The seven-year enrichment: Macrofaunal succession in deep-sea sediments around a 30-ton whale fall in the Northeast Pacific

RUNNING HEAD: Infaunal succession at deep-sea whale fall

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ABSTRACT. Whale falls cause massive organic and sulfide enrichment of underlying sediments, yielding energy-rich conditions in oligotrophic deep-sea ecosystems. While the fauna colonizing whale skeletons has received substantial study, sediment macrofaunal community response to the geochemical impacts of deep-sea whale falls remains poorly evaluated. Here we present a seven-year case study of geochemical impacts, macrofaunal community succession, and chemoautotrophic community persistence in sediments around a 30-ton gray-whale carcass implanted at 1675 m in the well oxygenated Santa Cruz Basin on the California margin. We find that the 30-ton whale fall yielded intense, patchy organic-carbon enrichment (>15% organic carbon) and pore-water sulfide enhancement (> 5 mM) in nearby sediments for 6-7 yr, supporting a dense infaunal assemblage of enrichment opportunists and vesicomyid clams. Infaunal succession in the whale-fall sediments resembled the scavenger-opportunist-sulfophile sequence previously described for epifaunal communities on sunken whale skeletons. The intense response of enrichment opportunists functionally resembles responses to organic loading in shallow-water ecosystems, such as at sewer outfalls and fish farms. Ten species of abundant whale-fall respondents were unique to whale-fall sediments suggesting that there is a deep-sea, sediment fauna specializing on intense organic/sulfide loading. In addition, from a total of 100 macrofaunal species in the whale-fall sediments, six were shared with cold seeps, five with hydrothermal vents, and 12 with nearby kelp and wood falls. Thus, whale-fall sediments may provide dispersal stepping stones for some generalized reducing-habitat species, but also support distinct macrofaunal assemblages and appear contribute significantly to beta diversity in deep-sea ecosystems.

KEY WORDS: Whale fall, Succession, Organic enrichment, Sulfide, Deep sea, Diversity, Chemoautrophy, Disturbance

INTRODUCTION

The carcasses of large cetaceans, with masses of 10 to 150 tons, constitute the largest marine detrital particles (Smith 2006). Sunken whale carcasses are rich in labile organic material, occur widely in the modern ocean, and cause substantial organic and sulfide enrichment in normally organic/sulfide-poor deep-sea settings (e.g., Smith & Baco 2003, Goffredi et al. 2008, Treude et al. 2009).

The fauna attracted to the soft tissues and skeletons of deep-sea whale falls has received substantial study (e.g., Smith et al. 1989, Bennett et al. 1994, Baco & Smith

2003, Smith & Baco 2003, Glover et al. 2005, Braby et al. 2007, Fujiwara et al. 2007, Lundsten et al. 2010, Amon et al. 2013). Large whale carcasses at the deep seafloor can harbor species-rich, trophically complex assemblages and have been documented to pass through a series of overlapping successional stages, including: (1) a mobile scavenger stage, (2) an enrichment opportunist stage and (3) a sulphophilic or chemoautotrophic stage (Smith & Baco 2003, Fujiwara et al. 2007, Treude et al. 2009, Lundsten et al. 2010). However, infaunal dynamics *in* the sediments around large whale falls in the deep sea remain very poorly studied (Smith 2006).

A 30,000-kg great whale carcass contains about 1.2 x 10^6 g of labile organic carbon in soft tissue (Smith 2006, Higgs et al. 2011). Since most deep-sea sediments receive approximately 2-10 g of particulate organic carbon flux per year (Lutz et al. 2007), a sunken 30,000 kg whale carcass is equivalent to $\geq$1000 yr of background organic-carbon flux to the underlying 100 m^2 of deep-sea floor (Smith 2006). As a consequence, carcass disintegration, sloppy scavenging, and the release of fecal material by necrophages (Smith 1985) can lead to substantial organic enrichment and reducing conditions in surrounding sediments (Smith et al. 2002, Smith & Baco 2003, Goffredi et al. 2008, Treude et al. 2009). If sedimentary organic enrichment persists around large whale carcasses for many years, whale-falls could foster a large infaunal community well adapted to exploit whale-fall oases. Such whale-fall assemblages may resemble those occurring in organic-rich sediments around large kelp and wood falls, in oxygen-minimum zones, and in submarine canyons (Vetter 1994, 1996, Levin 2003, Bernardino et al. 2010, De Leo et al. 2010, McClain & Barry 2010), or they might harbor whale-fall endemic species, just as wood falls, seagrass accumulations, and squid beaks appear to harbor their own specialists (Turner 1973, Wolff 1979, Gibbs 1987, Marshall 1987, Warén 1989, McLean 1992, Marshall 1994, Voight 2007). Given a persistence time of >5 yr for organic enrichment beneath bathyal whale falls (Treude et al. 2009), the average nearest neighbor distance between eutrophic whale-fall sites within the NE Pacific gray-whale range is likely to be <20 km (Smith & Baco 2003). Because organic-rich settings can sustain high macrofaunal growth rates and fecundities (e.g., Tyler et al. 2009), larval-dispersal between whale carcasses separated by 10's of kilometers seems quite plausible (cf. dispersal distances of vent and seep species; e.g., Marsh et al. 2001, Young et al. 2008, Mullineaux et al. 2010, Vrijenhoek 2010), suggesting that whale falls conceivably could support a specialized, sediment-dwelling (as well as a bone-dwelling) fauna.

Sediment microbial studies indicate that sulfidogenic and methanogenic assemblages are altered around whale falls over time scales up to 7 yr (Smith & Baco 2003, Goffredi et al. 2008, Treude et al. 2009). For the sediment-dwelling *macrofauna*, an enrichment-opportunist stage has been documented for whale-fall infaunal assemblages after 0.33 – 1.5 yr (Smith et al. 2002, Smith & Baco 2003). However, these time scales are short relative to the geochemical impacts of large whale falls on deep-sea sediments (Naganuma et al. 1996, Goffredi et al. 2008, Treude et al. 2009), suggesting that whale falls may influence infaunal communities over much longer periods. Rates and patterns of infaunal community succession around deep-sea whale falls are of broad ecological interest because they can provide insights into metacommunity dynamics and organic-matter recycling in the deep sea (e.g., Leibold et al. 2004), and help to predict the intensity and duration of disturbance resulting from anthropogenic organic enrichment at the seafloor (e.g., derived from sewage sludge emplacement, dumping of trawl by catch, or the disposal of animal and medical wastes; Gage & Tyler 1991, Debenham et al. 2004, Smith et al. 2008). Whale-fall successional studies can also provide insights into the evolution of life-history and feeding strategies that exploit ephemeral, food-rich habitat islands in typically oligotrophic deep-sea ecosystems (e.g., Rouse et al. 2004, Glover et al. 2008, Tyler et al. 2009, Johnson et al. 2010).

To more fully evaluate sediment community succession and chemoautotrophic community persistence at deep-sea whale falls, we conducted a 7-yr case study of selected geochemical variables and macrobenthic community structure around a 30-ton whale gray-whale carcass implanted at the 1675-m deep floor of Santa Cruz Basin, off southern California, USA. This whale fall has been the focus of previous, detailed sediment microbial studies (Treude et al. 2009). Here we address the following questions: *(1) How does macrofaunal community structure vary in space and time in sediments geochemically impacted by the whale fall? (2) How long can chemoautotrophic assemblages persist in whale-fall enriched sediments? (3) Does whale-fall community succession follow classic predictions from shallow-water successional models of organic enrichment (e.g., Pearson & Rosenberg 1978)? (4) What is the faunal overlap between the whale-fall sediment community and other organic- and/or sulfide-rich reducing habitats (e.g., wood falls, kelp falls, cold seeps) on the southern California margin?*

We find that the 30-ton whale fall yielded intense organic-carbon and sulfide enrichment in surrounding sediments for at least 7 yr, supporting a speciose infaunal assemblage including organic-enrichment opportunists and species with chemoautotrophic endosymbionts.

MATERIALS AND METHODS

Study site and field sampling

A 13-m, ~30 ton, gray whale carcass (*Eschrichtius robustus* Gray, 1864) was experimentally implanted on 28 April 1998 in Santa Cruz Basin, California (33°27’N, 119°22’W; See Bernardino et al. (2010) for a bathymetric map of the study area).The site has a depth of 1675 m depth, and bottom water temperature and oxygen concentration of ~ 4ºC, and 260 µM, respectively (Treude et al. 2009).. The whale carcass was studied after intervals of 0.12 y and 1.5 y with the HOV *Alvin* (Jun 1998 and Oct 1999 respectively), and after 4.5 y, 5.8 y and 6.8 y with the ROV *Tiburon* (Oct-Nov 2002, Feb-Mar 2004, and Feb-Mar 2005, respectively). During each visit to the carcass, photographic and video surveys of the whale fall were conducted (for methods see Bennett et al. 1994, Smith & Baco 2003, Treude et al. 2009), and sediment cores were taken along five different randomly located transects radiating outward from the carcass.

During the first dive of each series, the *HOV Alvin* or *ROV Tiburon* flew over the carcass along lines paralleling the long axis of the skeleton to conduct photosurveys. Digital photographs were taken from a camera oriented vertically downward and used to estimate bacterial mat and black sediment cover on the whale carcass and on surrounding sediments (Treude et al. 2009). Photomosaics of the carcass were constructed using the methods of Treude et al. (2009) at the 1.5 and 5.8 y time points. Detailed visual and video observations, as well as oblique digital photographs, were used to characterize the general condition of the carcass, surrounding sediments, and associated biota.

Macrofaunal samples were collected at all time points with tube cores at distances of 0, 1, 3, and 9 m along the five replicate, randomly located transects radiating from the carcass; cores for macrofauna were also collected on the transects at distances of 0.5 m at the 5.8 y and 6.8 y time points (i.e., when the whale-fall "footprint" appeared to be smaller). Macrofauna from the background community was sampled at 1.5 y, 4.5 y, and 5.8 y, with a total of 13 replicate tube cores at distances of $\geq$20 m from the whale fall. Four cores sampled at 9 m from the whale carcass at 6.8 y were pooled with the background samples to increase our temporal replication; based on macrofaunal abundance and species composition, there was no evidence of whale carcass influence beyond 3 m at 6.8 y. At the 0.12 y time point, cores were 10 cm in diameter; at 1.5 y, both 10 and 7 cm diameter cores were used; and from 4.5 – 6.8 y, cores 7-cm in diameter were used because of more limited payload and basket space on the ROV *Tiburon* compared to the HOV *Alvin.* All cores for macrofaunal analyses were extruded immediately on board ship and the 0-10 depth interval preserved in a 4% buffered seawater formaldehyde solution.

Replicate 7-cm cores were also taken at selected distances from the carcass for analyses of sediment organic carbon and pore-water profiles of sulfide. On shipboard, the top centimeter of cores for organic-carbon analyses were immediately extruded and frozen at –20 ^{o}C. Cores for pore-water sulfide analyses were immediately placed in an oxygen-free, nitrogen-flushed glove bag and sliced into 1-3 cm intervals. Sediment from each interval was transferred to 50-mL syringes and pore waters then expressed through 0.2 µm polycarbonate in-line filters (Jahnke 1988). The first milliliter of filtered pore water was discarded and the second was transferred into a scintillation vial containing 0.5

mL of 0.05 mol.L^{-1} zinc acetate; sulfide samples thus preserved were stable for weeks (Cline 1969).

At the 4.5, 5.8 and 6.8 y time points, vesicomyid clams were sampled at random locations within ~ 0.5 m of the skeleton using a 20-cm diameter, circular scoop net (2-cm stretch mesh). The net was scooped horizontally by the ROV to sediment depths of 10-20 cm. The approximate area sampled with each scoop-net deployment was estimated to be 0.1 m^2 (0.2 m by 0.5 m) from flyover photographs (see Bennett et al. 1994, for estimation methods). Scoop-net samples were immediately washed on a 2-mm sieve, and all recovered vesicomyid clams counted and stored on ice. Tissue samples were then quickly dissected from the foot of most clams and frozen at -80 ^{o}C or fixed in 95% ethanol for DNA analyses. Vesicomyid clams were also collected near the carcass in some tube cores; most of these clams were also placed on ice and foot tissue similarly dissected and fixed for DNA analyses.

Laboratory analysis

Fixed macrofaunal samples were sieved on 300-µm mesh with all animals, excluding the traditional meiofaunal taxa nematodes, harpacticoids and foraminiferans, sorted and identified to the lowest attainable taxonomic level. Animals were assigned to the trophic groups Carnivores/Scavengers/Omnivores (CSO), Surface-Deposit Feeders (SDF), and Subsurface-Deposit Feeders (SSDF) based on (Fauchald & Jumars 1979, Kukert & Smith 1992). Species thought to graze on microbial mats (dorvilleids and *Hyalogyrina* n. sp.) were assigned to the group Microbial Grazers (MG) based on (Warén & Bouchet 2009, Wiklund et al. 2009, Wiklund et al. 2012, Levin et al. 2013). Species with chemoautotrophic symbionts (e.g., *Idas washingtonia*; Deming et al. 1997) were placed in the Chemosymbiont (Chemo) trophic group. Species unassignable to any of the above trophic groups were placed in the group OTHER.

Sediment samples for organic-carbon analyses were acidified to remove carbonates by repeated additions of sulfurous acid (8 % v/v) until effervescence ceased (Verardo et al. 1990) and then analyzed using a Perkin-Elmer 2400 CHN Elemental Analyzer, with a precision of 0.3 % and 0.4 % for C and N, respectively. CHN standards were made with acetanilide. Analyses of pore-water sulfide were conducted as in Treude et al. (2009) using the colorimetric method (Cline 1969) to assess total dissolved sulfide, i.e., $H_2S + HS^- + S^{2-}$. The detection limit was 2 μM, and precision was 1.9 %.

Vesicoymid clams are challenging to identify morphologically, and include many undescribed species (e.g., Peek et al. 1997, Goffredi et al. 2003, Audzijonyte et al. 2012). Barcoding of a region of the mitochondrial cytochrome oxidase I gene has been widely used for vesicomyid identifications. From each individual vesicomyid clam, a ~700 bp region of the COI gene was amplified and sequenced using the primers VesHCO and VesLCO as in Peek et al (1997). The resulting sequences were aligned in Sequencher v4.8 and each unique haplotype was run through the NCBI Blast search engine using the “nucleotide blast” option with the “other” taxa database.

Photomosaics were produced using the methods of Pizarro & Singh (2003) and Treude et al. (2009).

Statistical methods

Because we were forced by logistical constraints to use core samples of different sizes at different time points, we analyzed macrofauna patterns using statistics that are robust to differences in sample size. Macrofaunal abundances were normalized to $1m^2$, rank abundance comparisons across time were only made for dominant species, and diversity comparisons were made with rarefaction [an approach developed to compare samples of different sizes (Sanders 1968, Hulbert 1984)] and evenness metrics (Magurran 2004). Differences in faunal densities versus distance from the whale carcass were examined with the non-parametric Kruskal-Wallis test performed at specific time points for similar core sizes. For significant Kruskal-Wallis results, *post-hoc* tests were used to examine differences in means [using the statistical package BioEstat© (Zar 1996)]. Species diversity was evaluated for pooled replicate cores at each distance sampled due to low macrofaunal densities in some samples. Hulbert's rarefaction curves ($ES(_n)$) were used to compare species diversity between treatments, with $ES_{(n)}$ at n=15 and for whole rarefaction curves. Background replicate cores (n=17) from 1.5 – 6.8 y were combined to calculate a composite diversity from the background community. Pielou's evenness (*J*') was used to provide information on the evenness component of species diversity (Clarke & Warwick 2001).

Cluster analyses and non-metric multi-dimensional scaling (NMDS) based on species-abundance data from standardized quantitative samples (PRIMER v6; Clarke & Gorley 2006) were used to compare community structure across distance and time. Square-root transformations were used prior to multivariate analyses to balance the importance of common and rare species (Clarke & Warwick 2001). Analysis of similarities (ANOSIM) were performed on groups of standardized quantitative samples, identified a priori, to determine the significance differences observed in multivariate plots (Clarke & Warwick 2001).

Comparisons of species overlap between whale-fall, kelp, wood, and other reducing habitats were restricted to vesicomyids and the relatively abundant macrofaunal species as in Bernardino et al. (2010, 2012).

RESULTS

Visual and video observations of the whale fall

At 0.12 y, the whale carcass was largely intact, with 400-800 hagfish (*Eptatretus deani*), 1-3 sleeper sharks (*Somniosis pacifica*), and clouds of lysianassid amphipods (many thousands) actively feeding on the carcass soft tissue (Fig. 1; Smith et al. 2002). During the scavenger feeding activity, small particles of whale tissue were visible settling onto the surrounding seafloor to distances of meters, and sediment was resuspended from the seafloor within one meter of the carcass by the thrashing activities of sleeper sharks. Some areas of seafloor within ~ 1m of the carcass where covered with a pinkish “carpet” of lysianassid amphipods resting on the sediment-water interface.

After 1.5 y, nearly all the soft tissue had been removed from the whale skeleton and most of the large mobile scavengers, except for ~10-20 hagfish, had dispersed (Figs. 1 - 2). The sediment-water interface within ~1 m of the whale skeleton was darker in color than the surrounding sediment, and in many areas was covered with millimeter-scale white spots, which appeared to be the shells of very small gastropods and bivalves (Figs. 1 - 2). Biogenous sediment structures, e.g., centimeter-scale worm tubes, burrows and mounds, were not visible within ~1 m of the carcass. The skeleton appeared wholly intact (Fig. 2), and harbored patches of the chrysopetalid polychaete *Vigtorniella flokati*, the “bone-eating” worm *Osedax* n. sp., and mud colored polychaete worm tubes on the bones.

After 4.5 y, most of the whale skeleton was covered with white microbial mats, with patches of *Osedax* interspersed; microbial mats extended tens of centimeters onto the sediment in some areas (Fig. 1). Other areas of sediment within 50-100 cm of the skeleton were blackish in color. Large centimeter-scale worm tubes, formed by the polychaete Ampharetid n. g. n. sp., were abundant (~ 50 m^{-2}) within ~1 m of the skeleton, gradually declining to zero abundance by 2-3 m (Fig. 1). At 5.8 and 6.8 y, the skeleton and surrounding sediments were similar in appearance to 4.5 y, with the bones highly intact, most of the bones and some nearby sediments covered with microbial mats (white, yellow and red), patches of blackened sediments (10-50 cm diameter) visible within 1 m of the carcass, and with numerous Ampharetid n. g. n. sp. tubes occurring on the sediment surface to distances of ≥1m from the skeleton (Figs. 1 - 2).

Sediment Organic Carbon

Sediment organic carbon content in the top centimeter of sediment exhibited substantial, but patchy, organic enrichment around the carcass at all times sampled (1.5 – 6.8 y; Fig. 3). The greatest enrichment was observed adjacent to the carcass at 0 – 0.5 m, with organic carbon contents of 9 - 15% (1.5 to 3 times background levels) even after 4.5 – 6.8 y. Sediment organic enrichment penetrated to substantial depths in some areas around the carcass, with organic carbon contents of 11 - 20% at depths of 2-8 cm and at distances of 0 - 0.5 m even after 5.8 - 6.8 y (Treude et al. 2009). At distances of 1-3 m, sediment organic carbon was enriched above background levels up to 4.5 y; by 5.8 – 6.8 y, limited data suggest that organic carbon concentrations in surface sediments at these distances had returned to near background levels (Fig. 3). At 9 m distance, surface sediment organic carbon appeared to be slightly elevated after 4.5 y, but fell in the low range of background-community levels after 5.8 – 6.8 y. In summary, organic enrichment of surface sediments was intense (albeit heterogeneous) at distances of 0 – 0.5 meters for up to 6.8 y, with some enrichment indicated to distances of 3 m for up to 4.5 y (Fig. 3).

Pore-water Sulfide Concentrations

Pore-water sulfide concentrations also exhibited intense, heterogeneous enhancement adjacent to the whale carcass for a number of years. At 0.12 y, pore-water sulfides were low around the carcass, generally falling within the range (< 0.010 mM) of background community levels (Fig. 4). By 1.5 y, pore-water sulfides at 0 - 1 m distances had attained high levels in some locations, reaching 7-10 mM at sediment depths of 0-6 cm, but remaining low in the single core at 3 m. After 4.5 y, pore-water sulfides at 0 m sites remained very high (0.7 – 10 mM) at sediment depths of 0 - 10 cm, with concentrations at greater distances (1-3 m) reaching substantial levels (0.05 mM) in some cores (Fig. 4). At 5.8 y, some cores from 0 m showed high sulfide enrichment, reaching 0.5 – 5 mM, while other profiles from 0 – 1 m exhibited little difference from background levels. Thus, for at least 4.5 - 5.8 years, sediments within 0 - 1 m of the whale fall sustained high enrichment of pore-water sulfides (≥5 mM), with marked meter-scale patchiness.

Vesicomyid Clams

Large vesicomyid clams in the subfamily Pliocardiinae, which are known to harbor chemoautotrophic endosymbionts in their gills and specialize on sulphide-rich habitats (Krylova & Sahling 2010), were observed and collected in sediments around the whale carcass at 4.5, 5.8 and 6.8 y. Clam siphons and shells protruded from the sediment in video and still images at numerous sites around the carcass in both blackened and brown sediments at distances from 0 to ≥ 0.5 m from the skeleton (Fig. 1). Clams were collected in randomly located cores at distances of 0 – 0.5 m from the whale fall beneath a yellow microbial mat (n=1), in blackened sediments (n=4), and in brown sediments (n=2; Table 1). A total of 72 vesicomyid clams were also collected with the scoop net at random locations within 0.5 m of the carcass at 4.5, 5.8 and 6.8 y (Table 1). The occurrence of vesicomyids to distances of 0.5 m from the carcass essentially matches the footprint of high pore-water sulfides around the whale carcass after 4.5 – 5.8 y (Fig. 4).

Barcoding of 58 vesicomyid individuals collected at the whale fall, using a ~700 base-pair region of the mitochondrial gene COI, indicated that four pliocardiin species occurred at the site (Table 1): (1) 51 individuals of *Archivesica gigas* (GenBank accession no. KF990208), all with 100% concordance with *A. gigas* sequences in GenBank (Audzijonyte et al. 2012); (2) three individuals (GenBank accession no. KF990209) showing 98% sequence overlap with two divergent molecular taxonomic units, "*Archivesica" packardana* and *"Pliocardia" stearnsii* in GenBank (Audzijonyte et al. 2012); (3) three individuals (GenBank accession nos. KF9902010 and KF9902011) with 93% sequence overlap with *Pliocardia ponderosa*; and (4) one *Calyoptogena pacifica* (GenBank accession no. KF9902012) with 100% sequence overlap with *C. pacifica* in GenBank. Sequence divergences above 1.5-2% are considered indications of species-level differences between vesicomyid in this portion of the COI gene (Peek et al. 1997, Baco et al. 1999, Kojima et al. 2004, Audzijonyte et al. 2012) so we consider our species 3 certainly to be a new species, and species 2 likely to be new. Based on these barcoding results, *A. gigas* was the overwhelming dominant vesicomyid (93%), while the other three species constituted $\leq$5% of the clam population around the whale carcass between 4.5 and 6.8 y.

Assuming that the scoop net sampled a seafloor area of 0.1 m^2, mean clam densities within 0.5 m of the skeleton ranged from 52 to 93 ind. m^{-2} at 4.5 - 6.8 y (Table 1). Treude et al. (2009) estimated that the seafloor area within 0.5 m of the whale skeleton was 18 m^2; this yields estimated vesicomyid clam population sizes of approximately 900-1600 individuals around the whale carcass at 4.5 – 6.8 y (Table 1).

Macrofaunal abundance and community structure

Macrofaunal abundance exhibited major, time-dependent changes around the whale carcass. After 0.12 y, mean macrofaunal abundances at distances of 0 – 9 m were not significantly different from background community levels ($p > 0.05$; Fig. 5; Table S1). However, by 1.5 y, macrofaunal abundances at all distances (0 to 9 m) exhibited a dramatic response to the whale fall, exceeding background community levels by at least 7 fold ($p < 0.01$; Fig. 5; Table S1); abundances at 0 m were especially high (mean = 51,460 ind. m^{-2}), i.e., 28 times mean background levels. After 4.5 y, macrofaunal abundances remained very high at 0 m (~10 times background abundances, $p = 0.001$), were significantly elevated (~3 times background) at 1 m, but had declined to background community levels at greater distances (3 and 9 m). After 5.8 – 6.8 y, macrofaunal abundance followed a similar pattern of very high levels at 0 m (10-12 times background;

$p < 0.05$), with modest enhancement at 0.5 – 1 m distances, and no enhancement above background levels at 3 - 9 m.

Macrofaunal community composition also exhibited strong, time-dependent responses to the whale carcass. At 0.12 y, the sediment within 1 m of the carcass was dominated by amphipods, with one species of mobile scavenger, Lysianassid sp. A, constituting >85% of community abundance (Table 2); this amphipod also was dominant at 9 m, and was absent from background community samples. Based on mean amphipod densities in core samples at 0-m and 1- m distances (2800 m^{-2}) and the seafloor area (>40 m^2) within 1 m of the carcass (Treude et al. 2009), the total population size of Lysianassid sp. A at the carcass exceeded 100,000 individuals. Other macrofaunal species occurring near the carcass at this time were rare or absent in the background community, and included juveniles of the bivalve *Idas washingtonia* (a bone inhabiting species with sulfur-oxidizing endosymbionts; Smith & Baco 2003), the omnivorous enrichment opportunist cumacean *Cumella* sp. A (Smith 1986, Smith et al. 2002, Bernardino et al. 2010), and the omnivorous oedicerotid amphipod, *Monoculodes* sp. A (Table 2).

By 1.5 y, the sediment macrofaunal community around the carcass had changed dramatically, with the high abundances at 0 to 1 m dominated by bivalve juveniles and a single species of gastropod, which were absent from background sediments (Fig. 6; Table 2). The bivalve juveniles, most likely in the family Vesicomyidae, and the gastropod *Hyalogyrina* n. sp., constituted 50 to >90% of total macrofaunal abundance (Table 2). The vesicomyid bivalves appear to have recruited in response to high sulfide levels in sediments adjacent to the carcass (Fig. 4). *Hyalogyrina* n. sp. is known from microbial mats at kelp falls in Santa Cruz Basin (Bernardino et al. 2010) and this genus is common in other habitats supporting sulfur oxidizing bacterial mats, including hydrothermal vents, cold seeps, wood falls, and whale falls (Smith & Baco 2003, Warén & Bouchet 2009), so this gastropod likely was attracted to microbial mats around the Santa Cruz whale carcass. At 3 m at this time, the sediment community was dominated by a dorvilleid polychaete, a spionid polychaete, and cumacean crustaceans (Fig. 6); the dorvillied, *Parougia* sp. A, and the two cumaceans (*Cumella* sp. A, and Cumacea sp. A; Table 2) are attracted to organic enrichment around fish, kelp and wood falls and are considered enrichment opportunists feeding on microbial mats and/or labile sediment organic matter (Smith 1986, Smith et al. 2002, Bernardino & Smith 2010). The spionid, *Prionospio* sp. B, also falls in a family with many enrichment opportunists (Smith & Baco 2003). At 9 m at this time (1.5 y), non-background taxa continued to dominate the macrofaunal community (Table 2), including many species apparently responding to organic enrichment, such as the cumaceans *Cumella* sp. A and Cumacea sp. K, dorvilleid polychaetes (*Parougia* sp. A and *Subadyte mexicana*), spionid and ampharetid polychaetes (Table 2).

After 4.5 y, the sediment macrofauna at 0 m was dominated (>75%) by high abundances of dorvilleids, cumaceans and ampharetids (Table 2, Fig. 6). The dominant species at this distance included the omnivorous enrichment opportunists *Ophryotrocha* sp. A, *Cumella* sp. A, and other apparently opportunistic ampharetids and dorvilleids (e.g., *Parougia* sp. A, *Ophryotrocha platykephale*), which were all absent from the background community. At 1 m, the enrichment opportunist Cumacea sp. K and some dorvilleids were still dominant, but dominant background species (the cirratulids *Tharyx* sp. A and *Monticellina* sp. A) had become common. By 3 to 9 m, the cirratulids common in the background community had become dominant, with a few dorvilleids present (Fig. 6, Table 2).

Macrofaunal community composition at 5.8 y and 6.8 y was quite similar. Sediments with enhanced macrofaunal abundances at distance of 0 – 0.5 m (Fig. 5) were dominated (55-75%) by dorvilleids, cumaceans, and ampharetids (Fig. 6). Species dominants at these distances included the omnivorous opportunists *Ophryotrocha* sp. A, *Cumella* sp. A (Bernardino et al., 2010), and other apparently opportunistic ampharetids and dorvilleids (e.g., Ampharetid sp. 14, *Parougia* sp. A, *Ophryotrocha* sp. E, *Exallopus* sp. A), all absent from background community samples. At a distance of 3 m, background community cirratulid and cossurid polychaetes had become common, with a few presumably opportunistic dorvilleids still present. By 9 m, the macrofaunal community at 5.8 y and 6.8 y resembled the background community in terms of higher-level taxa and dominant species (Fig. 6, Table 2).

In summary, the macrofaunal community exhibited strong successional patterns in space and time around the whale carcass in both higher taxonomic composition and dominant species. The sediment macrofaunal community near the whale carcass was dominated (1) initially (0.12 y) by patches of mobile lysianassid scavenging amphipods to distances of 1-9 m, (2) then (at 1.5 y) by sulphophilic juvenile vesicomyids and hyalogyrinid gastropods near the carcass ($\leq$1 m), and enrichment opportunists including dorvilleids (Menot et al. 2009), cumaceans, and ampharetids at greater distances (3 – 9 m), and (3) finally by enrichment opportunists in a diminishing zone extending outward from the carcass to 3 m, 1 m, and 0.5 m after 4.5, 5.8, and 6.8 y, respectively.

The occurrence of sulphophilic and opportunistic macrofauna and megafauna roughly matched the spatial impacts of sulfide and organic-carbon enrichment around the whale carcass (Figs. 3 - 4). For example, juvenile vesicomyids apparently recruited into sulfide-rich sediments adjacent to the carcass by 1.5 y (Fig. 4), leading to the development of the megafaunal vesicomyid clam populations present in sulfide-rich sediments within 0.5 m after 4.5-6.8 y. In addition, the decline in the spatial extent of enrichment-opportunist assemblages roughly matched the declining spatial extent of organic enrichment measured around the whale carcass from 4.5 to 6.8 y (Fig. 3).

Non-metric multi-dimensional scaling (NMDS) analysis provided strong additional evidence of macrofaunal community succession around the whale carcass over both time and distance (Fig. 7). At 0.12 y, nearly all macrofaunal community samples around the whale fall clustered separately from all other time points (ANOSIM R=0,693, p=0.001), indicating a highly distinct community, consistent with a mobile scavenger assemblage (Smith & Baco 2003). At 1.5 y, the 0 m and 1 m samples also formed a largely distinct cluster, consistent with the dominance by sulphophilic bivalve juveniles and gastropods. Samples from 3 - 9 m at 1.5 y, and from 0 - 1 m from 4.5 – 6.8 y, generally grouped together in the central portion of the NMDS plot (Fig. 7), consistent with a community of enrichment opportunists (ANOSIM R=0,693, p<0.01). Samples from > 1 m at 4.5 – 6.8 y formed a cluster that gradually merged with the background community samples, consistent with transitions from enrichment-opportunist to background-community assemblages (Fig. 7).

Macrofaunal species diversity

Sediment macrofaunal rarefaction diversity also exhibited strong patterns in space and time at the whale fall. At 0.12 y, $ES_{(15)}$ at 0 - 3 m from the carcass was very low relative to the background community, and remained low to a distance of 9 m (Fig. 8). At 1.5 y, $ES_{(15)}$ was very low at 0 m, but gradually increased to near background levels by 9 m. At 4.5 y, $ES_{(15)}$ had increased at 0 – 3 m distances but still remained below the diversity levels of 9 m and in background sediments. By 5.8 – 6.8 y, all distances showed $ES_{(15)}$ levels similar to the background community. In summary, species diversity was very low within 3 m of the carcass at 0.12 y, and then increased essentially monotonically with distance from the carcass and time after implantation, recovering approximately to background levels by 5.8 y. Diversity patterns of whole rarefaction curves (Fig. S1), were essentially identical to those of $ES_{(15).}$

Patterns of macrofaunal species evenness were not as dramatic as those of rarefaction diversity. Pielou's Evenness (J') was reduced at 0 – 1 m from the carcass at 0.12 y, and remained low from 0 to 3 m after 1.5 y (Fig. 5B). At all other times and distances, macrofaunal species evenness resembled that in the background community.

Trophic group patterns

The relative abundance of macrofaunal trophic groups changed dramatically with distance and time at the whale carcass, with whale-fall effects persisting to 6.8 y. At 0.12 y, carnivores/scavengers/omnivores (CSO) (especially lysiannassid amphipods) overwhelmingly dominated at distances of 0 – 1 m compared with the background sediments (H= 1057,1, DF=27, $p<0.01$; Fig. 9). The relative abundance of surface deposit-feeders (SDF) was low at 0 - 1 m ($p<0.05$) but remained similar to background sediments at $\geq$3 meters from the carcass. After 1.5y, microbial grazers (MG) and species with chemoautotrophic symbionts (Chemo), *Hyalogyrina* n. sp. and vesicomyid juveniles, respectively), dominated the fauna at 0 – 1 m ($p<0.02$), with CSO becoming important at 3 m (p=0,05; Fig 9). After 4.5 y, microbial grazers (MG), composed of dorvilleids, dominated at 0 m, and the CSO group (now mainly cumaceans) dominated at 1 m ($p <0.05$). At 5.8 to 6.8 y, the MG group (dorvilleids) and the CSO group (mostly cumaceans) were enhanced at 0 – 0.5 m relative to background sediments ($p<0.05$), and subsurface deposit feeders (SSDF) were absent or rare near the carcass at 5.8 to 6.8 y, compared to their relatively high abundance (>25%) in background sediments ($p<0.05$; Fig. 9). In summary, the whale fall led to unusually high relative abundances of macrofaunal (1) carnivores/scavengers/omnivores after 0.12 y, (2) species with chemoautotrophic symbionts and microbial grazers after 1.5 yr, and (3) microbial grazers and carnivores/scavengers/omnivores after 4.5 – 6.8 y (Fig. 9). The radius of these trophic-group effects declined gradually from 9 m at 0.12 y, through a distance of 3 m at 1.5 y, to distances of ~1 m by 4.5 – 6.8 y (Fig. 9).

Faunal overlap of whale-fall species with other deep-sea habitats

Twenty-eight of the 100 collected species of sediment macrofauna and megafauna were abundant adjacent to the whale fall but were not collected in the background community (Table 3); we call these *whale-fall species*. Ten of these whale-fall species, consisting of ampharetid, cirratulid and dorvilleid polychaetes, were absent from nearby seep, kelp and wood falls and have not been reported from seep and vent habitats (Table 3); these species could be whale-fall specialists.

There was modest overlap between the sediment-dwelling whale-fall species and the fauna of other deep-sea reducing habitats. Approximately 20-40% of the whale-fall species were shared with kelp- and wood-fall habitats in Santa Cruz Basin; these included apparent enrichment opportunists (*Samytha cf. californiensis*, dorvillied polychaetes in several genera, and cumacean crustaceans), and one species with chemoautotrophic endosymbionts (*Idas washingtonia*; Table 3). Twenty-one percent (six) of the whale-fall species were shared with cold seep faunas, including two species of vesicomyids, and three species of dorvilleid polychaetes. Eighteen percent (5 species) of these whale-fall species have been found at hydrothermal vents, including two polychaetes, a bathymodiolin bivalve (*I. washingtonia*) and two species of vesicomyids. There was more overlap between the whale-fall fauna and that of vents and seeps at the generic level, with at least 8 genera shared with seep faunas and six genera shared with hydrothermal vents (Table 3).

DISCUSSION

The 30-ton gray whale carcass had major structural and geochemical impacts for at least seven years on the bathyal benthic community in the well oxygenated bottom waters (260 μM) of Santa Cruz Basin. The skeleton itself provided physical structure, and a source of sulfide to sulfur oxidizing bacterial mats (Treude et al. 2009), for at least 6.8 years with little evidence of bone erosion (Figs. 1 - 2). This is consistent with the findings of Smith and Baco (2003) and Schuller et al. (2004) that the intact skeletons of large adult whales can persist for many years to decades at bathyal depths on the southern California margin, even under well oxygenated conditions (>45 μM) and in the presence of abundant bone-boring *Osedax* (Baco & Smith 2003, Smith & Baco 2003, Smith & Demopoulos 2003, Treude et al. 2009). Our results contrast with the more rapid degradation of juvenile whale skeletons observed in Monterey Canyon (Lundsten et al. 2010) and off southern California (Smith & Baco 2003) and indicate that adult whale skeletons likely persist much longer than juvenile carcasses because of much larger bone volumes and greater bone calcification, even with large *Osedax* populations (Smith & Baco 2003, Schuller et al. 2004, Higgs et al. 2011).

Sediment geochemical impacts of the whale carcass in Santa Cruz Basin were also intense and persistent, and required some months to develop. After 0.12 y, there was no evidence from either pore-water sulfides or visual observations of geochemical impacts on the sediment. However, by 1.5 y, organic loading and pore-water-sulfide enhancement were intense, with organic enrichment similar to that near sewer outfalls and under fish farms (Hall et al. 1990, Hyland et al. 2005) and sulfide concentrations (up to 10 mM) comparable to those at hydrothermal vents and cold seeps (Van Dover 2000, Levin et al. 2003, Levin 2005, Treude et al. 2009). This interval of organic and sulfide buildup coincided with the apparent recruitment of sulfophilic species to the sediment, including vesicomyid and bathymodiolin mussels, and microbial-mat grazing gastropods (*Hyalogyrina* sp.). Organic loading and sulfide enhancement persisted patchily in sediments within a meter of the skeleton for 5.8 to 6.8 years. The abundance of species with chemoautotrophic symbionts, including large vesicomyids, and the prominence of microbial-mat grazers within the sediment after 6.8 y confirmed the provision of a significant reducing habitat in the whale-fall sediments throughout this period. Thus, the persistence times of reducing habitats *in sediments* around a large whale fall may begin to approach the persistent times (years to decades) of reducing habitats at some individual hydrothermal vents (Van Dover 2000). Of course, provision of reducing habitat on the bones of adults whale falls can be even longer, i.e., many decades (Smith & Baco 2003, Schuller et al. 2004).

Smith and Baco (2003) described three "overlapping stages of ecological succession" occurring on the carcasses of large, adult whales on the deep California margin, including (1) a mobile scavenger stage, (2) an enrichment opportunist stage characterized by heterotrophic opportunists, and (3) a sulfophilic stage characterized by chemoautotrophic production. However, their data set included only one time point for sediment dwelling macrofauna from any whale fall. Our seven-year time series indicates that sediment macrofaunal succession around the Santa Cruz whale fall resembled the Smith and Baco (2003) successional model, with substantial overlap between successional stages. In particular, highly mobile scavengers (e.g, lysianassid amphipods) overwhelming dominated sediments around the whale fall at the earliest sampling point (0.12 y), with opportunistic heterotrophic species (e.g., cumacean crustaceans, ampharetid and dorvilleid polychaetes) succeeding them as adult dominants in whale-fall impacted sediments after 1.5 years. Nonetheless, sulfophilic species with chemoautotrophic endosymbionts, as well as grazers of sulfur-oxidizing bacteria, were recruiting heavily during this "enrichment opportunist stage," as indicated by the abundance of juvenile vescomyid clams, bathymodiolin mussels and *Hyalogyrina* gastropods very close to the whale fall. By later time points (5.8 – 6.8 years), the abundance of enrichment opportunists remained high only very near the whale fall while a sizable (900-1600 individuals), multispecies assemblage of large, relatively long-lived vescomyid clams

(Barry et al. 2007) with chemoautotrophic endosymbionts had become established. This pattern of vesicomyid population persistence near the whale fall as the enrichment opportunist assemblage was contracting is consistent with studies of much older whale-fall assemblages off southern California, in which vesicomyids persist after organic enrichment and enrichment opportunists have disappeared from whale-fall sediments (Smith et al. 1998, Smith & Baco 2003, Smith 2006).

The successional patterns we observed around the Santa Cruz whale fall, both in space and time, resembled patterns described for intense point sources of organic enrichment in shallow-water ecosystems, such as sewer outfalls, dredge spoil dumps, and fish farms (e.g., Pearson & Rosenberg 1978, Weston 1990, Newell et al. 1998, Karakassis et al. 2000, Tomassetti & Porrello 2005). In particular, the large peak in abundance of enrichment opportunists combined with reduced species diversity in organically enriched sediments near the whale fall at 1.5 y, is similar to the Pearson and Rosenberg (1978) model, which has been widely applied to organic-enrichment disturbance in shallow-water ecosystems (e.g., Newell et al. 1998, Norkko et al. 2006). At later times (4.5 – 6.8 y) diversity adjacent to the whale fall had recovered to background community levels even while patchy organic enrichment and opportunists persisted; this resembled the transition zone in the Pearson and Rosenberg (1978) model, in which enrichment-opportunists and background species coexist as enrichment conditions began to ameliorate in space or time (e.g., Newell et al. 1998). We also observed some overlap at the family level between the whale-fall and shallow-water enrichment opportunists, with dorvilleid polychaetes dominating enriched sediments both around the whale fall and in many shallow-water, fine-sediment habitats (e.g., Karakassis et al. 2000, Wiklund et al.

2009). Nonetheless, there were some major taxonomic differences between the deep-sea whale-fall and shallow-water enrichment opportunists, with the shallow-water enrichment indicator families Capitellidae (e.g., Pearson & Rosenberg 1978, Norkko et al. 2006) and Thyasiridae (Danise et al. 2014) notably absent from the sediments around our whale falls as well as around kelp and wood falls on the California margin (Smith et al. 2002, Bernardino et al. 2010). Furthermore, cumacean crustaceans were prominent opportunists around the whale fall, as has observed for other organically enriched deep-sea sediments (Smith 1985, 1986, Snelgrove et al. 1994, Bernardino et al. 2010), while this group, to our knowledge, does not routinely respond to organic enrichment in shallow-water settings. Overall, the opportunistic response in the sediment macrofauna to the Santa Cruz whale fall functionally matches predictions for intense, large-scale disturbances (Norkko et al. 2006), suggesting that similar processes of resource enhancement and release from competition allow opportunists to flourish in ephemeral, enriched habitats in both shallow-water and deep-sea sediment ecosystems.

The enriched sediments around the Santa Cruz whale fall harbored some of the highest macrofaunal densities (>50,000 m^{-2}) ever recorded in the deep sea (Wei et al. 2010, Bernardino et al. 2012, Thurber et al. 2013), including ten highly abundant species not recorded either in the background community or in other deep-sea reducing habitats, including kelp falls, wood falls, and seeps within 200 km of the whale fall (Bernardino & Smith 2010, Bernardino et al. 2010, Bernardino et al. 2012). This suggests that the combination of intense organic enrichment and pore-water sulfide buildup associated with deep-sea whale falls might attract a species rich and endemic infauna. The sunken carcasses of very large sharks and other marine mammals (e.g., elephant seals) might create comparable, persistent organic- and sulfide-rich conditions to support such a specialized fauna in the deep-sea, but we know of no infaunal data to address this hypothesis. In any event, it appears that whales contribute to significantly beta diversity in deep-sea habitats (Bernardino et al. 2012).

The species overlap between the Santa-Cruz whale-fall infauna and the fauna of eastern Pacific seeps (six species shared) and hydrothermal vents (five species in common; Table 3) indicates that sulfide-rich whale-fall sediments could provide dispersal stepping stones for some generalized reducing-habitat species. Whale-fall stepping stones may be particularly important for vesicomyid clams such as *Archivesica gigas*, which can be abundant both in seep and whale fall sediments in the northeast Pacific, and the polychaete *Bathykurile guaymensis*, which can be abundant at both vents and whale falls (Table 3).

Finally, the whale-fall infaunal community in Santa Cruz Basin exhibited surprisingly modest species-level overlap with large, organic-rich kelp and wood falls located only ~100 m away (Bernardino et al. 2010). Thus, each of these organic-fall types appears to contribute distinct beta diversity to deep-sea soft sediment habitats, supporting both generalized opportunists and specialists adapted to the distinct geochemical conditions of the enrichment type (Bernardino et al. 2012, Bienhold et al. 2013). The full suite of reducing habitats in the deep sea (ranging from organic falls to hydrothermal vents) offers remarkable opportunities for studying niche partitioning, population connectivity, and adaptive radiation in food-rich metacommunities dispersed across the vast, oligotrophic deep-sea ecosystems (Smith et al. 2008, Levin & Sibuet 2012).

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LITERATURE CITED

Amon DJ, Glover AG, Wiklund H, Marsh L, Linse K, Rogers AD, Copley JT (2013) The discovery of a natural whale fall in the Antarctic deep sea. Deep-Sea Research II 92:87-96

Audzijonyte A, Krylova EM, Sahling H, Vrijenhoek RC (2012) Molecular taxonomy reveals broad trans-oceanic distributions and high species diversity of deep-sea clams (Bivalvia: Vesicomyidae: Pliocardiinae) in chemosynthetic environments. Systematics and Biodiversity 10:403-415

Baco A, Smith CR (2003) High species richness in deep-sea chemoautotrophic whale skeleton communities. Marine Ecology Progress Series 260:109-114

Baco AR, Smith CR, Peek A, Roderick G, Vrijenhoek RC (1999) The phylogenetic relationships of whale-fall vesicomyid clams based on mitochondrial COI DNA sequences. Marine Ecology Progress Series 182:137-147

Barry JP, Kochevar RE, Baxter CH (1997) The influence of pore-water chemistry and physiology on the distribution of vesicomyid clams at cold seeps in Monterey Bay: Implications for patterns of chemosynthetic community organization. Limnology and Oceanography 42:318-328

Barry JP, Whaling PJ, Kochevar RK (2007) Growth, production and mortality of the chemosynthetic vesicomyid bivalve *Calyptogena kilmeri* from cold seeps off central California. Marine Ecology 28:169-182

Bennett BA, Smith CR, Glaser B, Maybaum HL (1994) Faunal community structure of a chemoautotrophic assemblage on whale bones in deep northeast Pacific Ocean. Marine Ecology Progress Series 108:205-223

Bernardino AF, Levin LA, Thurber AR, Smith CR (2012) Comparative composition, diversity and trophic ecology of sediment macrofauna at Vents, Seeps and Organic Falls. PLOS One 7:e33515

Bernardino AF, Smith CR (2010) Community structure of infaunal macrobenthos around vestimentiferan thickets at the San Clemente cold seep, NE Pacific. Marine Ecology 31:608-621

Bernardino AF, Smith CR, Baco AR, Altamira I, Sumida PYG (2010) Macrofaunal succession in sediments around kelp and wood falls in the deep NE Pacific and community overlap with other reducing habitats. Deep-Sea Research I 57:708-723

Bienhold C, Ristova PP, Wenzhofer F, Dittmar T, Boetius A (2013) How deep-sea wood falls sustain chemosynthetic life. PLOS One 8:e53590

Blake JA, Hilbig B (1990) Polychaetes from the vicinity of deep-sea hydrothermal vents in the eastern Pacific, 2. New species and records from the Juan de Fuca and Explorer Ridge systems. Pacific Science 44:219-253

Braby CE, Rouse GW, Johnson SB, Jones WJ, Vrijenhoek RC (2007) Bathymetric and temporal variation among Osedax boneworms and associated megafauna on whale-falls in Monterey Bay, California. Deep-Sea Research I 54:1773-1791

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial, Plymouth

Clarke KR, Warwick RM (2001) Change in marine commuities: an approach to statistical analysis and intepretation PRIMER-E. University of Plymouth, Plymouth

Cline JD (1969) Spectrophotometric determination of hydrogen sulfide in natural waters. Limnology and Oceanography 14:454-458

Danise S, Dominici S, Glover AG, Dahlgren TG (2014) Molluscs from a shallow-water whale-fall and their affinities with adjacent benthic communities on the Swedish west coast. Marine Biology Research 10:3-16

De Leo FC, Smith CR, Rowden AA, Bowden DA, Clark MR (2010) Submarine canyons: hotspots of benthic biomass and productivity in the deep sea. Proceedings of the Royal Society of London Series B:1-10

Debenham NJ, Lambshead PJD, Ferrero TJ, Smith CR (2004) The impact of whale falls on nematode abundance in the deep sea. Deep-Sea Research I 51:701-706

Deming JW, Reysenbach A, Macko SA, Smith CR (1997) Evidence for the microbial basis of a chemoautotrophic invertebrate community at a whale fall on the deep seafloor: Bone-colonizing bacteria and invertebrate endosymbionts. Microscopy Research and Technique 37:162-170

Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. Oceanography and Marine Biology an Annual Review 17:193-284

Fujiwara Y, Kawato M, Yamamoto T, Yamanaka T, Sato-Okoshi W, Others (2007) Three-year investigations into sperm whale-fall ecosystems in Japan. Marine Ecology 28:219-232

Gage JD, Tyler PA (1991) Deep-Sea Biology: a natural history of organisms at the deep-sea floor, Vol. Cambridge University Press, Cambridge

Glover AG, Kallstrom B, Smith CR, Dahlgren TG (2005) World-wide whale worms? A new species of *Osedax* from the shallow north Atlantic. Proceedings of the Royal Society of London Series B 272:2587-2592

Glover AG, Kemp KM, Smith CR, Dahlgren TG (2008) On the role of bone-eating worms in the degradation of marine vertebrate remains. Proceedings of the Royal Society of London Series B 275:1959-1961

Goffredi SK, Hurtado LA, Hallam S, Vrijenhoek RC (2003) Evolutionary relationships of deep-sea vent and cold seep clams (Mollusca: Vesicomyidae) of the "*pacifica/lepta*" species complex. Marine Biology 142:311-320

Goffredi SK, Wilpiszeski R, Lee RW, Orphan V (2008) Temporal evolution of methane cycling and phylogenetic diversity of archaea in sediments from a deep-sea whale-fall in Monterey Canyon, California. ISME 2:204-220

Hall POJ, Anderson LG, Holby O, Kollberg S, Samuelsson M-O (1990) Chemical fluxes and mass balances in a marine fish cage farm. I. Carbon. Marine Ecology Progress Series 61:61-73

Higgs ND, Little CTS, Glover AG (2011) Bones as biofuel: a review of whale bone composition with implications for deep-sea biology and palaeoanthropology. Proceedings of the Royal Society of London Series B 278:9-17

Huber M (2010) Compendium of bivaves. A full-color guide to 3,300 of the world's marine bivalves. A status on Bivalvia after 250 years of research., Vol. ConchBooks, Hackenheim

Hulbert SM (1984) Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54:187-211

Hyland J, Balthis L, Karakassis I, Magni P, al. e (2005) Organic carbon content of sediments as an indicator of stress in the marine benthos. Marine Ecology Progress Series 295:91-103

Jahnke RA (1988) A simple, reliable and inexpensive pore-water sampler. Limnology and Oceanography 33:483-487

Johnson SB, Warén A, Lee RW, Kano Y, Kaim A, Davis A, Strong EE, Vrijenhoek RC (2010) *Rubyspira*, New Genus and two new species of bone-eating deep-sea snails with ancient habits. Biological Bulletin 219:166-177

Karakassis I, Tsapakis M, Hatziyanni E, Papadopoulou K-N, Plaiti W (2000) Impact of cage farming of fish on the sabed in three Mediterranean coastal areas. ICES Journal of Marine Science 57:1462-1471

Kojima S, Fujikura K, Okutani T (2004) Multiple tras-Pacific migrations of deep-sea vent/seep-endemic bivalves in the family Vesicomyidae. Molecular Phylogenetics and Evolution 32:396-406

Krylova EM, Sahling H (2010) Vesicomyidae (Bivalvia): Current taxonomy and distribution. PLOS One 5

Kukert H, Smith CR (1992) Disturbance, colonization and succession in a deep-sea sediment community: artificial-mound experiments. Deep-Sea Research 39:1349-1371

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzales A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601-613

Levin LA (2003) Oxygen minimum zone benthos: adaptation and community response to hypoxia. Oceanography and Marine Biology an Annual Review 41:1-45

Levin LA (2005) Ecology of cold seep sediments: interactions of fauna with flow, chemistry and microbes. Oceanography and Marine Biology: an Annual Review 43:1-46

Levin LA, Sibuet M (2012) Understanding Continental Margin Biodiversity: A New Imperative. Annual Review of Marine Science 4:1-34

Levin LA, Ziebis W, Mendoza GF, Growney-Cannon V, Tryon MD, Brown KM, Mahn C, Gieskes JM, Rathburn AE (2003) Spatial heterogeneity of macrofauna at northern California methane seeps: influence of sulfide concentration and fluid flow. Marine Ecology Progress Series 265:123-139

Lundsten L, Schlining KL, Frasier K, Johnson SB, Kuhnz LA, Harvey JBJ, Clague G, Vrijenhoek RC (2010) Time-series analysis of six whale-fall communities in Monterey Canyon, California, USA. Deep-Sea Research I 57:1573-1584

Lutz MJ, Caldeira K, Dunbar RB, Behrenfeld MJ (2007) Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of biological pump in the global ocean. Journal of Geophysical Research: Oceans 112:C10011

Magurran A (2004) Measuring species diversity, Vol. Blackwell Science, Oxford

Marsh AG, Mullineaux LS, Young CM, Manahan DT (2001) Larval dispersal potential of the tubeworm *Riftia pachyptila* at deep-sea hydrothermal vents. Nature 411:77-80

McClain CR, Barry JP (2010) Habitat heterogeneity, disturbance and productivity work in concert to regulate biodiversity in deep submarine canyons. Ecology 91:964-976

Menot L, Crassous P, Desbruyeres D, Galéron J, Khripounoff A, Sibuet M (2009) Colonization patterns along the equatorial West African margin: implications for functioning and diversity maintenance of bathyal and abyssal communities. Deep-Sea Research II 56:2313-2325

Mullineaux LS, Adams DK, Mills SW, Beaulieu SE (2010) Larvae from afar colonize deep-sea hydrothermal vents after catastrophic eruption. PNAS 107:7829-7834

Naganuma T, Wada H, Fujioka K (1996) Biological community and sediment fatty acids associated with the deep-sea whale skeleton at the Torishima seamount. Journal of Oceanography 52:1-15

Newell RC, Seiderer LJ, Hitchcock DR (1998) The impact of dredging works on coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the sea bed. Oceanography and Marine Biology an Annual Review 36:127-178

Norkko A, Rosemberg R, Thrush SF, Whitlatch RB (2006) Scale- and intensity-dependent disturbance determines the magnitude of opportunistic response. Journal of Experimental Marine Biology and Ecology 330:195-207

Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution in the marine environment. Oceanography and Marine Biology an Annual Review 16:229-311

Peek AS, Gustafson RG, Lutz RA, Vrijenhoek RC (1997) Evolutionary relationships of deep-sea hydrothermal vent and cold-water seep clams (Bivalvia: Vesicomyidae): results from the mitochondrial cytochrome oxidase subunit I. Marine Biology 130:151-161

Pizarro O, Singh H (2003) Towards large area mosaicing for underwater scientific applications. IEEE Journal of Oceanic Engineering 28:651-672

Rouse GW, Goffredi SK, Vrijenhoek RC (2004) *Osedax:* bone eating marine worms with dwarf males. Science 305:668-671

Sanders HL (1968) Marine benthic diversity: a comparative study. American Naturalist 102:243-282

Schuller D, Kadko D, Smith CR (2004) Use of 210Pb/226Ra disequilibria in the dating of deep-sea whale falls. Earth and Planetary Science Letters 218:277-289

Smith CR (1985) Food for the deep-sea: utilization, dispersion and flux of nekton falls at the Santa Catalina Basin floor. Deep-Sea Research 32:417-442

Smith CR (1986) Nekton falls, low-intensity disturbance and community structure of infaunal benthos in the deep-sea. Journal of Marine Research 44:567-600

Smith CR (2006) Bigger is better: The roles of whales as detritus in marine ecosystems. In: Estes J (ed) Whales, Whaling and Marine Ecosystems. University of California, California

Smith CR, Baco AR (2003) Ecology of whale falls at the deep-sea floor. Oceanography and Marine Biology: an Annual Review 41:311-354

Smith CR, Baco-Taylor AR, Glover AG (2002) Faunal succession on replicate deep-sea whale falls: time scales and vent-seep affinities. Cahiers de Biologie Marine 43:293-297

Smith CR, De Leo FC, Bernardino AF, Sweetman AK, Arbizu PM (2008) Abyssal food limitation, ecosystem structure and climate change. Trends in ecology and evolution 23:518-528

Smith CR, Demopoulos AWJ (2003) The deep Pacific ocean floor. In: Tyler PA (ed) Ecossystems of the World, Vol 27, p 179-218

Smith CR, Kukert H, Wheatcroft RA, Jumars PA, Deming JW (1989) Vent fauna on whale remains. Nature 34:127-128

Smith CR, Maybaum HL, Baco-Taylor A, Pope RH, Carpenter SD, Yager PL, Macko SA, Deming JW (1998) Sediment community structure around a whale skeleton in the deep Northeast Pacific: macrofaunal, microbial and bioturbation effects. Deep-Sea Research II 45:335-364

Snelgrove PVR, Grassle JF, Petrecca RF (1994) Macrofaunal response to artificial enrichments and depressions in a deep-sea habitat. Journal of Marine Research 52:345-369

Thurber AR, Levin LA, Rowden AA, Sommer S, Linke P, Kroger K (2013) Microbes, macrofauna and methane: a novel seep community fueled by aerobic methanotrophy. Limnology and Oceanography 58:1640-1656

Tomassetti P, Porrello S (2005) Polychaetes as indicators of marine fish farm organic enrichment. Aquaculture International 13:109-128

Treude T, Smith CR, Wenzhofer F, Carney E, Bernardino AF, Hannides AK, Kruger M, Boetius A (2009) Biogeochemical processes at a deep-sea whale fall: rates of sulfate reduction, sulfide efflux and methanogenesis. Marine Ecology Progress Series 382:1-21

Tunnicliffe V, McArthur AG, McHugh D (1998) A biogeographical perspective of the deep-sea hydrothermal vent fauna. Advances in Marine Biology 34:353-442

Tyler PA, Marsh L, Baco-Taylor AR, Smith CR (2009) Protandric hermaphroditism in the whale-fall bivalve mollusc *Idas washingtonia*. Deep-Sea Research II 56:1689-1699

Van Dover CL (2000) The ecology of deep-sea hydrotermal vents, Vol. Princeton University Press, New Jersey

Verardo DJ, Froelich PN, McIntyre A (1990) Determination of organic carbon and nitrogen in marine sediments using the Carlo Erba NA-1500 Analyzer. Deep-Sea Research 37:157-165

Vetter EW (1994) Hotspots of benthic production. Nature 372:47

Vetter EW (1996) Enrichment experiments and infaunal population cycles on a Southern California sand plain: response of the leptostracan *Nebalia daytoni* and other infauna. Marine Ecology Progress Series 137:83-93

Vrijenhoek RC (2010) Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations. Molecular Ecology 19:4391-4411

Warén A, Bouchet P (2009) New gastropods from deep-sea hydrocarbon seeps off West Africa. Deep-Sea Research II 56:2326-2349

Wei C-L, Rowe GT, Escobar-Briones E, Boetius A, Soltwedel T, Caley MJ, Soliman Y, Huettmann F, Qu F, Yu Z, al. e (2010) Global patterns and predictions of seafloor biomass using random forests. PLOS One 5:e15323

Weston DP (1990) Quantitative examination of macrobenthic community changes along an organic enrichment gradient. Marine Ecology Progress Series 61:233-244

Wiklund H, Glover AG, Johannessen PJ, Dahlgren TG (2009) Cryptic speciation at organic-rich marine habitats: a new bacterivore annelid from whale-fall and fish farms in the North-East Atlantic. Zoological Journal of the Linnean Society 155:774-785

Young CM, Fujio S, Vrijenhoek RC (2008) Directional dispersal between mid-ocean ridges: deep-ocean circulation and gene flow in *Ridgeia piscesae*. Molecular Ecology 17:1718-1731

Zar JH (1996) Bioestatistical analysis, Vol. Prentice Hall

Table 1. Vesicomyid clam collections, species barcoding, and population densities and sizes. All clams were sampled from 0 – 0.5 m from the whale-fall. TD stands for ROV Tiburon dive. *Archivesica* = *A; Calayptogena* = *C.; Pliocardia* = *P.** assuming a scoop net sampling area of 0.1 m^2; ** total individuals based on estimated area within 0.5 m of the whale-fall (Treude et al., 2009). *** Cores collected in blackened sediments. $^{\#}$ Core collected in yellow microbial mat. $^{\$}$ Core collected in brown sediment.

Time	Date	Dive	Sample Type	# of clams in sample	*A. gigas*	Nr. *'V.' packardana/ 'P.' stearnsi*	*P.* nr. *ponderosa*	*C. pacifica*	Unbarcoded clams	Mean clam density m^{-2} ± s.e. *	Clam pop. size ± s.e. **
4.5 y	10/27/2002	TD 498	Scoop net	6	5			1			
	10/28/2002	TD 500	Scoop net	2	2						
	10/29/2002	TD 502	Scoop net	4	2	1			1		
	10/24/2002	TD 491	TC #67***	1	1						
	10/24/2002	TD 491	Scoop net	8	8						
	10/28/1002	TD 495	Scoop net	6					6		
	Total			27						52 ± 10	900 ± 180
5.8 y	3/1/2004	TD 653	Scoop net	1	1						
	3/1/2004	TD 653	TC #44$^{\#}$	1	1						
	3/2/2004	TD 654	Scoop net	21	13	2	2		4		

	3/2/2004	TD 654	TC #50[***]	1					1		
	3/2/2004	TD 655	Scoop net	6	3		1		2		
	Total			30						93 ± 60	1620 ± 600
6.8 y	2/26/2005	TD 822	TC #62[***]	2	2						
	2/26/2005	TD 822	TC #79[$]	2	2						
	2/27/2005	TD 823	Slurps	3	3						
	2/27/2005	TD 823	Scoop net	8	8						
	Total			15						80	1440
Overall Total				**72**	**51**	**3**	**3**	**1**	**14**		
% of barcoded clams					**93%**	**5%**	**5%**	**2%**			

Table 2. Mean abundance m^{-2} (s.e.) and relative abundances of macrofaunal species as a function of time and distance from the whale fall, and in the background community. Species constituting ≥ 2.8 % of community abundance at any time-distance combination are included. Ranks indicated are for 0 m distances or background sediments. (P) Polychaeta, (Cr) Crustacea, (M) Mollusca. Dashes indicate no samples taken at that distance-time point.

		Whale 0.12 y									
Rank 0 m		**0 m**		**0.5m**		**1m**		**3m**		**9m**	
		Mean density	%	Mean density	%	Mean density	%	Mean density	%	Mean density	%
1	Lysianassid sp. A (Cr)	1565 (234)	86.0%	-	-	4034 (1476)	85.6%			424.7 (92)	41.7%
2	*Idas washingtonia* (M)	127.4 (23.5)	7.0%	-	-						
	Laonice sp. A (P)			-	-	169.9 (24.5)	3.6%	84.9 (24.5)	40.0%	127.4 (55.2)	12.5%
	Monoculodes sp. A (Cr)			-	-	127.4 (73.6)	2.7%				
	Cumella sp. A (Cr)			-	-	127.4 (42.5)	2.7%				
	Cossura rostrata (P)			-	-			84.9 (49)	40.0%	127.4 (55.2)	12.5%
	Aphelochaeta sp. A (P)			-	-			42.5 (24.5)	20.0%	254.8 (55.2)	25.0%
	Total percent		*93.0%*	-	-		*94.6%*		*100.0%*		*91.7%*
Rank 0 m		**Whale 1.5 y**									
1	Juvenile bivalve (M)	25112 (3550)	48.8%	-	-	1094 (186.2)	11.0%				
2	*Hyalogyrina* n. sp. (M)	23662 (1851)	46.0%	-	-	3956(568)	39.9%				
3	CRS Ampharetid sp. 14 (P)	1400 (168)	2.7%	-	-	527.2 (21.7)	5.3%				
	Parougia sp. A (P)			-	-	994.9(155.2)	10.0%	6985 (932)	40.1%	229.3 (33.2)	2.6%
	Cumella sp. A (Cr)			-	-	2552 (348.9)	25.8%	3990(658)	22.9%	203(42.6)	2.3%
	Cumacea sp. K (Cr)			-	-			3654(507)	21.0%	615(76.3)	6.9%
	Prionospio sp. B (P)			-	-			590.6(118.2)	3.4%	382(86.4)	4.3%
	CRS Ampharetid sp. 2 (P)			-	-					1070 (205)	12.0%
	Chaetozone sp. E (P)			-	-					918 (112)	10.3%

	Cossura rostrata (P)			-	-					408(48.8)	4.6%
	Subadyte mexicana (P)			-	-					254.8(113)	2.8%
	Gastropod sp. K			-	-					280(125)	3.1%
	Total percent		*97.5%*	-	-		*92%*		*92.8%*		
Rank 0 m					**Whale 4.5 y**						
1	*Ophryotrocha sp. A* (P)	6803(962)	39.4%	-	-						
2	CRS Ampharetid sp. 14 (P)	2513(298)	14.6%	-	-						
3	CRS Ampharetid sp. 12 (P)	1343(250)	7.8%	-	-	52.0(23.2)	1.2%				
4	*Ophryotrocha platykephale* (P)	1256(218)	7.3%	-	-						
5	*Cumella* sp. A (Cr)	780(219)	4.5%	-	-						
	Samytha cf. *californiensis* (P)	260(54.8)	1.5%	-	-						
	Cumacea sp. K (Cr)			-	-	2288(551)	53.0%				
	Tharyx sp. A (P)			-	-	260(63.7)	6.0%	104(28.5)	16.7%	260(90)	16.7%
	Parougia sp. A (P)			-	-	208(43.5)	4.8%			52(23.2)	3.3%
	Monticellina sp. A (P)			-	-			104(28.5)	16.7%	156(46.5)	10.0%
	Idas washingtonia (M)	260(106)	1.5%	-	-			52(23.2)	8.3%		
	Total percent		*76.6%*	-	-		*65.0%*		*33.4%*		*26.7%*
Rank 0 m					**Whale 5.8 y**						
1	*Ophryotrocha sp. A* (P)	4003(996)	22.6%	4246(1883)	23.1%						
2	Cumacea sp. K (Cr)	3692(988)	20.9%	1300(750)	7.1%			52(23.3)	2.3%		
3	*Ophryotrocha sp. E* (P)	1924(803)	10.9%	346.6(132.4)	1.9%						
4	*Cumella* sp. A (Cr)	1039(285)	5.9%	1387(727)	7.5%			52(23.3)	2.3%		
5	CRS Ampharetid sp. 14 (P)	728(216)	4.1%	1993(1150)	10.8%						
	Parougia sp. A (P)	312(67.8)	1.8%	780(378)	4.2%	208(23.3)	9.8%	156(46.5)	7.0%		
	Chaetozone cf. *commonalis* (P)					208(67.8)	9.8%	156(69.8)	7.0%	130(37.5)	9.1%
	Monticellina sp. A (P)					52(23.3)	2.4%	208(43.5)	9.3%	260(75)	18.2%
	Cossura cf. *rostrata* (P)							52(23.3)	2.3%	325(97.5)	22.7%
	Total percent		*66.2%*		*54.6%*		*22%*		*30.2%*		50.0%
Rank 0 m					**Whale 6.8 y**						

1	Cumacea sp. K (Cr)	4524(861)	19.4%	1872(476)	15.4%	312(57)	8.6%				
2	*Ophryotrocha* sp. A (P)	2652(334)	11.4%	572(182)	4.7%	51.9(23.3)	1.4%				
3	CRS Ampharetid sp. 14 (P)	2184(571)	9.4%	416(186)	3.4%						
4	CRS Ampharetid sp. 12 (P)	1976(245)	8.5%	884(340)	7.3%						
5	*Parougia* sp. A (P)	1664(499)	7.1%								
6	*Exallopus sp. A (P)*	728(297)	3.1%	1040(465)	8.5%						
	Cumella sp. A (Cr)	104(28.5)	0.4%	623(203)	5.1%	156(46.5)	4.3%				
	Cossura cf. *rostrata* (P)			208(23.3)	1.7%	416(130)	11.4%	52(23.3)	*2.8%*	260(90)	15.6%
	Chaetozone cf. *commonalis* (P)			364(78.9)	3.0%	468(43.5)	12.9%	156(46.5)	*8.3%*	156(28.5)	9.4%
	Ophryotrocha sp. E (P)			2444(1093)	20.1%						
	Monticellina sp. A (P)			104(46.5)	0.9%	260(52)	7.1%	260(73.5)	*13.9%*	260(73.5)	15.6%
	Total percent		*60.7%*		*70.1%*		*45.7%*		25.0%		*40.6%*

Rank Bkgd		**Background (> 9-20m)**	
		Mean density	%
1	*Cossura cf. rostrata* (P)	214(81.1)	16.9%
2	*Chaetozone sp. D* (P)	183(53.5)	14.5%
3	*Monticellina sp. A* (P)	168(58.7)	8.4%
4	*Tharyx sp. A* (P)	76.5(29.6)	6.0%
	Total percent		*45.8%*

Table 3. Occurrence of Santa Cruz whale-fall (SCr WF) sediment macrofaunal and megafaunal taxa at other organic/sulfide-rich reducing habitats in the deep sea. Included only are macrofaunal species or genera that (1) occurred at distances of 0 - 0.5 m from the whale fall and (2) were absent from the background community. Percentages indicate the proportion of total sediment macrofaunal community abundance contributed by that species or genus in the particular habitat. * Sediment macrofaunal species thus far found only at whale falls (a total of 10 species). References: 1 - (Smith & Baco 2003); 2 - (Bernardino et al. 2010); 3 - (Levin et al. 2003); 4 - (Levin 2005); 5 - (Blake & Hilbig 1990); 6 - (Tunnicliffe et al. 1998); 7 - (Bernardino & Smith 2010); 8 – (Krylova & Sahling 2010); 9 - (Barry et al. 1997); 10 – (Huber 2010); 11 - (Audzijonyte et al. 2012).

Species	SCr WF	Kelp	Wood	Seep	Vent	References
Polychaeta						
Ampharetidae						
*CRS Ampharetid sp. 1	>5%					
*CRS Ampharetid sp. 6	1-5%					
*CRS Ampharetid sp. 12	>5%					
*CRS Ampharetid sp. 14	>5%					
**Sosanopsis* sp. A	1-5%					
Samytha cf. californiensis	>5%	6.5%	13.2%			1, 2
Cirratulidae						
*CRS Cirratulid. sp. 1	>5%					
CRS Cirratulid. sp. 2	>5%		14.3%			2
Dorvilleidae						
Parougia sp. A	>5%		14.6%	P	P (genus)	1, 2, 3, 4, 5
Ophryotrocha sp. A	>5%	36.5%	33.8%	P (genus)	P (genus)	1, 2, 4
Ophryotrocha sp. B	1-5%		1.3%	P (genus)	P (genus)	1, 2, 4
**Ophryotrocha* sp. E	>5%			P (genus)	P (genus)	1, 4
**Ophryotrocha* sp. H	1-5%			P (genus)	P (genus)	1, 4
**Ophryotrocha* sp. K	1-5%			P (genus)	P (genus)	1, 4
Schistomeringos longicornis	>5%		1.4%	P		1, 4
Ophryotrocha platykephale	>5%			P	P	3, 5
**Exallopus* sp. A	>5%			P (genus)	P (genus)	1, 4, 5
Polynoidae						
Bathykurila guaymasensis	>5%				P	1, 5
Crustacea						
Cumella sp. A	>5%	34.4%	1.4%			1, 2

Cumacean sp. K	>5%	52.7%	32.3%			1, 2
Ilyarachna profunda	1-5%		6.9%			1, 2
Mollusca						
Hyalogyrina n. sp.	>5%	11.5%				1, 2
Idas washingtonia	>5%		2.8%	P	P	1, 2, 4, 6, 7
Bivalve sp. Q	1-5%	5.4%	9.7%			1, 2
Archivesica gigas	P			P	P	8,11
Near *'Archivesica' packardana* & *'Pliocardia' stearnsi*	P			P (genus)		9,11
Near '*Pliocardia' ponderosa*	P			P (genus)		10
Calyptogena pacifica	P			P	P	10, 11
Total species or genera	28	6	11	14	12	
% of 28 SCr WF species shared	100	21	39	21	18	

Figure Legends

Figure 1. (A-E). Similar, oblique views of the central left side of the gray whale carcass. For scale, the maximum rib diameter is ~15 cm. (A) *0.12 y after carcass emplacement.* Note the numerous hagfish (*E. deani)* feeding on the largely intact carcass. (B) *1.5 y after emplacement.* The soft tissue has been largely removed from the carcass, but a few hagfish remain. The sediments at lower right are speckled with the white shells of small gastropods and bivalves. (C) *4.5 y after emplacement.* Note the heavy cover on the bones of white mats of sulfur oxidizing bacteria, as well as darker patches on bone indicating ampharetid tubes and *Osedax* burrows. Muddy ampharetid tubes are also abundant within 1-2 m of the skeleton. (D*) 5.8 y after emplacement.* The bones continue to be covered with mats of sulfur oxidizing bacteria, ampharetid tubes, and patches of *Osedax*, with amphareitid tubes and black sulfidic patchs visible in nearby sediments. (E) *6.8 y after emplacement.* The skeleton is still largely intact and clad in sulfur oxidizing bacterial mats. Mats are encrouching further onto the sediment. Several vesicomyid clams are visible in the sediment near the ribs. (F) *Vertical view of the sediments adjacent to the ribs after 5.8 y.* The muddy tubes of the polychaete Ampharetid n. g. n. sp. are abundant. White spots visible in the sediments are the shells of vesicomyid clams (living and dead).

Figure 2. Photomosaics of the grey whale skeleton in the Santa Cruz Basin at 1.5 y (top) and 6.8 y (bottom) after emplacement. The photomosaic at 1.5 y is black and white because the down-looking camera in the HOV Alvin in 1999 was black and white. Note the darkened area of

sediment around the skeleton at 1.5 y. At 6.8 y, the skeleton is essentially intact, and largely covered with white microbial mats.

Figure 3. Variations in organic carbon content (% of dry weight) of the top centimeter of sediment with distance from the whale carcass. Samples from the background community (collected at distances of 20-100 m) are plotted at a distance of 30 m. Means ± 1 standard error are plotted.

Figure 4. Profiles of pore-water sulfide concentrations as a function of time and distance from the whale carcass. Data from single profiles are indicated by similar colored symbols (e.g., blue circles). Points are plotted at the middle of the depth interval sampled.

Figure 5. (A) Total macrofaunal community abundance as function of time and distance from the whale fall. The shaded bar is the mean (± 1 s.e.) of the background community abundance at distances of 20-100 m from the whale carcass.(B) Pielou's Evenness (J') as a function of time and distance from the carcass. Data points are means ± 1 s.e.

Figure 6. High-level taxonomic composition of macrofauna around the whale fall as a function of time and distance from the whale fall. (A) 0.12 y, (B) 1.5 y, (C) 4.5 y, (D) 5.8 y, (E) 6.8 y. Data are from pooled core samples for each time and distance.

Figure 7. Nonmetric Multidimensional Scaling (NMDS) plot for macrofauna from individual core samples at all times and distances from the whale fall. Numbers next to symbols indicate

distance in meters from the carcass. Samples enveloped by black lines have Bray-Curtis Similarities of $\geq$ 40%.

Figure 8. Macrofaunal rarefaction species diversity, $ES_{(15),}$ as function and time and distance from the whale carcass. Means of cores from each distance-time combination are plotted.

Figure 9. Trophic-group composition of the sediment macrofaunal community as a function of time and distance from the whale carcass. CSO = carnivores-scavengers-omnivores; SDF = surface-deposit feeders; SSDF = subsurface-deposit feeders; MG = microbial grazer; Chemo = containing chemoautotrophic endosymbionts; Other = trophic unknown or in none of the other major categories. “n.s.” means not sampled.

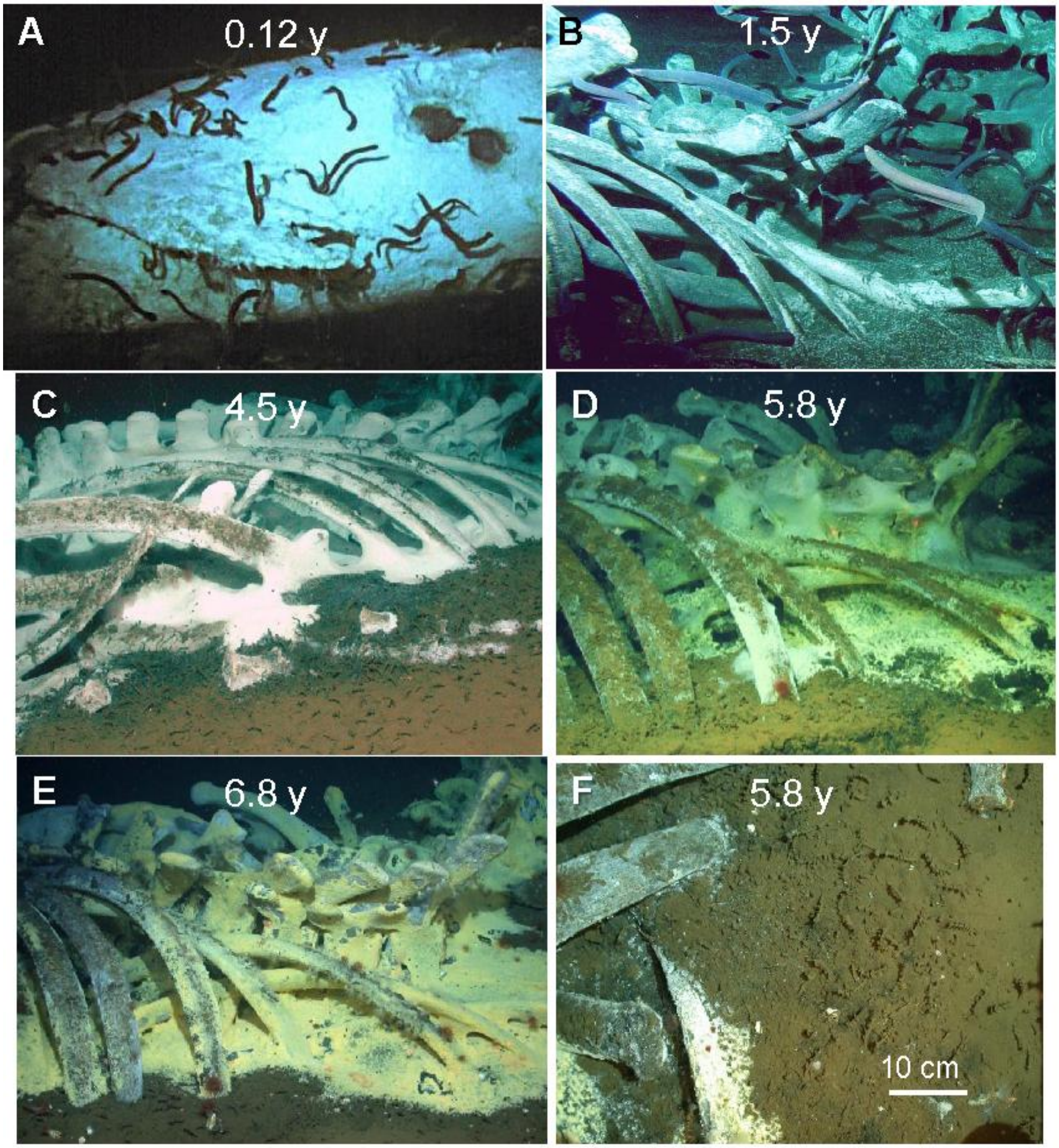


Figure 1

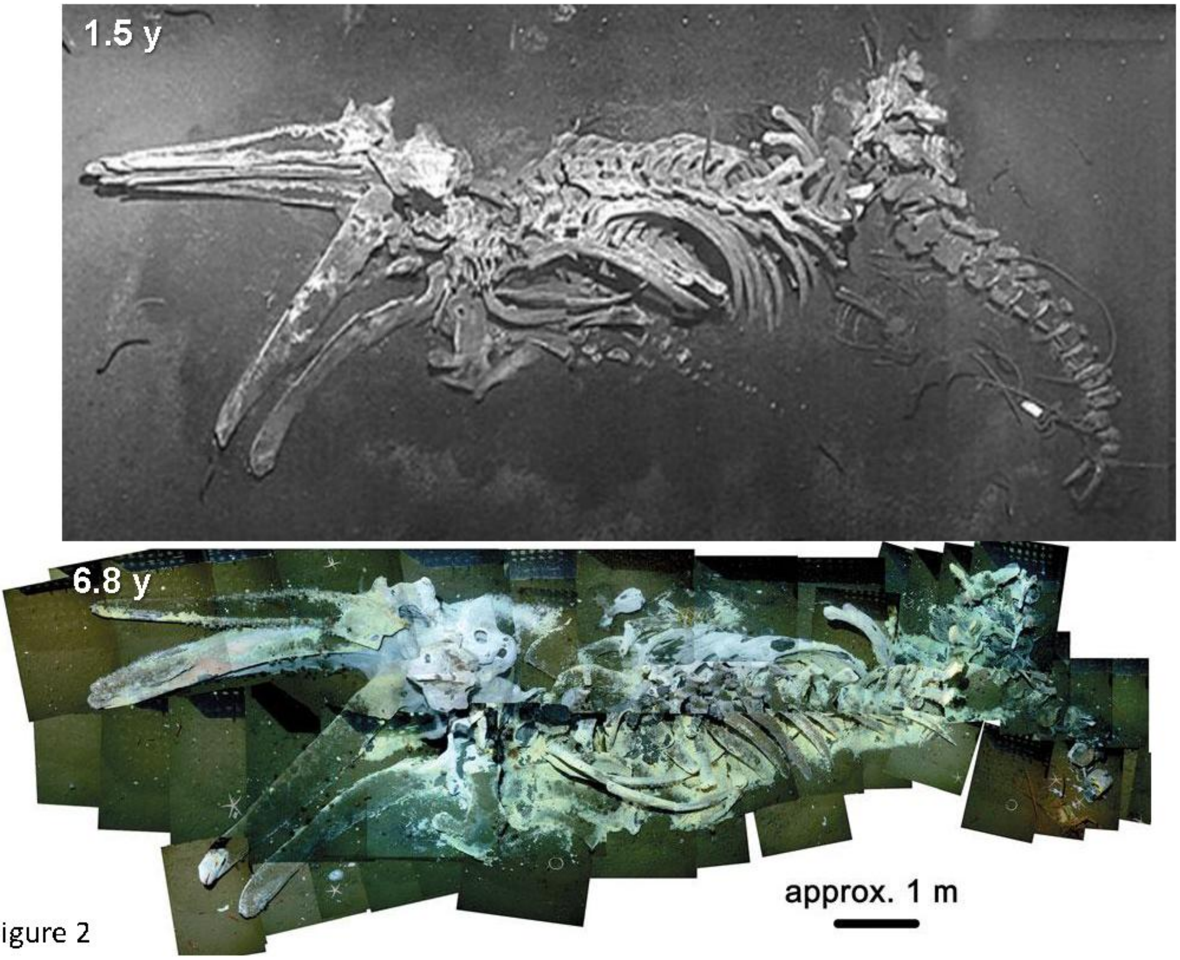
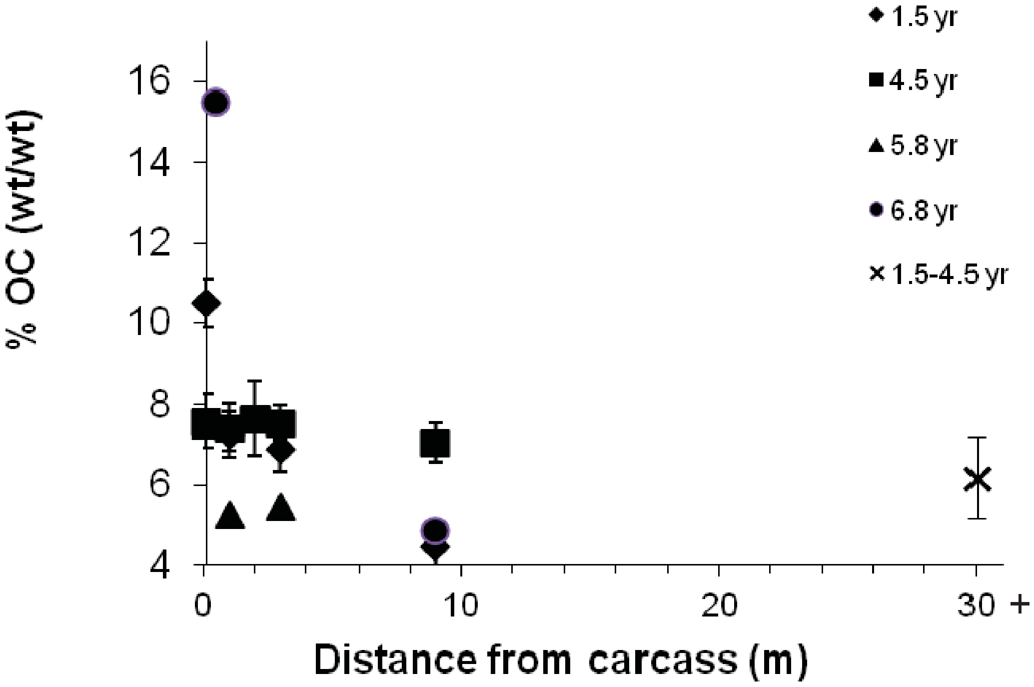


Figure 2



◆ 1.5 yr
■ 4.5 yr
▲ 5.8 yr
● 6.8 yr
× 1.5-4.5 yr
% OC (wt/wt)
16
14
12
10
8
6
4
0
10
20
30 +
Distance from carcass (m)

Figure 3

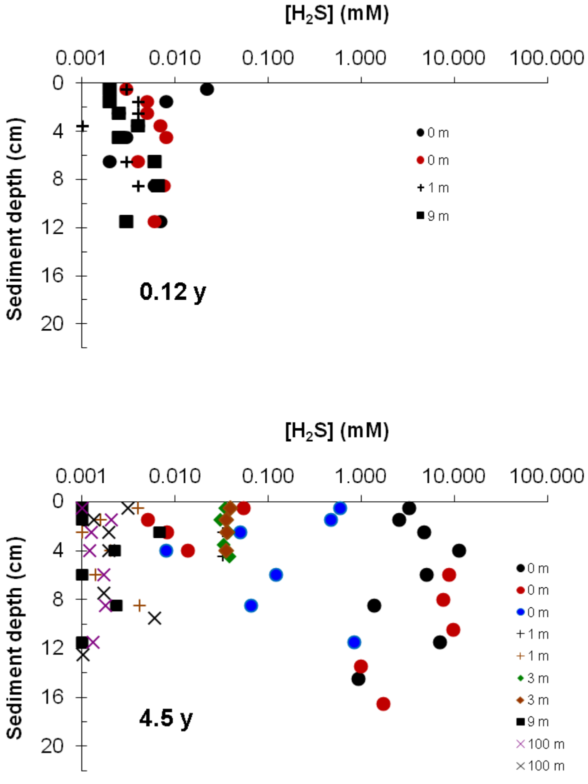


Figure 4

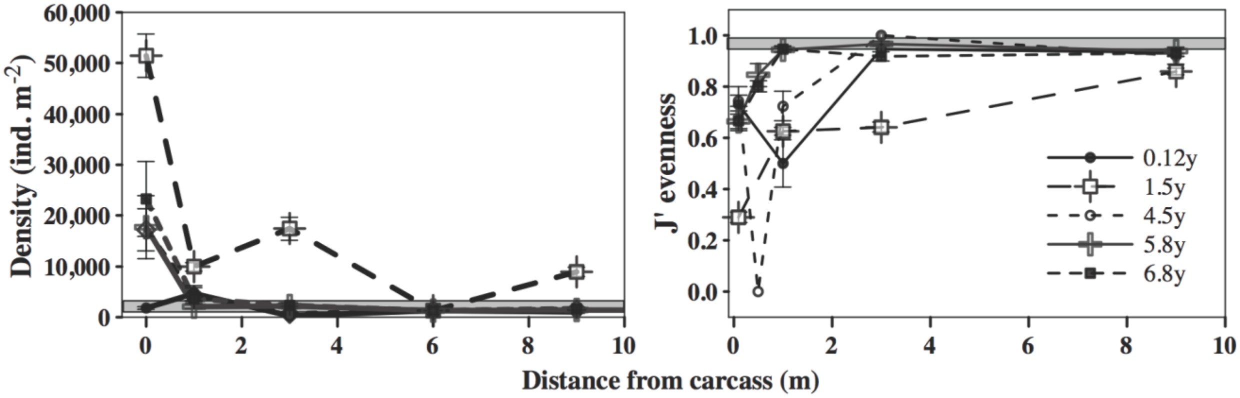


Figure 5

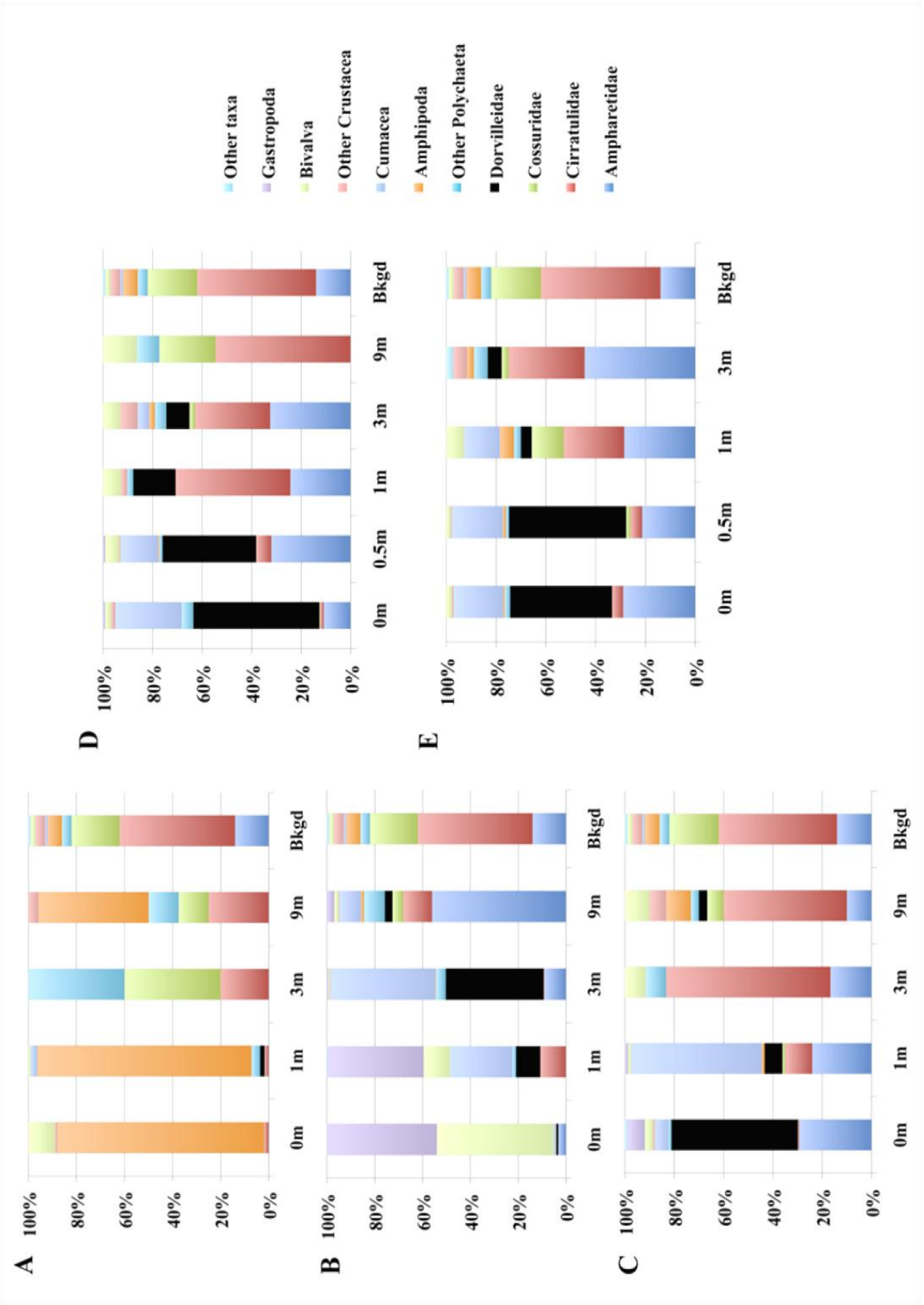

A
B
C
D
E
100%
80%
60%
40%
20%
0%
0m
0.5m
1m
3m
9m
Bkgd
Ampharetidae
Cirratulidae
Cossuridae
Dorvilleidae
Other Polychaeta
Amphipoda
Cumacea
Other Crustacea
Bivalva
Gastropoda
Other taxa

Figure 6

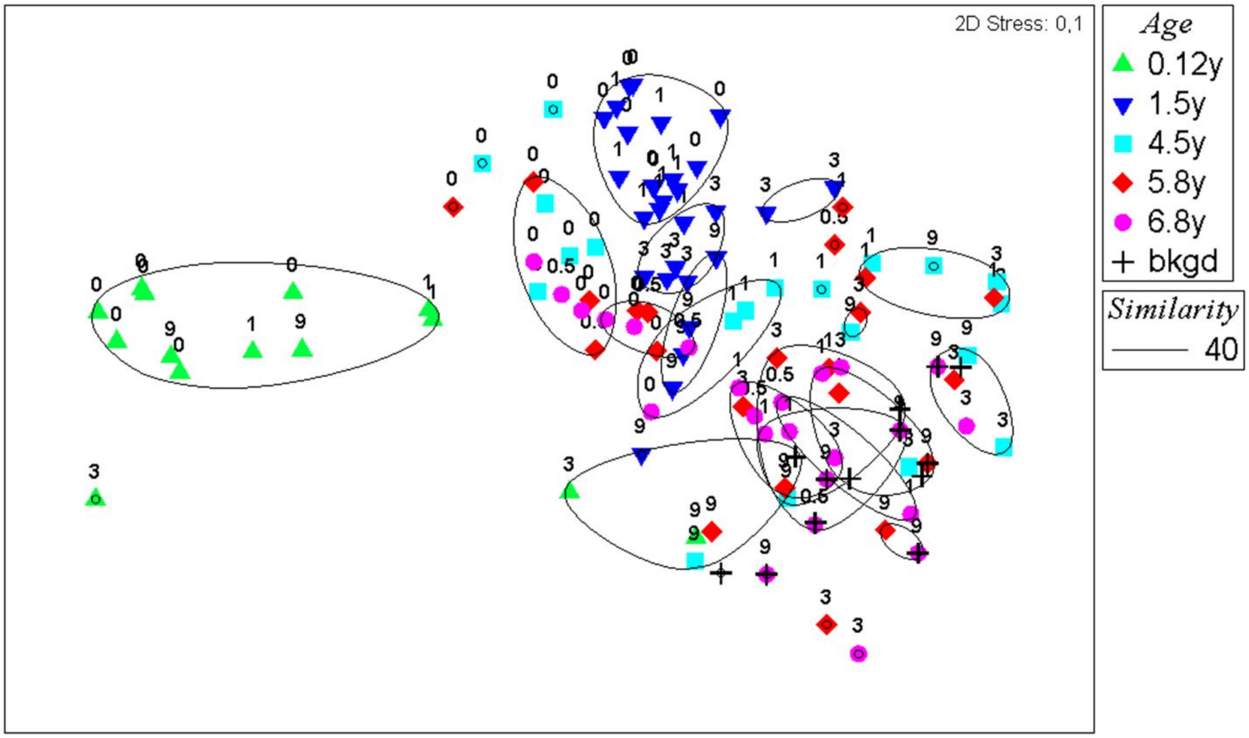


Figure 7

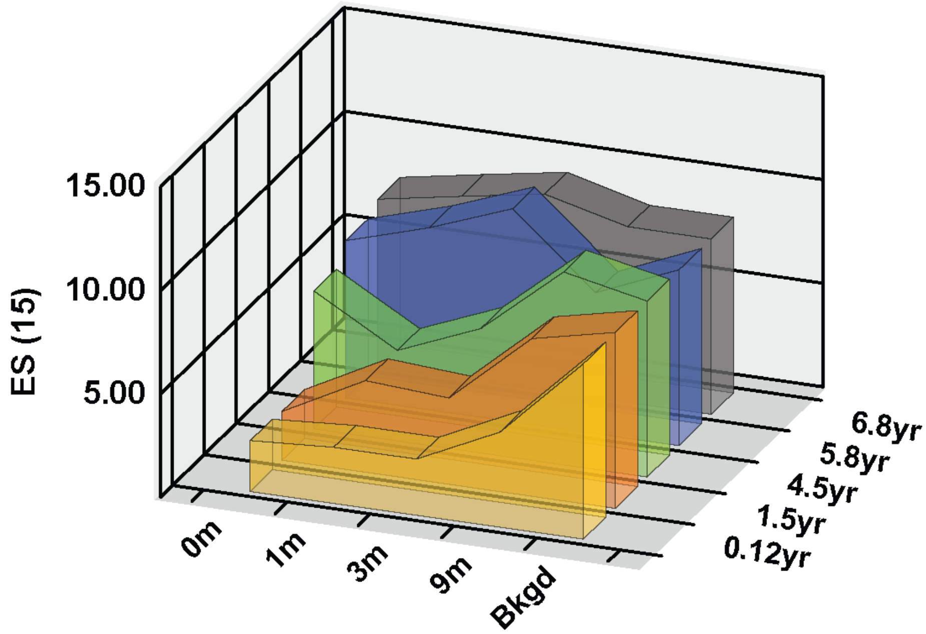


Figure 8

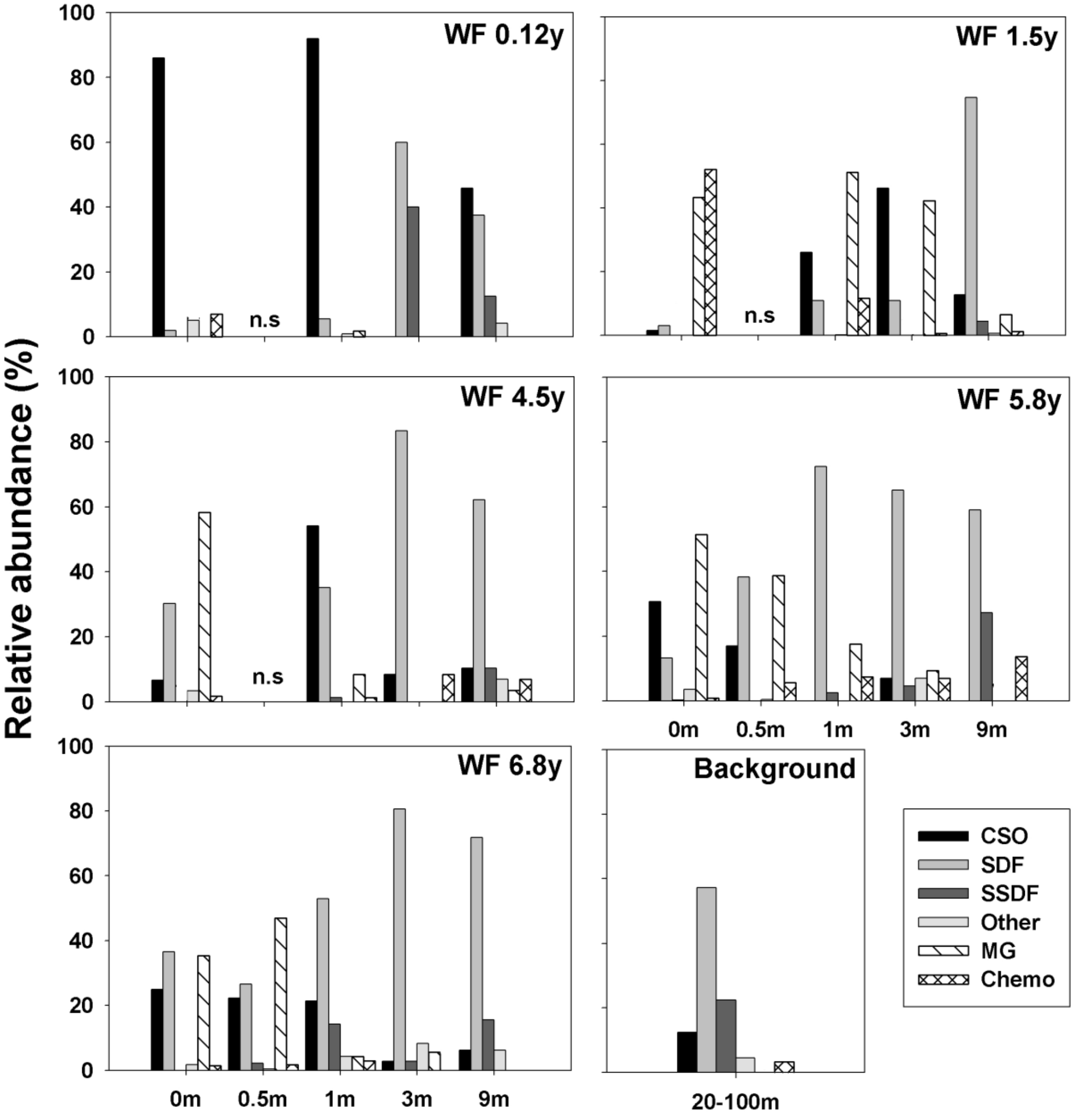

Relative abundance (%)
WF 0.12y
WF 1.5y
WF 4.5y
WF 5.8y
WF 6.8y
Background
n.s
n.s
n.s
0
20
40
60
80
100
0m
0.5m
1m
3m
9m
20-100m
CSO
SDF
SSDF
Other
MG
Chemo

Figure 9

SUPPLEMENTAL MATERIAL

Table S1. Student-t post-hoc tests of significant (p<0.05) Kruskal-Wallis tests on macrofauna abundance around the whale carcass. Values not presented indicate no statistical difference from background sediments.

Distance from whale-fall (m)	***0.12 y***		***1.5 y***				***4.5 y***		***5.8 y***			***6.8 y***		
	0m	**1m**	**0m**	**1m**	**3m**	**9m**	**0m**	**1m**	**0m**	**0.5m**	**1m**	**0m**	**0.5m**	**1m**
0m														
0.5m														
1m									0.05					
3m	.	0.05					0.001	0.03	0.05			0.04		
9m							0.02		0.01			0.01		
20-100m			<0.001	0.001	0.001	0.003	0.001	0.05	0.001	0.03		0.001	0.01	0.03

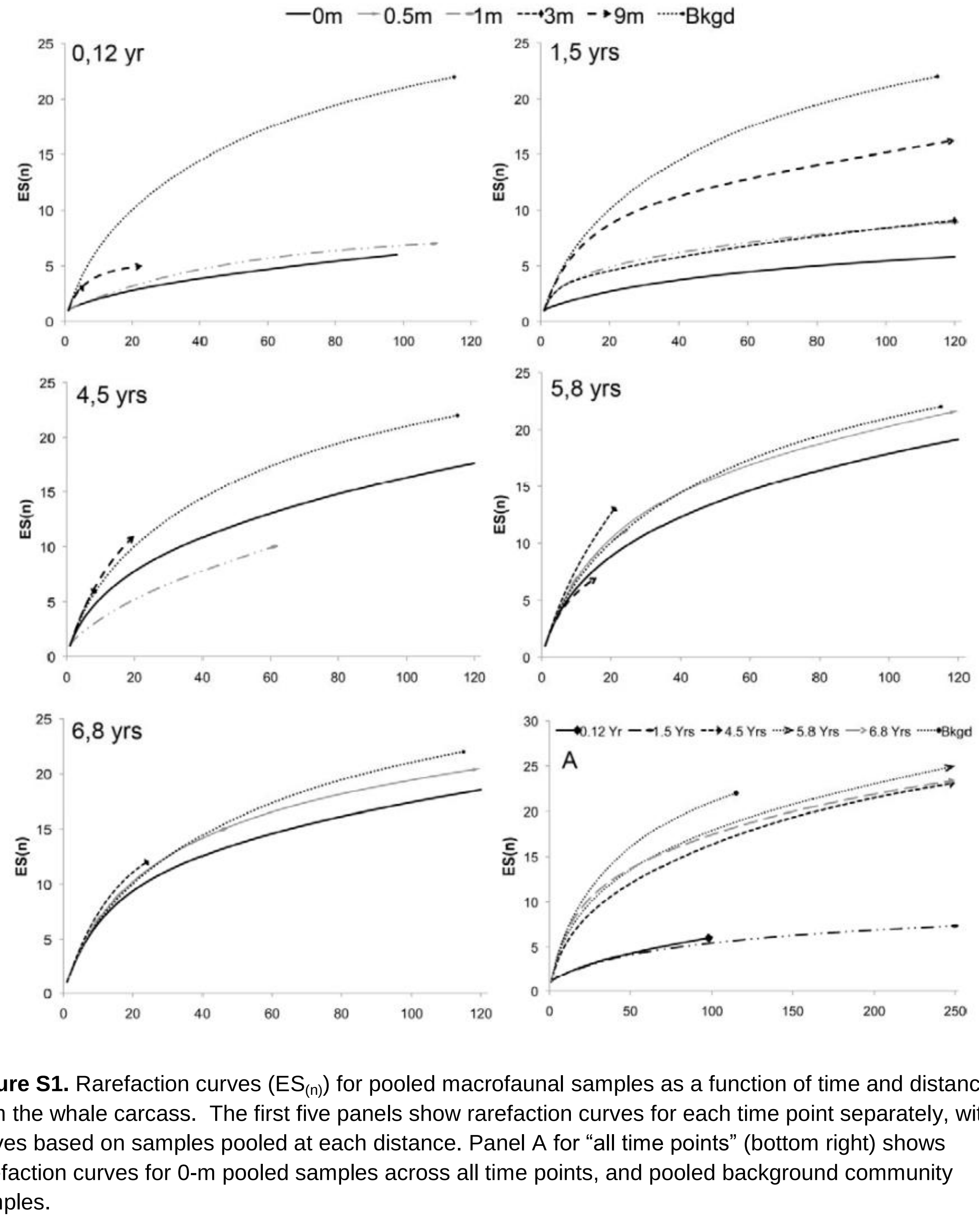


Figure S1. Rarefaction curves ($ES_{(n)}$) for pooled macrofaunal samples as a function of time and distance from the whale carcass. The first five panels show rarefaction curves for each time point separately, with curves based on samples pooled at each distance. Panel A for "all time points" (bottom right) shows rarefaction curves for 0-m pooled samples across all time points, and pooled background community samples.