

# Seven-year enrichment: macrofaunal succession in deep-sea sediments around a 30 tonne whale fall in the Northeast Pacific

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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. We present a 7 yr case study of geochemical impacts, macrofaunal community succession, and chemoautotrophic community persistence in sediments around a 30 t gray-whale carcass implanted at 1675 m in the well-oxygenated Santa Cruz Basin on the California margin. The whale fall yielded intense, patchy organic-carbon enrichment (>15% organic carbon) and pore-water sulfide enhancement (>5 mM) in nearby sediments for 6 to 7 yr, supporting a dense assemblage of enrichment opportunists and chemosymbiotic vesicomyid clams. Faunal 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. Of 100 macrofaunal species in the whale-fall sediments, 10 abundant species were unique to whale falls; 6 species were shared with cold seeps, 5 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 contribute significantly to beta diversity in deep-sea ecosystems.

**KEY WORDS:** Whale fall · Succession · Organic enrichment · Sulfide · Deep sea · Diversity · Chemoautotrophy · Disturbance

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## INTRODUCTION

The carcasses of large cetaceans, with masses of 10 to 150 t, constitute the largest marine detrital particles. 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 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 sulfophilic 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 t great whale carcass contains about  $1.2 \times 10^6$  g of labile organic carbon in soft tissue (Smith 2006). Since most deep-sea sediments receive approximately 2 to 10 g of particulate organic carbon flux per year (Lutz et al. 2007), a sunken 30 t whale carcass is equivalent to  $\geq 1000$  yr of background organic-carbon flux to the underlying 100 m<sup>2</sup> of deep-sea floor. 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, 2012, 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). Assuming that organic enrichment may persist for >5 yr 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 tens 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 enhanced 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 around whale falls after 0.33 to 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 (Nagatsuma 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 meta-community dynamics and organic-matter recycling in the deep sea (e.g. Leibold et al. 2004) and help to predict the community response to anthropogenic organic enrichment at the seafloor (e.g. from sewage sludge emplacement, dumping of trawl bycatch, or the disposal of animal and medical wastes; Smith & Hessler 1987, Gage & Tyler 1991, Debenham et al. 2004, Smith et al. 2008). Whale-fall successional studies can also elucidate life-history and feeding strategies used to 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 t 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, and cold seeps) on the southern California margin?

## MATERIALS AND METHODS

### Study site and field sampling

A 13 m, ~30 t gray whale (*Eschrichtius robustus* Gray, 1864) carcass was implanted on 28 April 1998 at 1675 m depth in Santa Cruz Basin, California (33° 27' N, 119° 22' W; see Bernardino et al. 2010 for a bathymetric map of the area). The site has a bottom-

water temperature of  $\sim 4^{\circ}\text{C}$  and an oxygen concentration of  $\sim 260\ \mu\text{M}$  (Treude et al. 2009). The whale carcass was studied 0.12 and 1.5 yr after implantation with the HOV 'Alvin' (June 1998 and October 1999 respectively) and 4.5, 5.8, and 6.8 yr after implantation with the ROV 'Tiburon' (October and November 2002, February and March 2004, and February and March 2005, respectively). During each visit to the carcass, photographic and video surveys of the whale fall were conducted. On 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 taking digital photographs from a camera oriented vertically downward. Photomosaics of the carcass were constructed using the methods of Pizarro & Singh (2003) and Treude et al. (2009) at the 1.5 and 5.8 yr 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 each time point by sampling along 5 new replicate, randomly located transects radiating outward from the carcass. Along each transect, 1 tube core was collected for macrofauna at distances of 0, 1, 3, and 9 m from remaining portions of the carcass (soft tissue or skeleton); for the 5.8 and 6.8 yr time points (i.e. when the whale-fall 'footprint' appeared to be smaller), cores were also collected at distances of 0.5 m. Macrofauna from the background community was sampled with tube cores at 1.5, 4.5, and 5.8 yr (4, 6 and 3 cores, respectively) at random locations  $\geq 20$  m from the whale fall. Four cores sampled at 9 m from the carcass at 6.8 yr were pooled with 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 yr. At the 0.12 yr time point, cores were 10 cm in diameter; at 1.5 yr, both 10 and 7 cm diameter cores were used; and from 4.5 to 6.8 yr, 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 to 10 cm depth interval was preserved in a 4% buffered seawater formaldehyde solution.

Replicate 7 cm cores were also taken at a subset of distances from the carcass for analyses of sediment organic carbon and pore-water profiles of sulfide (see Fig. 3 for distances). On board ship, cores for organic carbon analyses were extruded and the top centimeter frozen at  $-20^{\circ}\text{C}$ . Cores for pore-water sulfide analyses were immediately placed in an oxygen-free,

nitrogen-flushed glove bag and generally sliced into 1 cm intervals over depths of 0 to 3 cm, 2 cm intervals from 3 to 7 cm depths, and then 3 cm intervals to the bottom of the core. Sediment from each interval was transferred to a 50 ml syringe, and pore waters were then expressed through a  $0.2\ \mu\text{m}$  polycarbonate in-line filter (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  $0.05\ \text{mol l}^{-1}$  zinc acetate; sulfide samples thus preserved were stable for weeks (Cline 1969).

At the 4.5, 5.8 and 6.8 yr time points, vesicomid clams were sampled at random locations ( $n = 5, 3,$  and  $1,$  respectively) within  $\sim 0.5$  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 to 20 cm. The approximate area sampled with each scoop-net deployment was estimated to be  $0.1\ \text{m}^2$  (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 vesicomid clams were stored on ice. Tissue samples were then quickly dissected from the foot of most clams and frozen at  $-80^{\circ}\text{C}$  or fixed in 95% ethanol for DNA bar coding. Vesicomid clams were also collected near the carcass in some tube cores; most of these clams were also placed on ice, and the foot tissue was similarly dissected and fixed for DNA analyses.

### Laboratory analyses

Preserved macrofaunal samples were sieved on  $300\ \mu\text{m}$  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) (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) (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. The following taxonomic specialists assisted in morphospecies identifications and in com-

paring abundant whale-fall species with fauna from other reducing habitats: A. Glover, H. Wiklund, and I. Altamira for polychaetes; A. Waren for gastropods; and L. Watling for cumaceans.

Sediment samples for organic-carbon analyses were acidified to remove carbonates (Verardo et al. 1990) and analyzed using a Perkin-Elmer 2400 CHN Elemental Analyzer (precision of 0.3% and 0.4% for C and N, respectively). Acetanilide was used as a CHN standard. 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.  $\text{H}_2\text{S} + \text{HS}^- + \text{S}^{2-}$ . The detection limit was 2  $\mu\text{mol}$ , and precision was 1.9%.

Vesicomid 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 vesicomid identifications. From each individual vesicomid clam, a ~700 base-pair region of the COI gene was amplified and sequenced using the primers VesHCO and VesLCO as in Peek et al. (1997). 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.

### Statistical methods

Because we were forced by logistical constraints to use differently sized cores at different time points, we analyzed macrofauna patterns using statistics that are robust to differences in sample size. Macrofaunal abundances were normalized to 1 m<sup>2</sup>, 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, Hurlbert 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. Hurlbert's rarefaction curves ( $\text{ES}_{(n)}$ ) was used to compare species diversity between treatments, with  $\text{ES}_{(n)}$  at  $n = 15$  and with whole rarefaction curves. Background

replicate cores ( $n = 17$ ) from 1.5 to 6.8 yr were combined to calculate a composite diversity from the background community. Pielou's evenness ( $J'$ ) was used to assess species evenness (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). Analyses 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). Multivariate results were highly consistent across cores of different size (i.e. samples clustered by time and distance, not by core size).

Comparisons of species overlap between whale-fall, kelp, wood, and other reducing habitats were restricted to vesicomids and common species, i.e. those exceeding 1% of total macrofauna abundance.

## RESULTS

### Visual and video observations of the whale fall

At 0.12 yr, the whale carcass was largely intact, with 400 to 800 hagfish *Eptatretus deani*, 1 to 3 sleeper sharks *Somniosus pacifica*, and clouds of lysianassid amphipods (many thousands) actively feeding on the whale 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 several meters, and sediment was resuspended from the seafloor within 1 m of the carcass by the thrashing activities of sleeper sharks. Some areas of seafloor within ~1 m of the carcass were covered with a pinkish 'carpet' of lysianassid amphipods resting on the sediment-water interface.

After 1.5 yr, nearly all the soft tissue had been removed from the whale skeleton, and most of the large mobile scavengers, except for ~10 to 20 hagfish, had dispersed (Fig. 1, Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m515p133\\_supp.pdf](http://www.int-res.com/articles/suppl/m515p133_supp.pdf)). 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



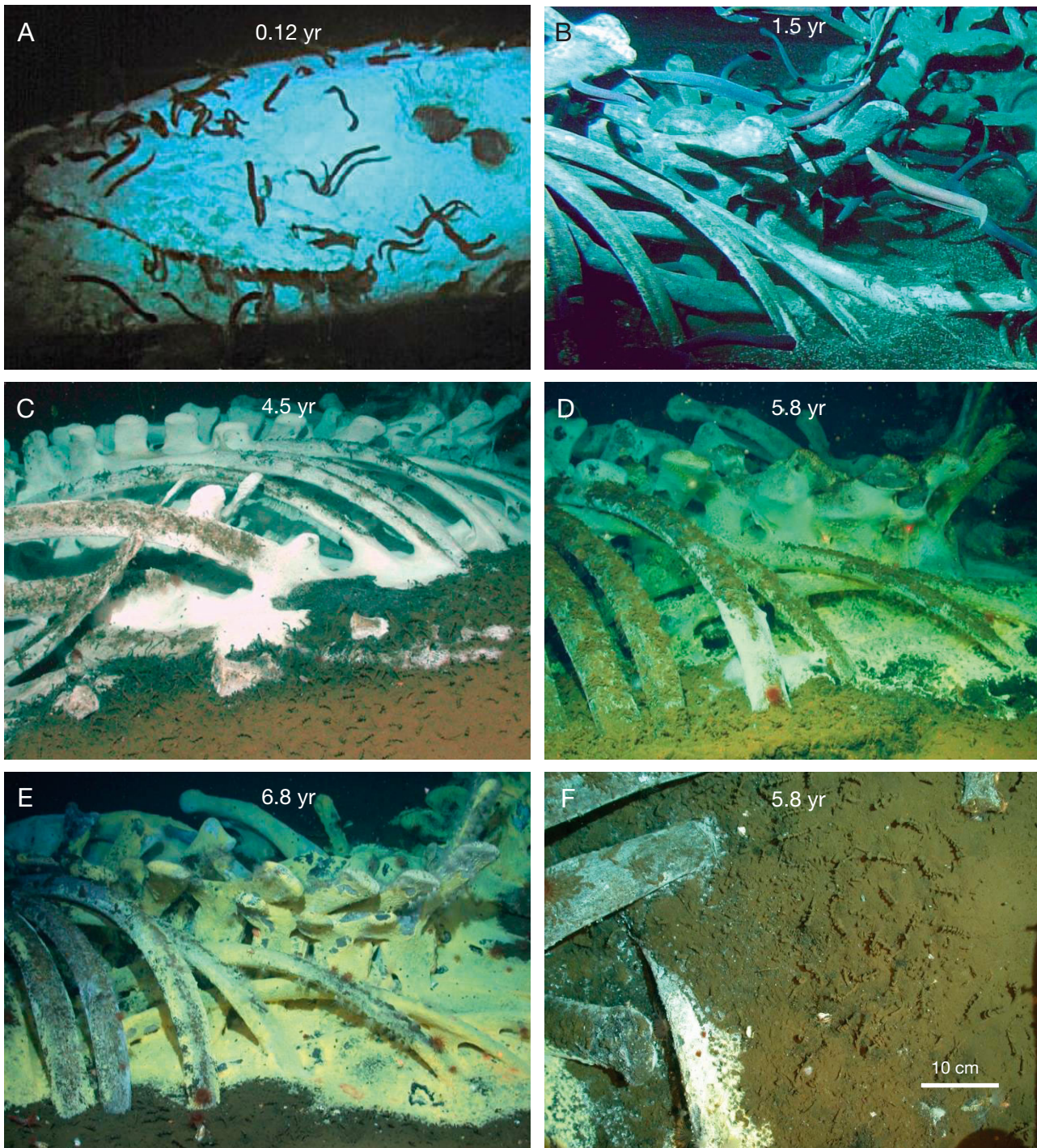


Fig. 1. (A–E) Similar, oblique views of the central left side of the gray whale carcass at stated times after carcass emplacement. For scale, the maximum rib diameter is ~15 cm. (A) 0.12 yr. Note the numerous hagfish *Eptatretus deani* feeding on the largely intact carcass. (B) 1.5 yr. The soft tissue 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 yr. 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 to 2 m of the skeleton. (D) 5.8 yr. The bones continue to be covered with mats of sulfur-oxidizing bacteria, ampharetid tubes and patches of *Osedax*, with ampharetid tubes and black sulfidic patches visible in nearby sediments. (E) 6.8 yr. The skeleton is still largely intact and clad in sulfur-oxidizing bacterial mats. Mats extend 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 yr. The muddy tubes of the polychaete *Ampharetid* n. g. n. sp. are abundant. White spots in the sediments are the shells of vesicomyid clams (living and dead)

(Figs. 1 & S1). Biogenous sediment structures, e.g. centimeter-scale worm tubes, burrows, and mounds, were common on background sediments but were not visible within ~1 m of the carcass. The skeleton appeared wholly intact (Fig. S1) 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 yr, 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 0.5 to 1.0 m of the skeleton were blackish in color. Siphons of buried vesicomid clams were visible within ~0.5 m of the skeleton. Large, centimeter-scale worm tubes, formed by the polychaete *Ampharetid n. g. n. sp.*, were abundant (~50 m<sup>-2</sup>) within ~1 m of the skeleton, gradually declining to zero abundance by 2 to 3 m (Fig. 1). At 5.8 and 6.8 yr, the whale bones continued to be highly intact, and the skeleton and surrounding sediments were similar in appearance to that at 4.5 yr, with vesicomid siphons visible and ampharetid tubes abundant within 0.5 m of the skeleton, and bones and nearby sediments covered with white, yellow, and red microbial mats (Figs. 1 & S1).

### Sediment organic carbon

Organic carbon content of the top centimeter of sediment exhibited substantial, but patchy, enrichment around the carcass at all times sampled (Fig. 2). The greatest enrichment occurred at 0 to 0.5 m from the carcass, with organic carbon contents of 9 to 15% even after 4.5 to 6.8 yr. At distances of 1 to 3 m, sediment organic carbon exceeded background levels up to 4.5 yr; by 5.8 to 6.8 yr, limited data (n = 2 profiles) suggest that organic carbon content at these distances had returned to near background levels (Fig. 2). At 9 m distance, surface-sediment organic carbon appeared to be slightly elevated after 4.5 yr, but fell in the low range of background-community levels after 5.8 to 6.8 yr. In summary, organic enrichment was intense (albeit heterogeneous) to distances of 0.5 m for up to 6.8 yr, with some enrichment to distances of 3 m for up to 4.5 yr (Fig. 2).

### Pore-water sulfide concentrations

Pore-water sulfide concentrations also exhibited intense, heterogeneous enhancement adjacent to the

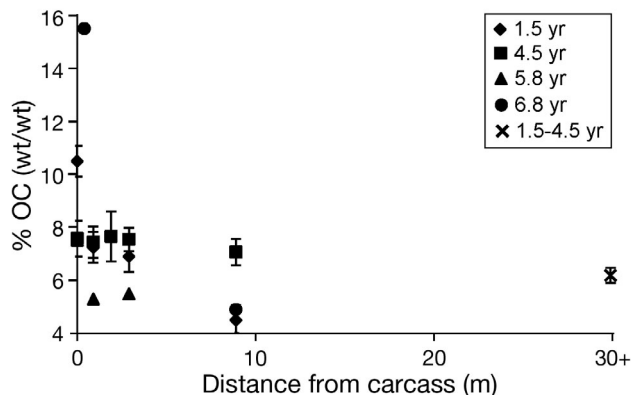


Fig. 2. Variations in organic carbon (OC) content (% of dry weight) of the top centimeter of sediment with distance from the whale carcass. Samples from the background community (collected at distances of 20 to 100 m) are plotted at a distance of 30 m. Means  $\pm$  1 standard error are plotted. Symbols without error bars represent n = 1

whale carcass for a number of years. At 0.12 yr, pore-water sulfides were low around the carcass, generally falling within the range of background community levels (Fig. 3). By 1.5 yr, pore-water sulfides at 0 to 1 m distances had attained high levels in at least some locations, reaching 7 to 10 mM at sediment depths of 0 to 6 cm, but remained low in the single core at 3 m. After 4.5 yr, pore-water sulfides at 0 m sites remained very high at depths of 0 to 10 cm, with concentrations at 1 to 3 m reaching substantial levels (0.05 mM) in some cores (Fig. 3). At 5.8 yr, some cores from 0 m exhibited high sulfide enrichment, while other profiles from 0 to 1 m exhibited little difference from background levels. Thus, for at least 4.5 to 5.8 yr, sediments within 0 to 1 m of the whale fall sustained high, patchy enrichment of pore-water sulfides.

### Vesicomid clams

Large chemosymbiotic vesicomid clams in the subfamily Pliocardiinae, which are known to specialize on sulfide-rich habitats (Krylova & Sahling 2010), were observed and collected in sediments at 0 to 0.5 m from the whale carcass at 4.5, 5.8, and 6.8 yr but were not observed at substantially greater distances (Figs. 1 & S1). Clams were collected in randomly located cores beneath a yellow microbial mat (n = 1), in blackened sediments (n = 4), and in brown sediments (n = 2; Table 1). In addition, 72 vesicomid clams were collected with the scoop net at a total 9 random locations within 0.5 m of the carcass at 4.5, 5.8, and 6.8 yr (Table 1). The occurrence of vesicomids to distances of 0.5 m from the carcass essen-



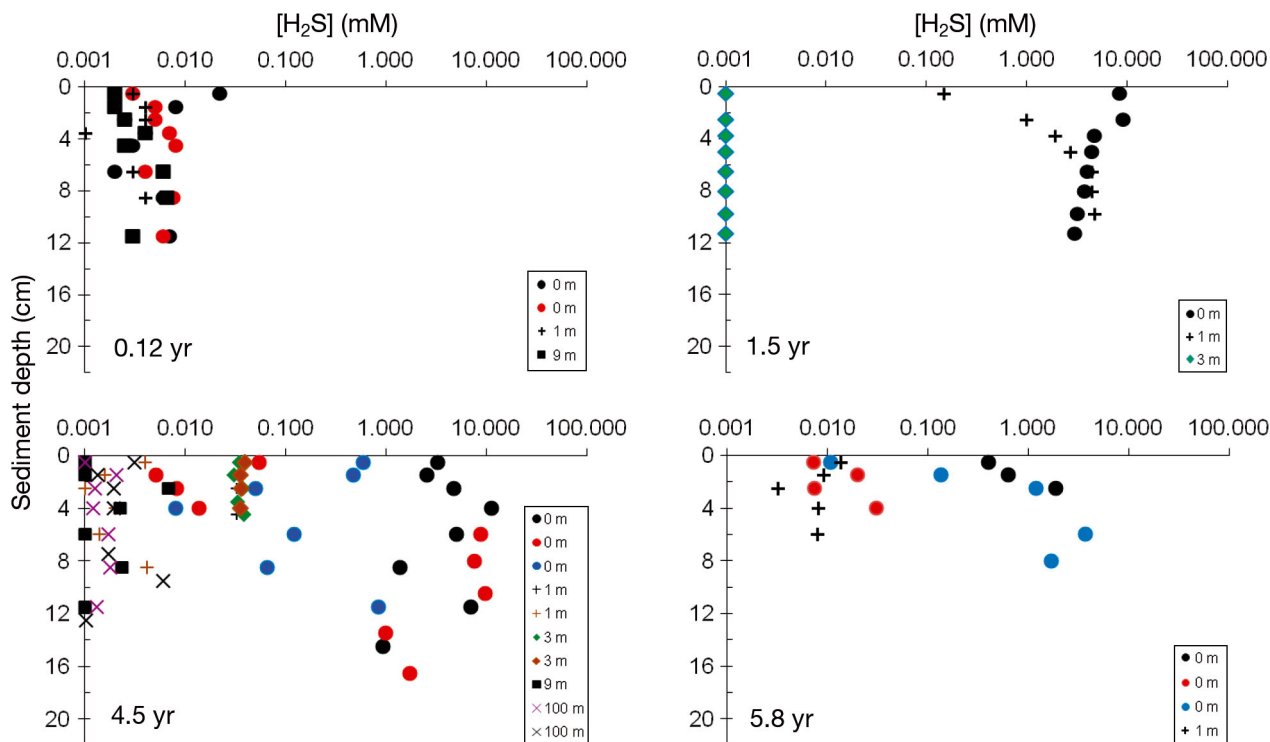


Fig. 3. Profiles of pore-water sulfide concentrations as a function of time and distance from the whale carcass. Data from single profiles are indicated by similarly colored symbols (e.g. blue circles). Points are plotted at the middle of the depth interval sampled

tially matches the footprint of high pore-water sulfides around the whale carcass after 4.5 to 5.8 yr (Fig. 3).

Barcoding of 58 vesicomyid individuals collected at the whale fall, using a ~700 base-pair region of the mitochondrial gene COI, indicated that 4 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) 3 individuals (GenBank accession no. KF990209) showing 98% sequence overlap with 2 divergent molecular taxonomic units, '*Archivesica*' *packardana* and '*Pliocardia*' *stearnsii* in GenBank (Audzijonyte et al. 2012); (3) 3 individuals (GenBank accession nos. KF9902010 and KF9902011) with 93% sequence overlap with *Pliocardia ponderosa*; and (4) 1 *Calyptoptogena pacifica* (GenBank accession no. KF9902012) with 100% sequence overlap with *C. pacifica* in GenBank. Sequence divergences above 1.5 to 2% are considered indications of species-level differences between vesicomyids 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 to certainly be a new molecular operational taxonomic unit, and Species 2 is likely to be new. Based

on these barcoding results, *A. gigas* was the overwhelming dominant vesicomyid (93%), while the other 3 species constituted  $\leq 5\%$  of the clam population around the whale carcass between 4.5 and 6.8 yr.

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

### Macrofaunal abundance and community structure

Macrofaunal abundance exhibited major, time-dependent changes around the whale carcass. After 0.12 yr, mean macrofaunal abundances at distances of 0 to 9 m were not significantly different from background community levels (Kruskal-Wallis test,  $p > 0.05$ ) (Fig. 4; Table S1, the latter in the Supplement at [www.int-res.com/articles/suppl/m515p133\\_supp.pdf](http://www.int-res.com/articles/suppl/m515p133_supp.pdf)). However, by 1.5 yr, macrofaunal abundances at

Table 1. Vesicomylid clam collections, species barcoding and population densities and sizes. All clams were sampled 0 to 0.5 m from the whale-fall. TD: ROV Tiburon dive; TC: tube core; A: *Archivesica*; C: *Calyptogena*; P: *Pliocardia*

Time	Date (mm/dd/ year)	Dive	Sample type	No. of clams in sample	A. <i>gigas</i>	Nr. 'V.' <i>packar- dana</i> ' <i>P.</i> <i>stearnsi</i>	P. nr. <i>ponde- rosa</i>	C. <i>pacifica</i>	Unbar- coded clams	Mean clam density m <sup>-2</sup> ± SE <sup>a</sup>	Clam pop. size ± SE <sup>b</sup>
4.5 yr	10/27/2002	TD 498	Scoop net	6	5			1		} 52 ± 10	} 900 ± 180
	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 <sup>c</sup>	1	1						
	10/24/2002	TD 491	Scoop net	8	8						
	10/28/1002	TD 495	Scoop net	6					6		
<b>Total 27</b>											
5.8 yr	3/1/2004	TD 653	Scoop net	1	1					} 93 ± 60	} 1620 ± 600
	3/1/2004	TD 653	TC #44 <sup>d</sup>	1	1						
	3/2/2004	TD 654	Scoop net	21	13	2	2		4		
	3/2/2004	TD 654	TC #50 <sup>c</sup>	1					1		
	3/2/2004	TD 655	Scoop net	6	3		1		2		
<b>Total 30</b>											
6.8 yr	2/26/2005	TD 822	TC #62 <sup>c</sup>	2	2					} 80	} 1440
	2/26/2005	TD 822	TC #79 <sup>e</sup>	2	2						
	2/27/2005	TD 823	Slurps	3	3						
	2/27/2005	TD 823	Scoop net	8	8						
<b>Total 15</b>											
<b>Overall total</b>				<b>72</b>	<b>51</b>	<b>3</b>	<b>3</b>	<b>1</b>	<b>14</b>		
<b>% of barcoded clams</b>					<b>93</b>	<b>5</b>	<b>5</b>	<b>2</b>			

<sup>a</sup>Assuming a scoop net sampling area of 0.1 m<sup>2</sup>; <sup>b</sup>Total individuals based on estimated area within 0.5 m of the whale-fall (Treude et al. 2009); <sup>c</sup>Cores collected in blackened sediments; <sup>d</sup>Core collected in yellow microbial mat; <sup>e</sup>Core collected in brown sediment

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. 4, Table S1), with abundances at 0 m 28-fold greater than mean background levels. After 4.5 yr, macrofaunal abundances remained very high at 0 m (10× background levels;  $p = 0.001$ ), were significantly elevated at 1 m, but had declined to background community levels at greater distances. After 5.8 to 6.8 yr, macrofaunal abundance followed a similar pattern of very high levels at 0 m (10 to 12 times background;  $p < 0.05$ ), modest enhancement at 0.5 to 1 m, and no enhancement above background levels at 3 to 9 m.

The sediment macrofaunal community also exhibited strong successional patterns in space and time around the whale carcass in both higher taxonomic composition and dominant species. The details of these changes are presented in the Supplement (see 'Patterns of macrofaunal community composition around the carcass in space and time' at [www.int-res.com/articles/suppl/m515p133\\_supp.pdf](http://www.int-res.com/articles/suppl/m515p133_supp.pdf)) and in Figs. 5 & S1. The sediment community patterns can be summarized as follows: (1) Macrofaunal community abundance was initially (at 0.12 yr) dominated

(42 to 86%) by dense patches of a mobile scavenging amphipod (*Lysianassid* sp. A) to distances of 1 to 9 m from the carcass. This amphipod achieved an estimated population size of >100000 around the carcass but was absent from the background community samples. Other macrofaunal species occurring near the carcass at this time were rare or absent in the background community and included juveniles of the chemosymbiotic bivalve *Idas washingtonia*, an enrichment-opportunist cumacean crustacean, and an omnivorous oedicerotid amphipod. (2) At 1.5 yr, a sulfophilic hyalogyrinid gastropod (*Hyalogyrina* n. sp.) and putative juvenile vesicomylids dominated sediments near the carcass ( $\leq 1$  m), with organic enrichment opportunists, including several species of dorvilleid polychaetes, cumaceans, and ampharetids, dominating at greater distances (3 to 9 m). These sulfophilic and enrichment opportunistic species were absent from background community samples. (3) At later time points, the enrichment opportunists, again including multiple species of dorvilleids, cumaceans, and ampharetids, dominated in a diminishing zone extending outward from the carcass to 3, 1, and 0.5 m after 4.5, 5.8, and 6.8 yr, respectively. At the outer



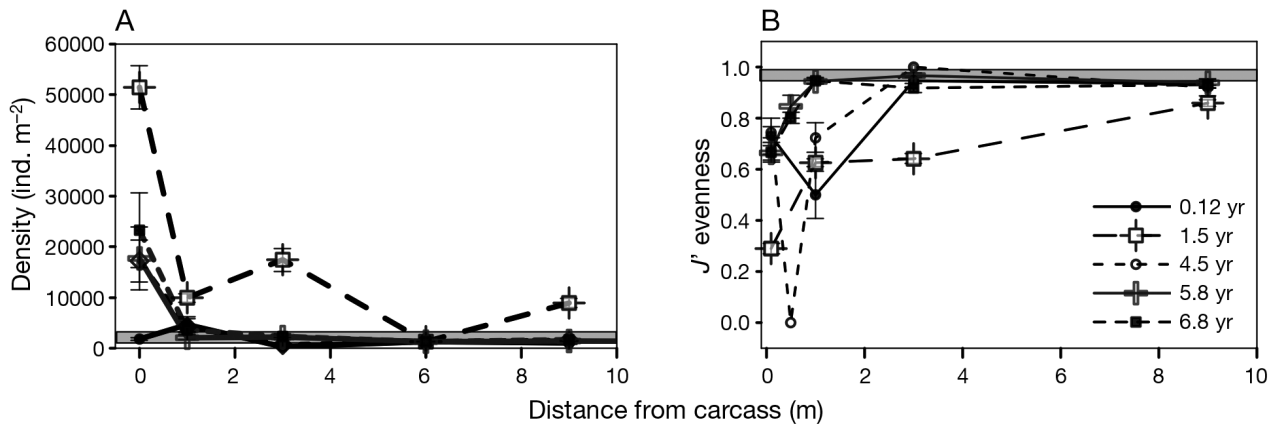


Fig. 4. (A) Total macrofaunal community abundance as function of time and distance from the whale fall. The shaded bar is the mean ( $\pm 1$  SE) of the background community abundance at distances of 20 to 100 m from the whale carcass. (B) Pielou's evenness ( $J'$ ) as a function of time and distance from the carcass. The shaded bar is the mean ( $\pm 1$  SE) of  $J'$  in the background community. Data points are means  $\pm 1$  SE

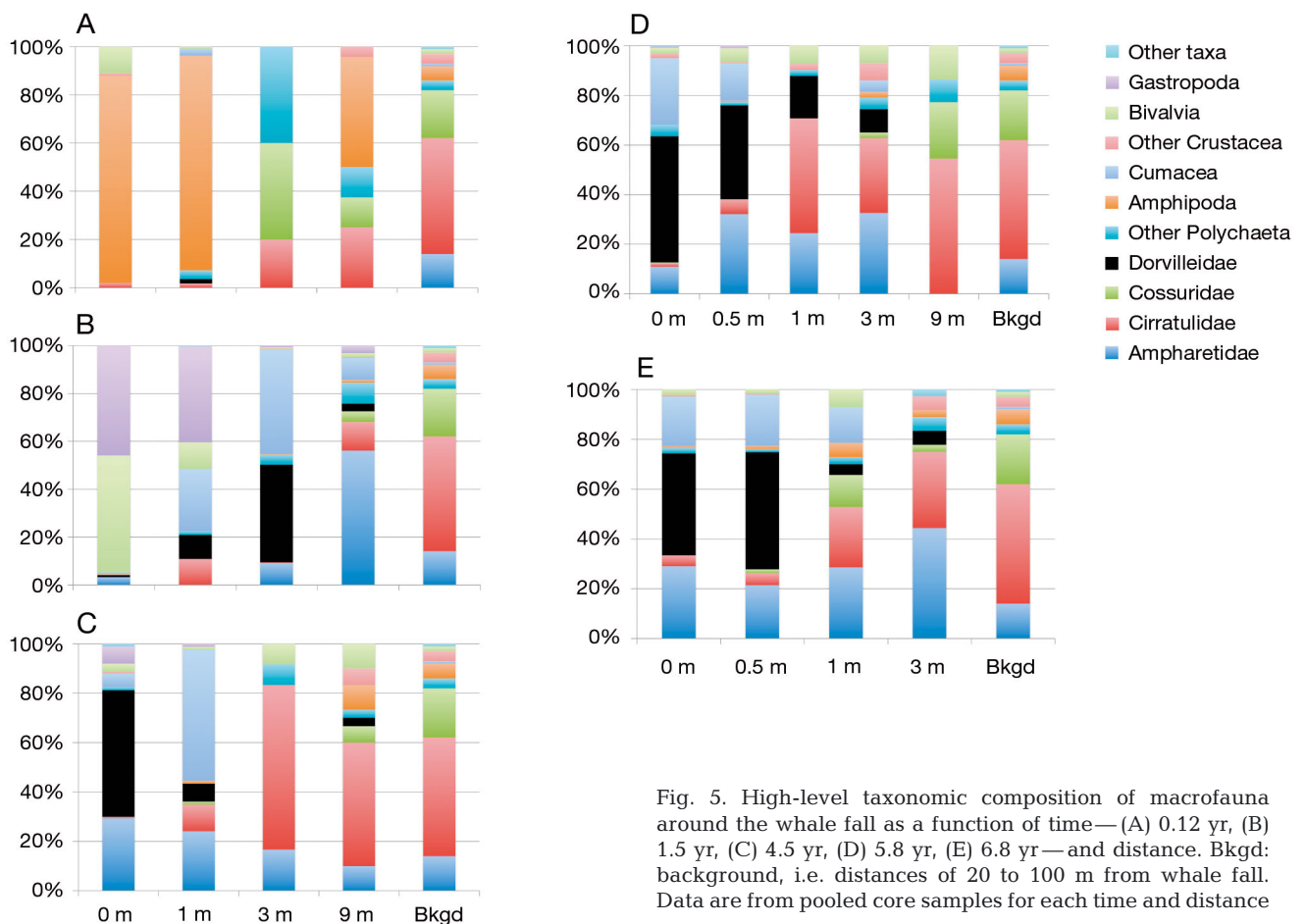
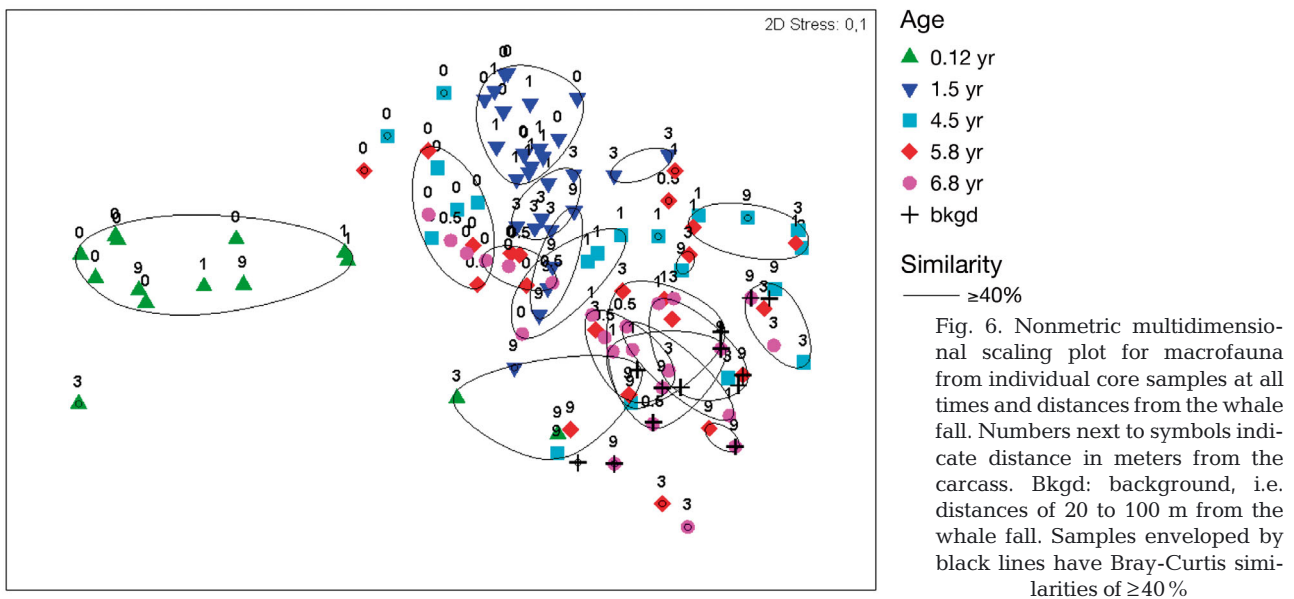


Fig. 5. High-level taxonomic composition of macrofauna around the whale fall as a function of time—(A) 0.12 yr, (B) 1.5 yr, (C) 4.5 yr, (D) 5.8 yr, (E) 6.8 yr—and distance. Bkgd: background, i.e. distances of 20 to 100 m from whale fall. Data are from pooled core samples for each time and distance

margin of the zone of opportunists, the most abundant background species (including 2 species of cirratulid polychaetes) became common, and then became dominant in this zone (Table S2 in the Supplement at [www.int-res.com/articles/suppl/m515\\_p133\\_supp.pdf](http://www.int-res.com/articles/suppl/m515_p133_supp.pdf)).

The occurrence of sulfophilic and opportunistic macrofauna and megafauna roughly matched the spatial scales of sulfide and organic-carbon enrichment around the whale carcass (Figs. 2 & 3). For example, juvenile vesicomids apparently recruited into sulfide-rich sediments adjacent to the carcass by



1.5 yr (Fig. 3), allowing the development of megafaunal vesicomyid clam populations within 0.5 m of the carcass after 4.5 to 6.8 yr. In addition, the decline in the spatial extent of enrichment opportunists roughly matched the declining spatial extent of organic enrichment measured around the whale carcass from 4.5 to 6.8 yr (Fig. 2).

NMDS analysis provided strong additional evidence of macrofaunal community succession around the whale carcass over both time and distance (Fig. 6). At 0.12 yr, 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 yr, the 0 and 1 m samples also formed a largely distinct cluster, consistent with dominance by sulfophilic bivalve juveniles and gastropods. Samples from 3 to 9 m at 1.5 yr, and from 0 to 1 m from 4.5 to 6.8 yr, generally grouped together in the central portion of the NMDS plot, consistent with a community of enrichment opportunists (ANOSIM  $R = 0.693$ ,  $p < 0.01$ ). Samples from  $> 1$  m at 4.5 to 6.8 yr formed a cluster that gradually merged with the background community samples, consistent with transitions from enrichment-opportunist to background-community assemblages.

#### Macrofaunal species diversity

Sediment macrofaunal rarefaction diversity also exhibited strong patterns in space and time at the

whale fall. At 0.12 yr,  $ES_{(15)}$  at 0 to 3 m from the carcass was very low relative to the background community and remained low to a distance of 9 m (Fig. 7). At 1.5 yr,  $ES_{(15)}$  was very low at 0 m but gradually increased to near background levels by 9 m. At 4.5 yr,  $ES_{(15)}$  had increased at 0 to 3 m distances but still remained below the diversity levels of 9 m and in background sediments. By 5.8 to 6.8 yr, 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 yr and then increased essentially monotonically with distance from the carcass and time after implantation, recovering approximately to background levels by 5.8 yr. Diversity patterns of whole rarefaction curves (Fig. S2 in the Supplement at [www.int-res.com/articles/suppl/m515p133\\_supp.pdf](http://www.int-res.com/articles/suppl/m515p133_supp.pdf)) 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 to 1 m from the carcass at 0.12 yr and remained low from 0 to 3 m after 1.5 yr (Fig. 4). 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 yr. The whale fall led to unusually high rel-

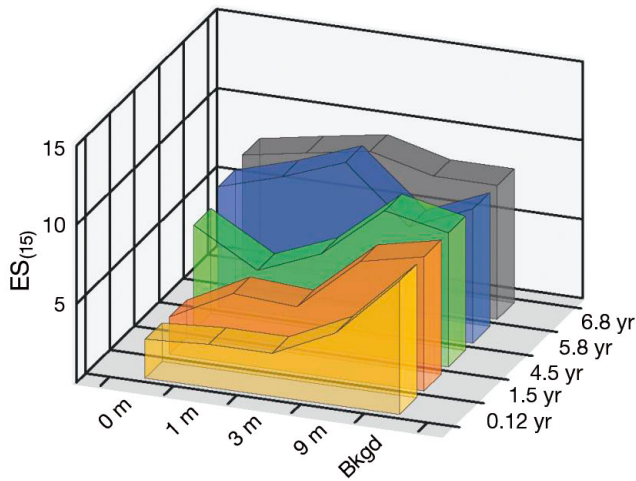


Fig. 7. Macrofaunal rarefaction species diversity,  $ES_{(15)}$ , as a function of time and distance from the whale carcass. Bkgd: background, i.e. distances of 20 to 100 m from the whale fall. Means of cores from each distance-time combination are plotted

ative abundances of (1) carnivores/scavengers/omnivores after 0.12 yr, (2) species with chemoautotrophic symbionts and microbial grazers after 1.5 yr, and (3) microbial grazers and carnivores/scavengers/omnivores after 4.5 to 6.8 yr (Fig. 8). The radius of these trophic-group effects declined gradually from 9 m at 0.12 yr, through a distance of 3 m at 1.5 yr, to distances of ~1 m by 4.5 to 6.8 yr (Fig. 8).

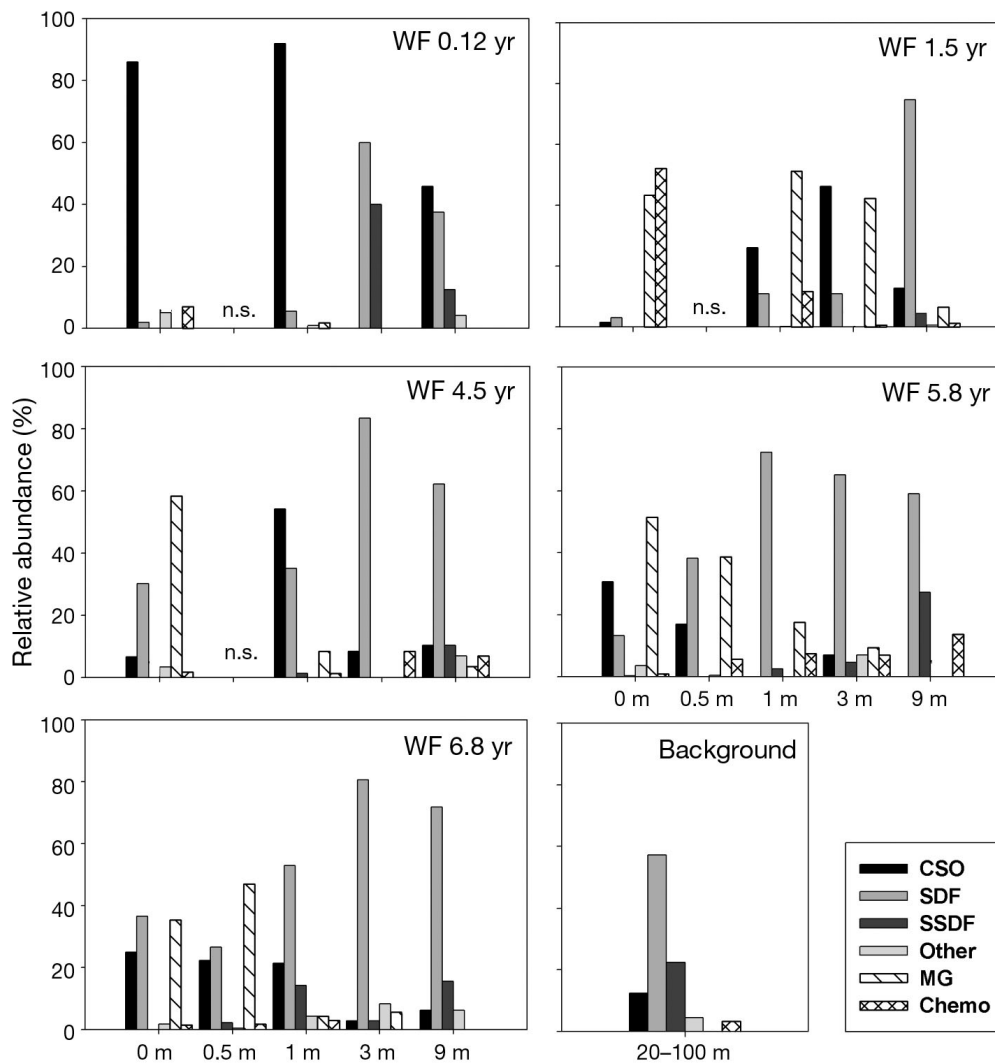


Fig. 8. Trophic-group composition of the sediment macrofaunal community as a function of time and distance from the whale carcass. WF: whale fall; CSO: carnivores-scavengers-omnivores; SDF: surface-deposit feeders; SSDF: subsurface-deposit feeders; MG: microbial grazer; Chemo: containing chemoautotrophic endosymbionts; Other: trophic group unknown or none of the other major categories. 'ns': not sampled



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

Twenty-eight of the 100 collected species of sediment macrofauna and megafauna were common (>1% of total abundance) adjacent to the whale fall but were not collected in the background community (Table 2); 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 2); these species could be whale-fall specialists.

There was modest overlap between the sediment-dwelling whale-fall species and the reported fauna of other deep-sea reducing habitats. twenty-one percent (6) of the whale-fall species were shared with kelp-fall habitats and 39% (11) with wood-fall habi-

Table 2. 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 are only macrofaunal species or genera that (1) occurred at distances of 0 to 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. Species with letter designations are working species in the C. R. Smith collection, i.e. they have been resolved to the species level but have not been successfully related to any described species. P: present. Sources: 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	Source
<b>Polychaeta</b>						
<b>Ampharetidae</b>						
Ampharetid sp. A <sup>a</sup>	>5%					
Ampharetid sp. F <sup>a</sup>	1–5%					
Ampharetid sp. L <sup>a</sup>	>5%					
Ampharetid sp. N <sup>a</sup>	>5%					
<i>Sosanopsis</i> sp. A <sup>a</sup>	1–5%					
<i>Samytha</i> cf. <i>californiensis</i>	>5%	6.5%	13.2%			1, 2
<b>Cirratulidae</b>						
Cirratulid sp. 1 <sup>a</sup>	>5%					
Cirratulid sp. 2	>5%		14.3%			2
<b>Dorvilleidae</b>						
<i>Parougia</i> sp. A	>5%		14.6%	P	P (genus)	1, 2, 3, 4, 5
<i>Ophryotrocha</i> sp. A	>5%	36.5%	33.8%	P (genus)	P (genus)	1, 2, 4
<i>Ophryotrocha</i> sp. B	1–5%		1.3%	P (genus)	P (genus)	1, 2, 4
<i>Ophryotrocha</i> sp. E <sup>a</sup>	>5%			P (genus)	P (genus)	1, 4
<i>Ophryotrocha</i> sp. H <sup>a</sup>	1–5%			P (genus)	P (genus)	1, 4
<i>Ophryotrocha</i> sp. K <sup>a</sup>	1–5%			P (genus)	P (genus)	1, 4
<i>Schistomeringos longicornis</i>	>5%		1.4%	P		1, 4
<i>Ophryotrocha platykephale</i>	>5%			P	P	3, 5
<i>Exallopus</i> sp. A <sup>a</sup>	>5%			P (genus)	P (genus)	1, 4, 5
<b>Polynoidae</b>						
<i>Bathykurila guaymasensis</i>	>5%				P	1, 5
<b>Crustacea</b>						
<i>Cumella</i> sp. A	>5%	34.4%	1.4%			1, 2
Cumacean sp. K	>5%	52.7%	32.3%			1, 2
<i>Ilyarachna profunda</i>	1–5%		6.9%			1, 2
<b>Mollusca</b>						
<i>Hyalogyrina</i> n. sp.	>5%	11.5%				1, 2
<i>Idas washingtonius</i>	>5%		2.8%	P	P	1, 2, 4, 6, 7
Bivalve sp. Q	1–5%	5.4%	9.7%			1, 2
<i>Archivesica gigas</i>	P			P	P	8, 11
Near ' <i>Archivesica</i> ' <i>packardana</i> & ' <i>Pliocardia</i> ' <i>stearnsi</i>	P			P (genus)		9, 11
Near ' <i>Pliocardia</i> ' <i>ponderosa</i>	P			P (genus)		10
<i>Calyptogena pacifica</i>	P			P	P	10, 11
<b>Total species or genera</b>	<b>28</b>	<b>6</b>	<b>11</b>	<b>14</b>	<b>12</b>	
<b>% of 28 SCr WF species shared</b>	<b>100</b>	<b>21</b>	<b>39</b>	<b>21</b>	<b>18</b>	

<sup>a</sup>Sediment macrofaunal species to date found only at whale falls (a total of 10 species)

tats in the Santa Cruz Basin; these included apparent enrichment opportunists (the ampharetid *Samytha cf. californiensis*, several dorvillied polychaetes, and cumacean crustaceans) and 1 species with chemoautotrophic endosymbionts (*Idas washingtonius*; Table 2). Twenty-one percent (6) of the whale-fall species were shared with cold seep faunas, including 2 species of vesicomids and 3 species of dorvilleid polychaetes. Eighteen percent (5) of these whale-fall species have been found at hydrothermal vents, including 2 polychaetes, a bivalve in the bathymodiolin lineage (*I. washingtonius*) (Thubaut et al. 2013), and 2 species of vesicomids. 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 6 genera shared with hydrothermal vents (Table 2).

## DISCUSSION

The 30 t gray whale carcass had major structural and geochemical impacts for at least 7 yr on the bathyal benthic community in the well oxygenated bottom waters (260  $\mu\text{M}$ ) 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 yr with little evidence of bone erosion. This is consistent with the findings of Smith & 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 ( $>45 \mu\text{M}$ ) 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, greater bone calcification and higher lipid content, even with large *Osedax* populations (Smith & Baco 2003, Schuller et al. 2004, Smith et al. 2015).

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 yr, there was no evidence from either pore-water sulfides or visual observations of geochemical impacts on the sediment. However, by 1.5 yr, 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 vesicomid clams and chemosymbiotic mussels as well as microbial-mat grazing gastropods (*Hyalogyrina* sp.). Organic loading and sulfide enhancement persisted patchily in sediments within 1 m of the skeleton for 5.8 to 6.8 yr. The abundance of species with chemoautotrophic symbionts, including large vesicomids, and the prominence of microbial-mat grazers within the sediment after 6.8 yr, 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 persistence times (years to decades) of reducing habitats at some individual hydrothermal vents (Van Dover 2000). Of course, persistence of reducing habitats on the bones of adult whale falls can be even longer, i.e. many decades (Smith & Baco 2003, Schuller et al. 2004).

Smith & Baco (2003) described 3 'overlapping stages of ecological succession' occurring on the carcasses of large, adult whales on the deep California margin. However, their data set included only 1 time point for sediment-dwelling macrofauna from any whale fall. Our 7 yr time series indicates that sediment macrofaunal succession around the Santa Cruz whale fall resembled the Smith & Baco (2003) successional model, with substantial overlap between successional stages. In particular, highly mobile scavengers (e.g. lysianassid amphipods) overwhelmingly dominated sediments around the whale fall at the earliest sampling point (0.12 yr), 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 yr. Nonetheless, sulfophilic species with chemoautotrophic endosymbionts, as well as grazers of sulfur-oxidizing bacteria, were recruiting heavily during the 'enrichment opportunist stage,' as indicated by the abundance close to the whale fall of putative juvenile vesicomid clams, mussels in the bathymodiolin lineage, and *Hyalogyrina* gastropods. By later time points (5.8 to 6.8 yr), the abundance of enrichment opportunists remained high only very near the whale fall, while a sizable (900 to 1600 individuals), multispecies assemblage of large, relatively

long-lived vesicomyid 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).

Faunal succession around the Santa Cruz whale fall 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 yr was similar to the classic, widely applied Pearson & Rosenberg (1978) successional model. At later times (4.5 to 6.8 yr), 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 & Rosenberg (1978) model, in which enrichment-opportunists and background species coexisted as enrichment conditions began to ameliorate (e.g. Newell et al. 1998). We also observed overlap at the family level between the whale-fall and shallow-water enrichment opportunists, with dorvilleid polychaetes dominating enriched sediments at the whale fall and in many shallow-water, fine-sediment habitats (e.g. Karakassis et al. 2000, Wiklund et al. 2009). Nonetheless, there appear to be some major taxonomic differences between the deep-sea 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 the whale fall, as well as around kelp/wood falls on the California margin (Smith et al. 2002, Bernardino et al. 2010). Furthermore, cumacean crustaceans were prominent opportunists around the whale fall and in other enriched deep-sea sediments (Smith 1985, 1986, Snelgrove et al. 1994, Bernardino et al. 2010), whereas this group, to our knowledge, does not routinely respond to organic enrichment in shallow water. 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 release from competition allow opportunists to flourish in ephemeral, enriched habitats in both shallow and deep-sea benthic ecosystems.

The enriched sediments around the Santa Cruz whale fall harbored some of the highest macrofaunal densities ( $>50000\text{ m}^{-2}$ ) ever recorded in the deep sea (Wei et al. 2010, Bernardino et al. 2012, Thurber et al. 2013), including 10 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 at 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 (Higgs et al. 2014), but we know of no infaunal data to address this hypothesis. In any event, it appears that whale falls contribute significantly to 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 (6 species shared) and hydrothermal vents (5 species in common; Table 2) 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 *Bathypurila guaymensis*, which can be abundant at both vents and whale falls (Table 2).

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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