away – as well as local soft sediment assemblages outside the study area – are dominated by long-lived pennatulacean sea pens (Kuhnz et al., 2011), which provide important habitat for a variety of taxa (Baker et al., 2012). The holothurian *Scotoplanes globosa* also comprises a large fraction of the abundance of bathyal, benthic megafauna (Kuhnz et al., 2011). *S globosa* is presumably an important bioturbator that introduces oxygen to sediments as they feed and move along on the seafloor. Organisms that oxygenate sediments or reduce sulfide concentrations through feeding, dwelling structures, and burrowing may indirectly facilitate other taxa (Widdicombe et al., 2000; Levin et al., 2001). In this way, low-level or local-scale disturbance (<10 m², e.g., bioturbation) can increase small-scale heterogeneity and thereby increase biodiversity, while high-level or regional-scale disturbance (>10 m², e.g., dredging, trawling) typically reduces biodiversity (Engel and Kvitek 1998; Thrush and Dayton 2002). The arrival of an intermodal container in the deep sea is arguably a high-level disturbance, suffocating the fauna in underlying sediments. Similarly, trawling reduces habitat heterogeneity and is expected to reduce biodiversity. However, even though diversity in sediments beneath a lost container is expected to decline, containers on sediment-covered deep-sea environments also provide new habitat (albeit man-made) that is likely to increase local diversity and richness. Containers sinking in rocky habitats may have little effect on local habitat heterogeneity, and thus a minor influence on diversity or species richness.

If the container caused the anomalies in nearby macrofaunal community patterns, its effects are relatively minor. Some infaunal shifts may also be related to slight differences in the physical character of deep-sea sediments. Larger grain size and lower TOC of sediments nearest the container, consistent with acceleration of bottom currents by the container, may be responsible for the observed minor shifts in taxa abundance. While it has not been well-studied in deep-sea species, there is abundant evidence that deposit feeding taxa in shallow sedimentary habitats selectively ingest sediments of particular size classes (Rhoads 1974;
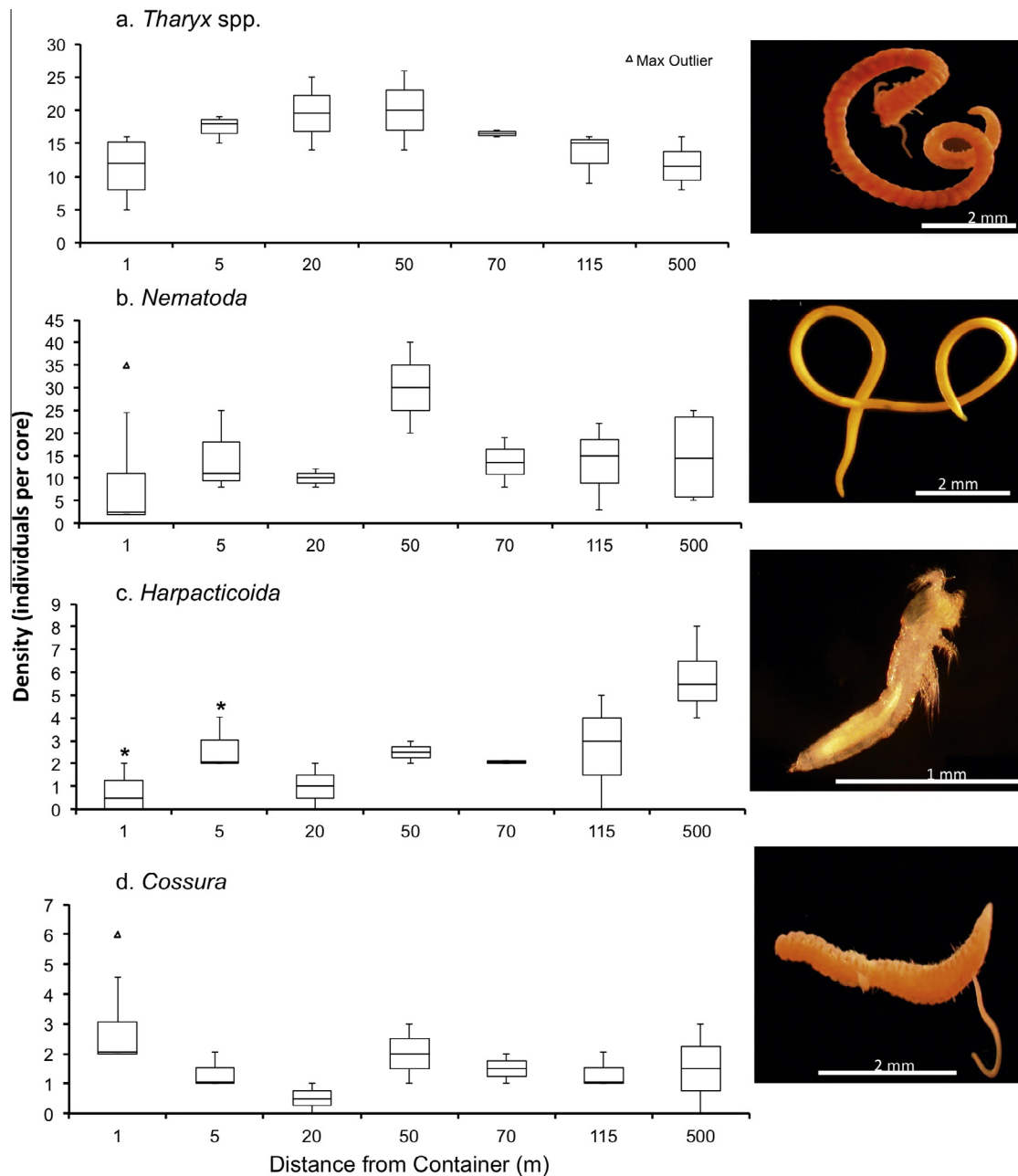
Fig. 8. Densities of dominant macrofauna taxa sampled from sediment push-cores taken 1, 5, 20, 50, 115, and 500 m from the container. Symbols and indicators of statistical significance as in Fig. 5.

Whitlatch 1981; Taghon 1982; Probert 1984; Wheatcroft and Jumars 1987); in this way, sediment characteristics correspondingly play an important role in structuring macrofaunal communities (Rhoads 1974; Levin et al., 2001). Trends in sediment grain-size near the container are very likely related to the hydrodynamic effects of the container on local flow patterns, promoting a higher range and variation in currents adjacent to the container, and net removal of fine sediments. Particulate organic matter (POM) flux or food supply has been suggested to ultimately play the most significant role in regulating the number of species (Levin et al., 2001). Interestingly, diversity typically declines at high levels of food supply; a phenomenon that is not well understood but may reflect a decrease in habitat heterogeneity, leading to increased dominance by a few species (Rosenzweig and Abramsky 1993; Mittelbach et al., 2001). Our results suggest that

a simple increase in organic matter availability is not responsible (Table 3) for the drop in benthic diversity and richness near the container site.

4.1. Consequences and Future Monitoring

Our results indicate that the container is a disturbance to the seabed that (1) alters local flow patterns, likely leading to changes in grain size assortment very nearby, (2) increases habitat heterogeneity and adds structure, leading to megafauna aggregation, (3) acts as hard substratum for settlement of different taxa than occur in soft sediments nearby, and (4) promotes a number of cascading indirect effects (e.g. changes in predation, competition, restructuring of sediment community due to change in grain size, and related biological effects). In sum, the container has conferred a mild
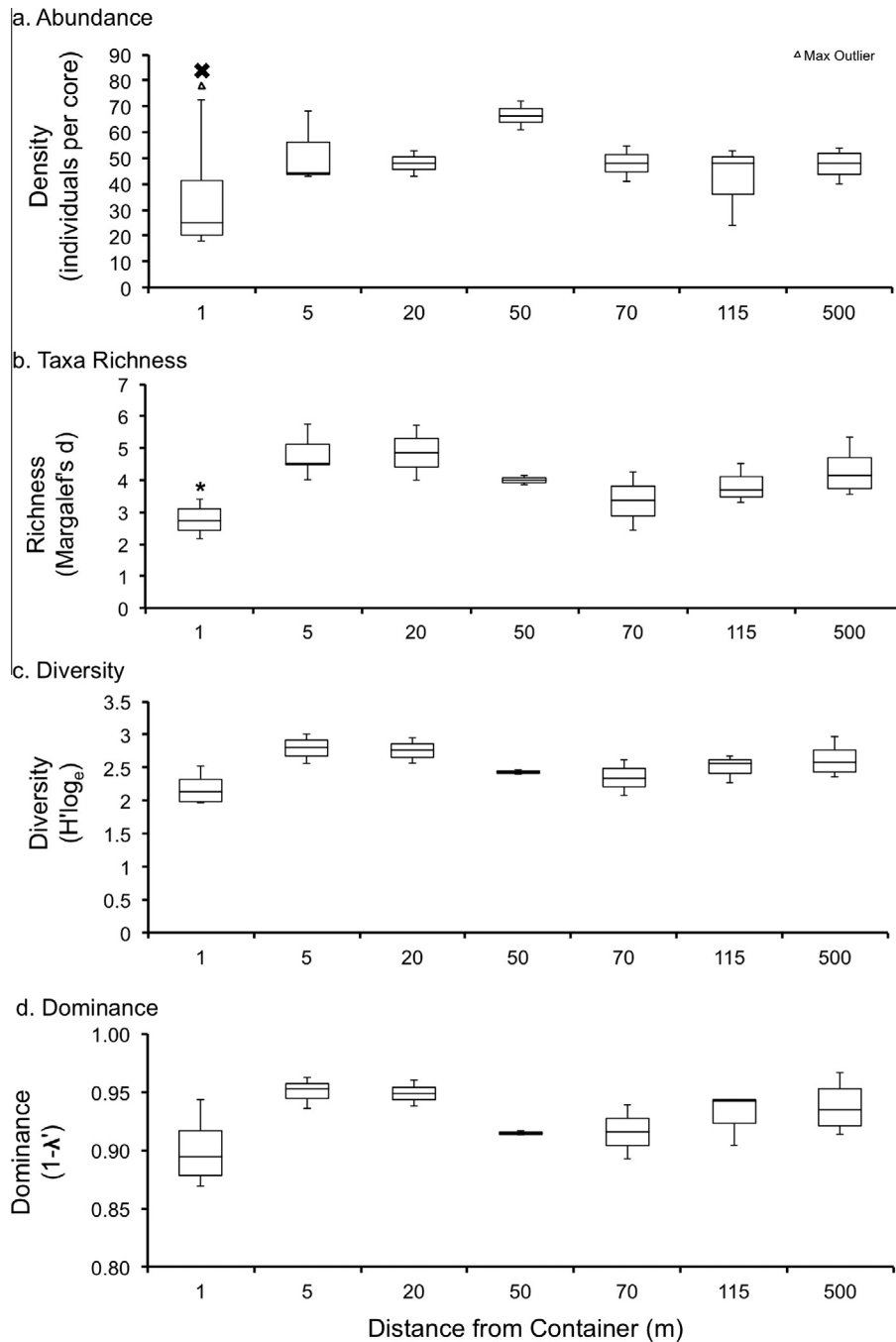
Fig. 9. Macrofauna assemblage data for each of seven sampling distances from the container: (a) abundance; (b) taxa richness; (c) diversity; and (d) dominance. Symbols and indicators of statistical significance as in Fig. 5.

Table 3
Characteristics of sediment collected from push-core samples at a range of distances from the shipping container. Measurements are reported as mean ± 95% CI.

Distance from container (m)	C:N	TOC (wt.%)	Grain size
1	9.51 ± 0.13	2.11 ± 0.08	18.06 ± 6.02
5	10.50 ± 0.89	2.16 ± 0.00	19.10 ± 2.74
20	[a]9.46	[a]2.06	[a]18.67
50	[a]10.24	[a]2.25	[a]15.50
70	[a]9.29	[a]2.13	[a]17.79
115	9.49 ± 0.44	2.20 ± 0.18	15.61 ± 1.86
500	9.59 ± 0.16	2.47 ± 0.13	15.84 ± 0.50

[a] Denotes measurements based on $n = 1$.

disturbance with very local scale effects (up to a 10 m halo of significantly altered biological patterns). Thus, the container's approx. 30 m² footprint with a 10 m halo gives approx. 600 m² of disturbance – or 20X its footprint. We are left with the unanswered question of why the container's megafauna assemblage is lacking the larger, longer-lived taxa that dominate local seamount communities. Continued monitoring of the site will help to discern whether the megafaunal assemblages on and near the container will ultimately become more similar to those associated with nearby rocky habitats, or whether further community development will be inhibited by the container's toxicity or other factors.

All 24 of the standard intermodal containers lost in this shipping incident are expected to have similar ecological effects to

those measured near the single container reported here. Considering the prevalence of similar incidents of cargo loss, the increasing dispersion of containers on the deep seafloor may promote population connectivity across vast sediment covered areas for taxa requiring hard substrata for survival and reproduction. The concept of evolutionary stepping stones in the deep-sea environment has long been considered, albeit predominantly with respect to chemosynthetic fauna (France et al., 1992; Vrijenhoek 1997; Tunnicliffe et al., 1998; Smith and Baco 2003) and seamount communities (Hamilton 1956; DeForges et al., 2000; Brewin et al., 2007). In an area of the deep sea with the spatial scale and habitat heterogeneity of Monterey Bay, it is unlikely that larvae are limited by natural hard substrata suitable for settlement; however, sunken containers regularly lost along shipping routes may provide stepping stones for some sessile, hard substrate taxa to migrate from port to port or coastline to coastline.

The episodic loss of intermodal containers along shipping routes is inevitable. In the years since the shipping container referenced here was lost, notable strides have been made in reducing the ecological impact of the shipping industry. For example, the Clean Cargo Working Group (CCWG), established by Business for Social Responsibility (BSR) in 2003, is a business-to-business initiative that creates practical tools for measuring and reducing the environmental impacts of global goods transportation. In particular, shippers and carriers holding membership with the CCWG (representing more than 60 percent of global container shipments) commit to the use of less-toxic or non-toxic antifouling coatings (Business Social Responsibility Report, 2011). To investigate the possibility of localized toxicity due to antifouling coatings, our next visit to the Monterey Bay National Marine Sanctuary container site will entail sampling of mineral and composite materials, as well as benthic organisms, found on and around the container for toxicological analyses.

Author contribution

Acknowledgments

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