Time-series analysis of six whale-fall communities in Monterey Canyon, California, USA

Lonny Lundsten a,*, Kyra L. Schlining a, Kaitlin Frasier b, Shannon B. Johnson a, Linda A. Kuhnza, Julio B.J. Harvey a, Gillian Clague a, Robert C. Vrijenhoeka

a Monterey Bay Aquarium Research Institute, 7700 Sandholdt Road, Moss Landing, CA 95039, USA
b Scripps Institution of Oceanography, 8602 La Jolla Shores Drive, La Jolla, CA 92037, USA

Abstract

Dead whale carcasses that sink to the deep seafloor introduce a massive pulse of energy capable of hosting dynamic communities of organisms in an otherwise food-limited environment. Through long-term observations of one natural and five implanted whale carcasses in Monterey Canyon, CA, this study suggests that: (1) depth and related physical conditions play a crucial role in species composition; (2) the majority of species in these communities are background deep-sea taxa; and (3) carcass degradation occurs sub-decadally. Remotely operated vehicles (ROVs) equipped with studio quality video cameras were used to survey whales during 0.8 to seven year periods, depending on the carcass. All organisms were identified to the lowest possible taxon. Community differences among whale-falls seemed to be most strongly related to depth and water temperature. The communities changed significantly from initial establishment shortly after a carcass' arrival at the seafloor through multiple years of steady degradation. The majority of species found at the whale-falls were background taxa commonly seen in Monterey Bay. While populations of species characterized as bone specialists, seep restricted, and of unknown habitat affinities were also observed, sometimes in great abundance, they contributed minimally to overall species richness. All whale carcasses, shallow and deep, exhibited sub-decadal degradation and a time-series of mosaic images at the deepest whale site illustrates the rapidity at which the carcasses degrade.

1. Introduction

Whale-falls, carcasses of dead whales that sink to the seafloor, host thriving and dynamic communities of organisms. Each whale arriving at the seafloor represents a massive influx of energy to an otherwise food-limited environment. Whale tissues and lipid-rich bones (over 60% lipids by weight) provide an energetic pulse to the region immediately surrounding the fall (Schuller et al., 2004). A 40-ton whale carcass may carry 2000–3000 kg of lipids in its skeleton alone, and represent 100–200 times the typical levels of organic carbon sinking annually to a hectare of seafloor (Smith et al., 2002; Smith and Baco, 2003; Smith, 2006).

Studies of natural and implanted whale-falls have spawned various theories on the structure and development of the communities that colonize these enriched habitats. Early research showed the presence of hydrothermal vent and cold seep organisms, although these taxa represented only a small percentage of species richness (Bennett et al., 1994; Deming et al., 1997; Feldman et al., 1998; Smith et al., 2002; Baco and Smith, 2003; Smith and Baco, 2003; Schuller et al., 2004). These authors also suggested that vent and seep animals may use whale carcasses as “stepping stones,” bridging spatial gaps between ephemeral seep and vent habitats (Bennett et al., 1994; Baco and Smith, 2003; Smith and Baco, 2003; Smith, 2006). Fujiwara et al. (2007) reported no overlap between whale-fall inhabitants and species found at nearby seeps and vents off the coast of Japan. Lundsten et al. (2010) report Lamellibrachia sp. living near a whale-fall off Vancouver Island, British Columbia. Several studies have suggested the existence of whale-fall specialists, organisms specifically adapted to the conditions at whale carcasses (Smith and Baco, 2003; Smith, 2006). Whale-fall specialists would seemingly include species of the unique siboglinid genus, Osedax (Rouse et al., 2004; Glover et al., 2005; Fujikura et al., 2006; Rouse et al., 2009; Vrijenhoek et al., 2009); however, the exclusive dependence upon whale bone for this genus has been the subject of recent debate (Jones et al., 2008; Glover et al., 2008; Vrijenhoek et al., 2008). Depth has also been posited to play a significant role in determining the overall species richness of whale-fall faunas (Goffredi et al., 2004; Fujiwara et al., 2007; Braby et al., 2007).

Bennett et al. (1994) proposed a four-stage model of succession at whale-falls which was later fully developed by...
including: (1) a "necrophage" stage, where scavengers remove flesh from the whale carcass; (2) an "enrichment-opportunist" stage, characterized by aggregations of polychaetes and crustaceans attracted to the enriched sediments; (3) a "sulphophilic" stage, composed of a chemoautotrophic bacterial assemblage and organisms fed by these chemoautotrophs; and (4) a "reef" stage, inhabited by suspension feeders exploiting the remaining nutrient-depleted hard substrate. Observations on whale-fall succession patterns suggested that carcasses persist for decades, depending on the whale age and size (Smith et al., 2002; Smith and Baco, 2003; Fujiwara et al., 2007). However, data from more recent studies indicate that some of these stages may not occur at all whale-falls and that where stages do occur, they most likely overlap (Smith et al., 2002; Smith and Baco, 2003; Goffredi et al., 2004; Smith, 2006; Braby et al., 2007). It also appears that succession can advance rapidly and the ultimate decomposition of the whale carcass may be quick, particularly for skeletons of sub-adult whales which have less calcified bones and smaller lipid reservoirs (Smith et al., 2002; Smith and Baco, 2003; Fujiwara et al., 2007; Braby et al., 2007). Succession of the microbial communities in sediments underlying whale-falls has also been demonstrated and is likely due to changes in the decompositional nature of the carcass over time (Goffredi et al., 2008; Treude et al., 2009; Goffredi and Orphan, 2010).

The present analyses of one natural and five implanted whale carcasses in Monterey Canyon, CA, allowed us to demonstrate that: (1) the variation in community structure is largely attributed to depth; (2) the majority of species found at whale-falls are typical background deep-sea taxa; and (3) whale carcasses can degrade rapidly (e.g., sub-decadally). Because these whale-fall sites span a variety of depths and physical conditions within a small geographical region, they provide a unique opportunity to compare community composition and development. An earlier subset of the present data was published by Braby et al. (2007) and since that study, two additional sites and three years of observations have been included.

2. Methods

Six whale-fall sites form the basis of this study. The natural carcass was discovered at a relatively early stage of degradation; however, the exact date of its arrival at the seafloor is unknown but estimated to be six months before discovery (Goffredi et al., 2004; Schuller et al., 2004). The five implanted carcasses were whales that stranded along neighboring coastlines and were subsequently towed out to sea and sunk to depth using iron train-wheel anchors. All sites are located within the Monterey Canyon (Fig. 1). Depths range from 382 to 2893 m (Table 1), and span the oxygen minimum zone (OMZ, defined by dissolved oxygen levels ≤ 0.5 ppm; Levin, 2003). Distances from bathymetric features such as seeps and ridges differ among sites, as do other environmental factors including disturbance, currents, and carcass orientation. Additionally, the whales themselves vary in species, age, and body size. Consequently, these sites are not treated as replicates, but as individual instances of whale-fall community development.

All whale-falls were surveyed using the Monterey Bay Aquarium Research Institute's (MBARI) ROVs Tiburon, Ventana, or Doc Ricketts. These ROVs are equipped with sensors that record and log environmental parameters such as geographic location, depth, salinity, oxygen concentration, pressure, and temperature. They have a variety of sampling capabilities and multiple video cameras. Studio-quality video cameras were used to survey the whale-falls and these observations were recorded to digital videotape. Video recordings were annotated using MBARI’s Video Annotation and Reference System (VARS, Schlining and Jacobsen Stout, 2006). Within VARS, all benthic and demersal organisms were identified to the lowest possible taxon. For animals that

![Fig. 1. Map of the Monterey Bay area whale study sites. The name of each whale corresponds to the depth (in m) at which it is geographically located.](image-url)
were unknown to the authors, voucher specimens were collected using the ROV manipulator arm, suction sampler, and push cores. For unknown species that were morphologically distinct, but not sampled, and therefore not identified to species level, a ‘tag’ name was applied within the VARS database (e.g., ‘Hesionidae sp.’). For some taxa, more than one species were identified from voucher specimens but species were indistinguishable in video. For these animals, a tag name was applied (e.g., ‘Amphipoda spp.’) and they were treated as a single ecological unit in analyses. ROV surveys varied in length and detail, depending upon the mission, surface weather, and seafloor conditions, but aimed to include a complete video survey along both sides as well as the center of the carcass. Under optimal condition (lighting, angle, suspended particulate), organisms down to ~0.5 cm could be resolved using the ROV’s high definition video camera. Taxa presence/absence lists were compiled for each ROV dive at each whale-fall and these taxa presence/absence list were considered one sample and used for further analysis. This method is appropriate for mega fauna, but cannot be used to assess micro- and infauna. Due to these sampling capability limitations, many of the species captured in previous whale-fall studies (i.e., macrofaunal polychaetes) are not represented in this work.

Samples-based species accumulation curves were calculated from presence/absence data using ESTIMATES (Colwell, 2009). The PRIMER software package (v6, Clarke and Gorley, 2001) was used to calculate the maximum potential value of Shannon Diversity, \( H_{\text{max}} \) (i.e., with perfect evenness) and these were compared using analysis of variance (ANOVA). PRIMER was also used for the following analyses on faunal composition: multidimensional scaling (MDS) plots and principal component analysis (PCA). For MDS plots, similarity matrices of Bray–Curtis coefficients were constructed. A combination of similarity matrices and Euclidian distances for normalized temperature, depth, and oxygen concentration data from each whale were used for PCA. Taxa were classified by habitat affinity including background fauna, bone specialist, vent specialist, and unknown fauna in an effort to determine the relative contribution of each category to total species richness. Here we define background fauna as organisms that have been observed and catalogued using MBARI’s VARS database from other habitats where MBARI has conducted research. The VARS database contains more than 4,000,000 observations.

Still image mosaics were created using Photo-Mosaic (Pizarro and Singh, 2003; Singh et al., 2004) and used to visualize changes in the whale carcasses over time. Mosaics were created using HD video frame grabs (1920 \( \times \) 1080) or Nikon Coolpix 990 digital still images (2048 \( \times \) 1536). Images were collected by carefully “flying” the ROV oriented perpendicular to the whale carcass along a parallel path using obliquely mounted video and still image cameras. Images were gathered such that each had 50% overlap with the next image in line, and stitched and blended using Photo-Mosaic in MatLab.

### 3. Results

#### 3.1. Physical characteristics

The physical data revealed differences in water column characteristics among sites (Table 1). Salinity was similar at all sites, increasing slightly from 34.05 to 34.53 ppm with the increase in depth. Temperature decreased from 7.15 °C at the shallowest sites, to 1.67 °C at the deepest. Data also revealed the presence of an oxygen minimum zone (OMZ), particularly at whales 633 and 1018. O2 concentrations reached a low of 0.476 ml L\(^{-1}\) at whale-1018 and a maximum of 2.426 ml L\(^{-1}\) at whale-2893.

### 3.2. Community similarity and diversity

Samples-based species accumulation curves (Fig. 2A) showed similarity (i.e., similar trajectories) between whale-fall communities. None of the curves appears to have reached asymptote. Analysis of variance of \( H_{\text{max}} \) (Appendix G) at each whale show a significant difference in diversity between sites (\( F(5, 51) = 9.514, \ p = <0.001 \); Fig. 2B).

An MDS plot of the Bray–Curtis similarities between samples (Fig. 3A) produced three major groupings with a 2D stress value of 0.17. The shallower sites (whales 382a, 382p, and 633) were pooled, showing resemblance of 

### Table 1

| Whale-fall characteristics by site, adapted from Braby et al. (2007). |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| Whale site      | Whale 382p      | Whale 382a      | Whale 633       | Whale 1018      | Whale 1820      | Whale 2893      |
| Depth (m)       | 382             | 382             | 633             | 1018            | 1820            | 2893            |
| Latitude        | 36.790N         | 36.790N         | 36.802N         | 36.772N         | 36.708N         | 36.613N         |
| Longitude       | −121.887 W      | −121.887 W      | −121.994 W      | −122.083 W      | −122.105 W      | −122.434 W      |
| Implant/Natural | Implanted       | Implanted       | Implanted       | Implanted       | Implanted       | Natural         |
| Carcass length (m) | 6              | 8               | 10              | 17              | 10              | 10              |
| Whale species   | Gray            | Gray            | Gray            | Blue            | Gray            | Gray            |
| Avg. salinity (ppm) | 34.05          | 34.18           | 34.24           | 34.44           | 34.42           | 34.53           |
| Avg. temperature (°C) | 7.15           | 7.11            | 5.52            | 3.86            | 2.30            | 1.67            |
| Avg. O2 (ml/L)  | 0.992           | 0.951           | 0.568           | 0.476           | 1.423           | 2.426           |
| Deployment date | 7 Feb., 2007    | 10 April, 2005  | 11 April, 2007  | 5 Oct., 2004    | 23 May, 2006    | Unknown         |
| Number of visits | 3              | 13              | 5               | 16              | 6               | 15              |
| Cumulative species richness (approx) | 36 | 66 | 57 | 68 | 72 | 90 |
| Months at bottom | 10             | 28              | 27              | 53              | 36              | 85              |

\* Underestimates species richness, because some identifications are not to species level.
3.3. Habitat affinity

Species habitat affinity showed that at all sites and times species richness was predominantly made up from background deep-sea fauna, with few exceptions (Fig. 4; 1820 M-2, 2893 M-85). Because many new species have been or are being described from specimens collected during these surveys, habitat affinities for some species are unknown; however, many of these organisms may not be restricted to whale-falls. Therefore, this analysis is most likely conservative. Bone specialists were abundant and included many \( n=16 \) species of *Osedax* as well as two bone-eating provannid gastropods (Johnson et al., in press). Seep associated species were observed infrequently at all sites. A vesicomyid clam was observed at the 2893 m site and dense populations of a bacterial mat-grazing dorvilleid species were observed at the 1820 m site.

3.4. Community characterizations

3.4.1. Whale-382a

This was an 8-m long gray whale implanted April 10, 2005 at a depth of 382 m. High disturbance and turbidity due to recurrent sediment flows are common at this site (Table 1). The carcass was surveyed 13 times during 28 months. It is the only one of the three shallowest sites visited earlier than four months post-deployment, allowing the flesh-removal stage to be directly
observed. Initial scavengers (at one month post-deployment) were thick swarms of amphipods in higher densities than observed at the whale-382p site, as well as an abundance of hagfish (*Eptatretus stoutii*), and a sleeper shark (*Somniosus pacificus*). At three months post-deployment, all flesh was gone and the numbers of amphipods and hagfish were greatly reduced. Over the next two years, diversity generally increased to a community predominantly composed of bone-eating *Osedax* worms, anemones, the fragile urchin, *Allocentrotus fragilis* (Fig. 5A&B), and *Rathbunaster californicus* (Fig. 5B). A surge of decapods and rockfish occurred during months 19 and 20. A total of 66 different taxa were observed.

### 3.4.2. Whale-382p

This 6-m long gray whale implanted during February 2007, at a depth of 382 m just 50 m from whale-382a, was the most recent of the Monterey whale-falls. It was also the smallest carcass, apparently from a stillborn or recently killed calf. We conducted three surveys over a 10-month period. All flesh on the carcass was gone when the site was first monitored at four months post-deployment. Amphipods and the sablefish, *Anoplopoma fimbria*, dominated initially. By 10 months, the site shifted to a community composed mainly of the siboglinid polychaete, *Osedax* ‘yellow collar’ (Vrijenhoek et al., 2009), growing on exposed bone surfaces. Three species of anthozoans and an echinoid, * Allocentrotus fragilis*, were observed on the bones as were two species of decapods. A total of 36 taxa were observed.

### 3.4.3. Whale-633

This 10-m long gray whale was implanted during April 2007 at a depth of 633 m in an area of relatively low oxygen concentration ($\text{mean} = 0.568 \text{ mL/L}$). All flesh had been removed by the first monitoring visit at four months post-deployment. We visited the site five times during 26 months. Initial observation revealed a wider variety of taxa than seen at the shallower sites. At four months post-deployment, extremely dense populations of amphipods (Fig. 5C) were present along with nine taxa of bony fishes, including *Anoplopoma fimbria* (present in greater numbers than at the shallower whales), *Merluccius productus*, and *Sebastes diploproa*. Hagfishes were present, although in low numbers, and provannid

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*Fig. 3.* (A) MDS plot of Bray–Curtis similarity indices using presence/absence data show clustering of samples by whale site, indicating depth related similarity. Stress is acceptable at 0.17. (B) Principal component analysis (PCA) relating three measured environmental factors on samples collected at each site. PC1 correlates most strongly with depth and temperature.
gastropods were common. In subsequent visits, the fish species shifted to more sedentary families (primarily Zoarcidae), and a variety of sessile and mobile invertebrates appeared, including actiniarians, asteroids, and holothurians. An increase in gastropods was also recorded. Osedax showed a species shift with *O. ‘orange collar’* being present initially, but replaced five months after
Fig. 5. Megafauna at whale-falls. The number in parentheses for each image refers to the ROV platform and dive number, i.e. T993 would be ROV Tiburon dive 993; the second number refers to months on bottom or months since initial visit for whale-2893. (A) Whale-382a: Fragile urchin, Allocentrotus fragilis (T993; 9). (B) Whale-382a: Fragile urchins, Allocentrotus fragilis, Rathbunaster californicus and drift kelp on whale bones (T933; 13). (C) Whale-633: Swarms of pink and yellow amphipods (T1120; 4). (D) Whale-1018: Pandalus tanneri feeding on whale tissue and dense Osedax sp. on whale bone. (T776; 3). (E) Whale-1018: Dover sole, Microstomus pacificus (T916; 13). (F) Whale-1820: Blob sculpin, Psychrolutes phrictus and soubhose eelpout, Pachycara bulkeps (T990; 2). (G) Whale-1820: Dense Osedax sp. on whale vertebrae, dense ophiuroids, and Pannychia moseleyi. (T1048; 7). (H) Whale-2893: New species of Osedax sp. and chaetopterid worms in sediment near whale carcass (T769; 34). (I) Whale-2893: Galatheid crabs, Munidopsis spp. (T742; 31). (J) Whale-2893: Scotoplanes globosa, bacterial mat, Amage cf. arieticornuta, and a new species of Spionidae (T406; 1). (K) Whale-2893: High densities of Scotoplanes globosa and Glyphanostomum sp. (T391; 0). (L) Whale-2893: Anthosactis pearseae, Osedax frankpressi, Munidopsis spp., collected with a piece of whale bone (T742; 31). (M) Whale-2893: Pycnogonid, Colossendeis gigas, feeding upon Liponema brevicornis tentacles (T391; 0). (N) Whale-2893: Liponema brevicornis and lithodid crab (T610; 18). (O) Whale-2893: Hesionid worm, Vrijenhoekia balaenophila, with abundant Osedax frankpressi (T610; 18).
deployment by dense populations of *O. roseus*. Dense populations of marine leaches (Hirudinea) were also observed throughout. A total of 57 taxa were observed.

3.4.4. Whale-1018

This 17-m long blue whale was implanted during October 2004 at a depth of 1018 m in an area with the lowest oxygen concentration for this study (mean = 0.476 ml/L). The head of this carcass had been removed for anatomical studies prior to our deployment. The carcass lies in a horseshoe-shaped orientation, and is located near a steep submarine canyon wall. Flesh was still present at three month post-deployment. Flesh consumers included hakfug, amphipods, and tanner crabs, *Chionoecetes tanneri* (Fig. 5D). All three taxa remained present although in slowly decreasing numbers until approximately 15 months post-deployment. These species were joined by *O. roseus* and relatively low numbers of amphipods by month three, when bone surfaces had become exposed. A dense bacterial mat, not observed at the shallower sites, developed on the sediment inside the U-shape. The total area covered by the bacterial mat peaked between months three and 19. This site exhibited its highest taxa-diverse period between months nine and 19, eventually leading to a low-diversity community of mobile scavengers. Through time, the bacterial mat became exposed. A dense bacterial mat, not observed at the shallower sites, developed on the sediment inside the U-shape. The total area covered by the bacterial mat peaked between months three and 19. This site exhibited its highest taxa-diverse period between months nine and 19, eventually leading to a low-diversity community of mobile scavengers. Through time, the bacterial mat became exposed. A dense bacterial mat, not observed at the shallower sites, developed on the sediment inside the U-shape.

3.4.5. Whale-2893

This naturally occurring carcass was discovered nearly three years prior to deployment of whale-1018, the first implanted carcass. The exact date of its arrival on the seafloor is unknown, but is estimated as roughly six months prior to discovery, based on the amount of flesh remaining and 210Pb/226Ra disequilibria (Goffredi et al., 2004; Schuller et al., 2004). Most of the flesh except for intestines and dense connective tissues were removed when it was found, so the earliest stages of degradation are not reflected in the data set. The intestinal remains disappeared eight months later. Species richness was elevated from the outset with exceptionally high annelid diversity and abundance. Initial taxa included *Osedax rubiplumis*, *O. frankpressi*, and *O. ‘spiral’* (Fig. 5H, Table 2), ampharetids (*Glymphastonomus* sp.), *Phylochaetopterus* sp., and dense populations of a new species of spinoid. Decapods, including two species of *Munidopsis* (Fig. 5I) and the lithodid crab, *Paralomis multispinosa*, were also abundant. A thick bacterial mat was observed near the whale’s abdominal region (Fig. 5J). Dense aggregations of the holothurian, *Scotoplanes globosa* (Fig. 5K), were noted until eight months post-discovery. This site exhibited the highest overall species richness, with 90 taxa observed over the course of 15 visits during 85 months.

At 18 months post-discovery, a variety of anthozoans appeared, succeeded by an increase in echinoderms after 45 months. Gastropod richness also increased, consisting primarily of three species of abundant spinoid gastropods. Ruby spira, *Paralomis multispinosa*, and *Munidopsis* spp. survived for numerous generations, demonstrated by the accumulation of carcasses and empty shells over time. Many observed taxa were not noted at the other Monterey whale-falls, including a newly described anemone, *Anthosactis pearseae* (Fig. 5L; Daly and Gusmão, 2007), pycnogonids, Ruby spira spp., sea pens and several species of *Munidopsis*. Two species of pycnogonids, *Colossendeis gigas* (Fig. 5M) and *C. japonica*, were observed at this site feeding on *Liponema brevicornis* (Fig. 5M and N) anemones that had collected around the whale bones as well as *A. pearseae* living attached to the bones (Braby et al., 2009). Fish diversity remained low throughout the duration of this study.

The carcass itself was highly degraded after two years with the exception of the baleen, which remained relatively intact. The skull was the slowest to degrade and the most species rich region of the whale-fall. When monitored 70 months post-discovery, only a small, highly degraded remnant of the skull remained. At this time, the site was still colonized by a diverse group of polychaetes (Fig. 5O), decapods, echinoderms, holothurians, and *Osedax* spp. that were living on the remnant bone fragments.

**Photo-mosaics**—High-resolution photo-mosaic images of whale-2893 illustrate the rapidity of whale carcass degradation (Fig. 6). A relatively intact skeleton and flesh is present at discovery (Fig. 6A); 34 months later (2.5 years) the carcass is already highly degraded with the bones becoming partially buried in sediment (Fig. 6B). By 45 months, the carcass is almost unrecognizable as a whale (Fig. 6C) and by 70 months post-discovery (almost six years) there are only a few remnants of bone and baleen (Fig. 6D). At 82 months, very little evidence of the sunken whale remains (Fig. 6E). Still images from the skull region of each whale-fall show similar trajectories of degradation at the time of the last survey for each site (Fig. 7).

4. Discussion

This study reveals that time and depth related faunal changes work together to facilitate the decomposition of whale carcasses on the seafloor. On arrival at the seafloor, carcasses host a relatively low-diversity community of mobile scavengers. Through time,
diversity increases, however, most of the increases in species richness come from background taxa that are merely exploiting the abundant nutrients provided by the whale carcass.

In addition to temporal changes, the whale-fall communities also differed according to water depth. We hypothesize that the differences among these whale-fall communities were constrained by the physical conditions at each depth as evidenced by ANOVA of $H_{\text{max}}$ (Fig. 2B), MDS, and PCA (Fig. 3A, B). The correlations of temperature and oxygen concentrations with depth appear to be primary factors and are well known to affect species presence and distribution in other benthic environments (Levin and Gage, 1998; Nilsson and Rosenberg, 2000). Oxygen minimum zones, characterized by $<0.5$ ml/L of O$_2$ tend to be associated with lower species diversity in the deep sea (Levin and Atkinson, 2003), but it remains unclear whether these trends can be extended to whale-falls implanted in Monterey Canyon (i.e., whales 633 and 1018; Braby et al., 2007). The longevity of the southern California whale carcasses reviewed in Smith (2006) may be due primarily to those carcasses being located within an anoxic basin. Recent studies have shown that deep-sea canyon systems may be areas with elevated diversity at both large and small spatial scales due to a variety of co-occurring processes (Vetter et al., 2010; De Leo et al., 2010; McClain and Barry, 2010). Vetter and Dayton (1998) link species diversity to reduced disturbance by currents, sedimentation, and organic enrichment, factors that typically decrease with increasing depth. Frequent disturbance is evident at whales 382a, 382p, and 633, which are located near the head of the Monterey Canyon, an area associated with high sediment deposition rates and frequent turbidity flows (Paull et al., 2003, 2005). Species richness in this study increased with depth, as observed by Braby et al. (2007), correlating with an apparent decrease in overall disturbance at the deeper sites.

Most of the taxa observed at these whale-falls are common deep-sea inhabitants of Monterey Canyon, nearby seamounts, and the continental slope (Figs. 4 and 5). We did not assess biomass or species abundance in this survey, but anecdotal information about the relative abundance of many species were noted here (Table 2; Appendices A–F) and in previous studies (Goffredi et al., 2004; Braby et al., 2007). Some of the most abundant organisms appeared to be specialists, including the bone-eating Osedax worms and Rubyspira gastropods (Johnson et al., in preparation). Some undescribed species (i.e., Spionidae at whale-2893) with unknown habitat affinities were also abundant. Many of the flesh-removing fishes were abundant, particularly hagfish, at depths shallower than 1018 m. Several species of amphipods were also abundant, although they could not be identified below the order level in video. Initial morphological assessments from collected amphipod specimens suggest the presence of a diverse amphipod assemblage with members of the orders and families Lysianassoidea, Melitidae, Alicellidae, and Ischyroceridae. Preliminary analyses of DNA

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sequence data from the nuclear coding gene Histone-3 (H3) suggests that the lyssianassids are restricted to the shallower sites (whales 382a/p and 633). Gammarideans, however, were found throughout the whole depth range of this study. These initial results have prompted a more detailed ecological and taxonomic study of the amphipods which is currently in progress (J. Harvey, MBARI).

We observed rapid (sub-decadal) degradation at both the shallow and the deep sites in contrast to earlier studies which suggested that heavily calcified adult whale carcasses may last for many decades. Our analysis agrees with earlier studies which suggested that the poorly calcified and relatively small lipid reserves of juvenile whales may degrade rapidly (Smith and Baco, 2003). Photo-mosaic and individual still images (Figs. 6 and 7) visually demonstrate the rapidity at which these Monterey Canyon whale-falls degrade. The deeper sites (whales 1018, 1820, and 2893) have degraded in a similar fashion and timescale. The shallower sites (whales 382a, 382p, and 633) have also degraded quickly, but these sites are subject to much more disturbance than the deeper sites. These carcasses are often partially buried in sediments, re-exposed, and partially buried again. The dynamic nature of canyon processes at these shallower sites might obscure the degradation processes, e.g., by burying carcasses (Paull et al., 2003; Paull et al., 2005; De Leo et al., 2010; McClain and Barry, 2010).

Evidence of four successional stages is lacking at these whale-falls. There clearly existed a necrophage stage, where flesh was removed by large (hagfish, sharks) and small (amphipods, crabs, and polychaetes) carrion feeders. This initial stage was followed by a multi-trophic community of mainly “enrichment/opportunists” (Smith and Baco, 2003); however, there is a great deal of overlap between these initial stages. Any evidence of a “sulphophilic” stage was short-lived at shallower depths, if it took place at all. At the 1018 m and 1820 m sites, a “sulphophilic” stage was more evident by the presence of a thick bacterial mats and elevated levels of sulfide (Goffredi et al., 2008). Bone specialists also increased at these sites during later stages of sampling (Fig. 4). At whale-2893, dense mats of methane-oxidizing bacteria were initially visible (Fig. 5). However, a sulfur-reducing bacterial community was not observed and very low levels of sulfide were detected (Goffredi et al., 2008). The presence of a “reef stage” consisting of suspension and filter feeders was not supported. Suspension feeding corals and sponges were observed at the deeper whales (i.e., Farrea, Asbestopluma, Bathypathes); however, these organisms appeared to have drifted down from nearby canyon walls and appeared to be dead or dying. Living mobile (Liponema brevicornis) and sessile (Hormathiidae) suspension feeders were observed in low abundance. However, based on the rate of degradation of these carcasses, a reef stage will never occur because the bones are so rapidly broken down. Ultimately, the nutrient-driven opportunist stage may actually outlast any structurally dependant stage. The longest-lasting feature of all the whale-falls was the head, characterized by large, lipid-rich bones that were slow to be colonized by Osedax and took the most time to degrade. Further monitoring of all sites may reveal additional changes in community structure; however, it appears highly unlikely that any trace of the whale carcasses will remain even a decade after deployment (Figs. 6 and 7). Smith and Baco (2003) first demonstrated truncated and overlapping successional stages, suggesting that the age of the whale at death and, therefore, the calcification of bone and lipid reservoir contained within it, might ultimately control the longevity of each stage.

Much of the motivation for this study derived from our interests in the extraordinary diversity of Osedax bone worms (Rouse et al., 2004, 2009; Vrijenhoek et al., 2009). Since initial discovery of the genus in 2002 at whale-2893, we have identified 15 species of Osedax on the bones deployed in Monterey Canyon. Relative abundance of Osedax species and bone-eating provannid
Osedax species were observed most clearly at whale-2893. *Osedax rubiplumus* was the first worm to occur in high abundance, but it was largely replaced during the next year by *O. frankpressi*. *O. 'spiral'* appeared later on baleen-laden sediments near the head region. It uses long sinuous roots to devour shards of bone buried in anaerobic sediments. Early colonization by *O. rubiplumus* and subsequent recruitment of *O. frankpressi* also occurred at whale-1820, but *O. 'spiral'* have not been observed there. Instead, we found abundant *O. roseus* co-occurring with *O. rubiplumus* at this site. *O. roseus* occurred abundantly in the early stages of whale-1018, where successional changes in *Osedax* species were also evident. *Osedax* species diversity appears to be higher at the deeper whale-falls, but the mid-depth whale-1018 is the most species-rich, with seven species. Sub-decadal degradation of these whale skeletons appears to be largely driven by *Osedax*, which excavate the lipid-rich bones with proliferative root-like structures that host heterotrophic bacterial endosymbionts (Goffredi et al., 2004; Rouse et al., 2004). In this sense, *Osedax* should be considered a foundation species that controls whale-fall community structure and longevity.

Two new species of bone-eating provannid gastropods have been described from these whale-falls (Johnson et al., in press). Like *Osedax* they may require bacterial symbionts to facilitate bone-decomposition. A new anemone (*Anthosactis pearseae*), a hesionid polychaete (*Vrijenhoekia balaenophila*), and three galatheid crabs (*Munidopsis bracteosa*, *M. albatrossae* and *M. cascadia*) have also been described from the 2893 m site (Daly and Gusmão, 2007; Jones and Macpherson, 2007; Pleijel et al., 2008). Species descriptions are pending for two more species of provannid gastropods, several new dorvellids, two additional species of *Vrijenhoekia*, a maldanid, a spionid, a new limpet, a new buccinid gastropod and a diversity of amphipods (Goffredi et al., 2004; Rouse, Scripps Inst. Oceanogr., La Jolla, CA, pers comm.). Future studies will include new species descriptions, life history studies, and attempts to reveal the dispersal mechanisms of the specialized organisms, like *Osedax* and the newly discovered provannids that depend on these tiny habitat islands. As these sites progress into their final stages of degradation, they will continue to reveal new insights into life and death on the deep seafloor.

**Acknowledgements**

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2010.09.003.

References


