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Unusual benthic fauna associated with a whale fall in Monterey Canyon, California

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Abstract

On February 6, 2002, we discovered an unusual assemblage of deep-sea animals associated with a well-preserved carcass of a gray whale (*Eschrichtius robustus*) at 2891 m depth in the axis of Monterey Canyon, California. The 9–10 m long carcass was found approximately 31 km off shore, where it settled to the bottom against the northern wall of the canyon's sedimented floor. This carcass delivered approximately 20,000 kg of organic material to a typically food-limited seafloor. Particularly noteworthy were the low occurrence of large mobile scavengers, the large number of opportunistic deep-sea species, and an abundance of unusual polychaetes. Two of these polychaetes, a spionid and a siboglinid, are new to science. Since this discovery, we visited the whale fall on two subsequent occasions (March and October 2002) to document faunal community changes in one of the deepest large food falls known to date.

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1. Introduction

Most deep-sea communities are limited by low food availability (Gage and Tyler, 1991). Even in highly productive surface waters, such as those found in Monterey Bay, California, deep-sea animals are generally adapted to a relatively low supply of carbon. Some deep-sea animals, how-

ever, can alter their metabolism, growth rate, feeding behavior, and reproduction to exploit episodic pulses of organic enrichment, such as animal carcasses, plant debris, and wood, as well as dissolved and particulate matter (Gage and Tyler, 1991; Levin, 2000). Decomposing whale carcasses, for example, deliver large pulses of organic material to the seafloor and serve as habitat islands for unique assemblages of deep-sea macrofauna (Brunn, 1957; Smith and Baco, 2003). Varying in time and space, these discrete resource patches are thought to contribute to habitat complexity and increase biodiversity in deep-sea

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environments (Grassle and Morse-Porteous, 1987; Butman et al., 1995b; Baco and Smith, 2003).

Based on the number of whale falls discovered during the past several decades of deep-sea exploration, these habitat islands may occur relatively frequently in time and space, especially along migration corridors for at least eight large whale species in the northeast Pacific. Smith et al. (1989) have estimated that hundreds of gray whales sink to the seafloor annually within an area of $8 \times 10^5 \text{ km}^2$ that includes Monterey Bay, California. If so, organic enrichment due to whale falls may play a significant role in regulating animal abundance and diversity in deep regions like Monterey Canyon. This includes enrichment of typical deep-sea animals such as holothuroids and ophiuroids, the occurrence of opportunistic polychaetes and crustaceans, as well as specific whale fall specialists.

Observations of natural and implanted whale falls along the California margin suggests that community succession typically progresses through three stages (Smith and Baco, 2003). (1) The mobile scavenger stage, comprised of about 40 species (mostly fish and crustaceans), removes more than 90% of the soft tissue, usually within 4 months after arrival on the seafloor depending on the size of the carcass. (2) The enrichment-opportunistic stage, comprised of about 20 species (mostly polychaetes and crustaceans), may last as long as 2 years. Finally, (3) the sulfophilic stage, which relies on the coupling between decomposition of bone lipids and seawater sulfate reduction and is dominated by microbial mats and more than 100 invertebrate species (including sulfide-tolerant and sulfide-dependent molluscs), may last for years and even decades depending on the size of the whale.

This paper describes a whale fall community found at 2891 m depth in the axis of Monterey Canyon, California. It is one of the deepest whale falls discovered to date, and, thus, provides a unique opportunity to study localized effects of organic enrichment at depths that exclude many of the large mobile scavengers found at shallower whale falls. We describe changes, including loss of soft tissue from the carcass, development of large microbial mats, and differences in polychaete

species composition, including two that we believe to be new to science, observed during three separate visits (at 0, 1, and 8 months after discovery). In addition, by mapping marine mammal remains discovered in Monterey Canyon we suggest that deposition occurs primarily within material transport conduits, thereby potentially affecting the diversity and structure of benthic communities in the axes of canyons like those off of Monterey, California. A long-term program has been established to monitor the fate of this large organic input to the benthic community.

2. Materials and methods

Canyon exploration, sample collection, and video surveillance were accomplished using the remotely operated vehicle (ROV) *Tiburón*, developed at the Monterey Bay Aquarium Research Institute. *Tiburón* is equipped with HMI (metallogen metal halide arc lamp) lighting, a suite of sensors to measure conductivity (salinity), temperature, depth, and oxygen (CTDO—approximately 2 m above the seafloor), and imaging sonar. The camera from which all video recordings were made was a high-resolution color digital camera (three chip Panasonic WVE550). Digital still images were taken from the *Tiburón* using a Coolpix 990 camera (Nikon) and a SB28 strobe light (Insight Tritech). Abundance estimates for *Scotoplanes* sp. and bacterial mat coverage areas were determined via seabed photographs taken with the *Tiburón* using a Coolpix camera. Approximately 16 h of video from ROV bottom-time was recorded, annotated, and analyzed from dives T391 (February 6, 2002), T406 (March 10, 2002), and T486 (October 9, 2002). Occurrences of all discernible animals were entered into a searchable database with corresponding environmental data from the CTDO sensors and observational (time, position) data. An acoustic homer beacon was placed near the whale skull to facilitate relocation and subsequent monitoring of the site.

Sediment push cores, bone samples, and animal specimens were collected with the manipulator arm of the *Tiburón*. On board the support vessel, tissue samples were dissected from specimens and

either frozen at -70°C or preserved in 95% ethanol, 10% formalin, or 2% cacodylate-buffered glutaraldehyde. Animal identifications were accomplished via either morphological or molecular characterizations. Morphological identifications, from both collections and video only, were made directly by the authors or through communications with taxonomic experts including G. Rouse (South Australian Museum), E. Southward (Marine Biological Association of the UK), J. Drazen (Monterey Bay Aquarium Research Institute), and the staff of the Monterey Bay Aquarium Research Institute video annotation lab. Voucher specimens of putative new species will be held at the Monterey Bay Aquarium Research Institute pending formal taxonomic descriptions.

Identification of the whale was determined via baleen structure and DNA sequencing of the mitochondrial control region. Preliminary classification of the two dominant polychaetes (annelid A (siboglinid) and annelid B (spionid)) was based on ribosomal 18S DNA sequences. The DNEASY kit (Qiagen) was used to extract total DNA from frozen or alcohol-preserved tissues, following the manufacturer's protocol. For the whale tissues, a 320 base pair fragment of the whale mitochondrial control region was amplified with primers TRO (5'-CCT CCC TAA GAC TCA AGG AAG-3') and D (5'-CCT GAA GTA AGA ACC AGA TG-3') (Arnason et al., 1993) using *Taq* polymerase (Promega) and the following polymerase chain reaction (PCR) protocol: initial denaturation at 94°C for 5 min; 35 cycles of (94°C for 1 min, 55°C for 1 min, and 72°C for 2 min); and a final extension at 72°C for 7 min. For the two dominant polychaetes (annelids A and B), a 1290 base pair fragment of the 18S region was amplified using the primers 18e and 18P and published PCR conditions (Halanych et al., 1998). Amplification products were purified using gel extraction following the manufacturer's protocol (Millipore Ultra DA-free columns). DNA sequencing was conducted with an ABI 3100 capillary sequencer (Perkin-Elmer/Applied Biosystems). Sequencing reactions were carried out according to the manufacturer's recommended protocols. Additional internal primers (18L and 18Q_∅) were used to sequence the entire 1290 base pair fragment of

the 18S region (Halanych et al., 1998). Sequences were aligned and proofread using Sequencher v 4.1 (Gene Codes Corp.). All phylogenetic comparisons were performed with PAUP*4.0b10 (Swofford, 1998). Sequence similarities (based on Kimura 2 parameter distances; Kimura, 1980) and supporting bootstrap values (based on maximum parsimony and NJ analyses) are reported in the text.

3. Results

3.1. Site description

The whale fall described here was discovered during *Tiburón* dive T391 on February 6, 2002. The skeleton was situated at 2891 m depth in the axis of Monterey Canyon at $36^{\circ}36.8'\text{N}/122^{\circ}26.0'\text{W}$ (star; Fig. 1). The surrounding floor of the canyon was composed of fine-grained clastic sediments. Trash (mostly plastic bags and trays), coastal macroalgae, and sea grass were observed near the fall, suggesting that this is an area of active sediment movement and deposition. Bottom water oxygen concentrations near the fall measured $97\text{--}110\ \mu\text{mol l}^{-1}$, at a depth that is far below the O_2 minimum zone in that area (700–800 m depth). Bottom temperatures were between 1.65°C and 1.69°C near the whale on all three dives. A limited number of bone, sediment, and animal samples were collected on all three dives, primarily to minimize disturbance for subsequent time course observations.

3.2. Whale description

The whale was identified as a gray whale (*Eschrichtius robustus*), based upon diagnostic baleen structure (short and rigid baleen with thick inner bristles) and confirmed by 99% DNA sequence similarity of the mitochondrial control region to known gray whales and only 81–89% similarity to six other extant baleen species known to inhabit Monterey Bay (Arnason et al., 1993). The whale measured approximately 9–10 m in length (determined via comparison to objects of known size and sonar readings). Because gray

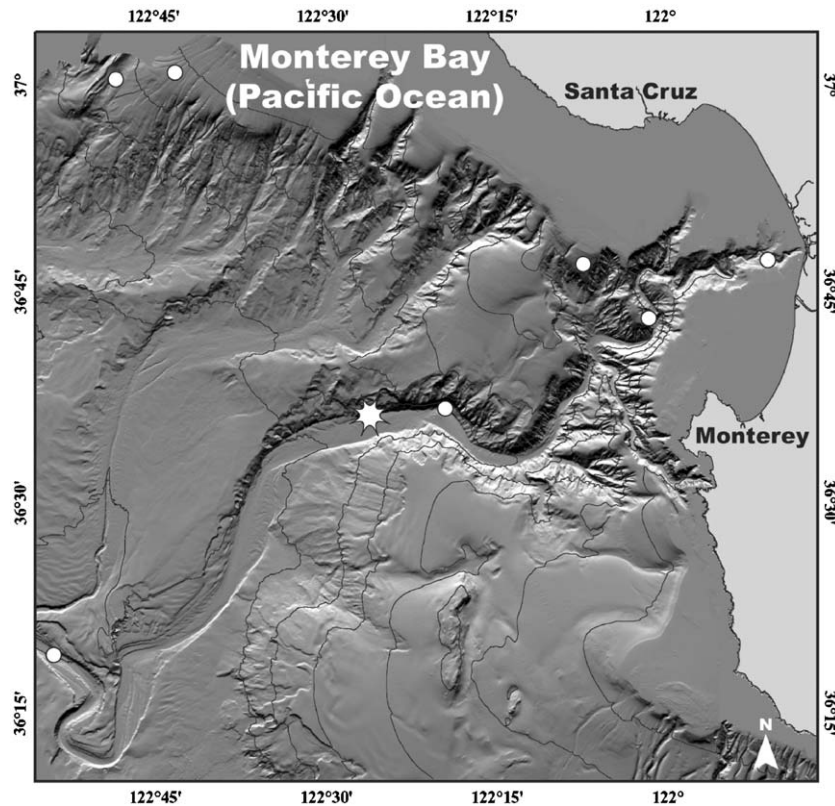


Fig. 1. Shaded relief map of the continental margin off Monterey Bay showing the whale fall location at 2891 m depth (large white star). Remains of seven other marine mammals are also shown (small white circles). Contour lines are 500 m depth intervals.

whales reach sexual maturity at 11–12 m in length this specimen was assumed to be a juvenile (Leatherwood et al., 1982). Based on weight to length correlations for gray whales, the biomass of the whale was assumed to be 20,000 kg (Leatherwood et al., 1982; Reeves et al., 2002). This animal presumably died during the 18,000 km round trip gray whale migration from the food-rich arctic Bering and Chukchi seas to the breeding grounds of Baja California, Mexico.

3.3. Whale fall community at time 1 (February 6, 2002)

Upon initial discovery, the remains of the whale included flesh, intestines, and baleen, suggesting relatively recent arrival on the seafloor (Figs. 2A–C). The skeleton was intact, with many of the bones still fused and only the tail vertebrae,

jawbones, and ribs exposed. Collections included one caudal vertebra and small pieces of baleen, flesh, and intestines with associated fauna. Bone and tissue surfaces were covered by a variety of organisms, including cnidarians, polychaetes, sipunculids, crustaceans, and echinoderms (Table 1). Filamentous bacterial mat was developing near the skull (area = $\sim 1 \text{ m}^2$), presumably facilitated by sulfide produced from microbial decay of lipids.

By far, the dominant animals associated with the whale fall were two unusual polychaetes (Figs. 2–3). Annelid A had a red plume, a dark green posterior brood sac, and no mouth or gut (Figs. 2A–B, 3A–D). Based on ribosomal 18S sequences (GenBank accession #AY240927) this worm is closely related to the Siboglinidae, a group including vestimentiferans and pogonophorans, which also lack digestive tracts as adults.

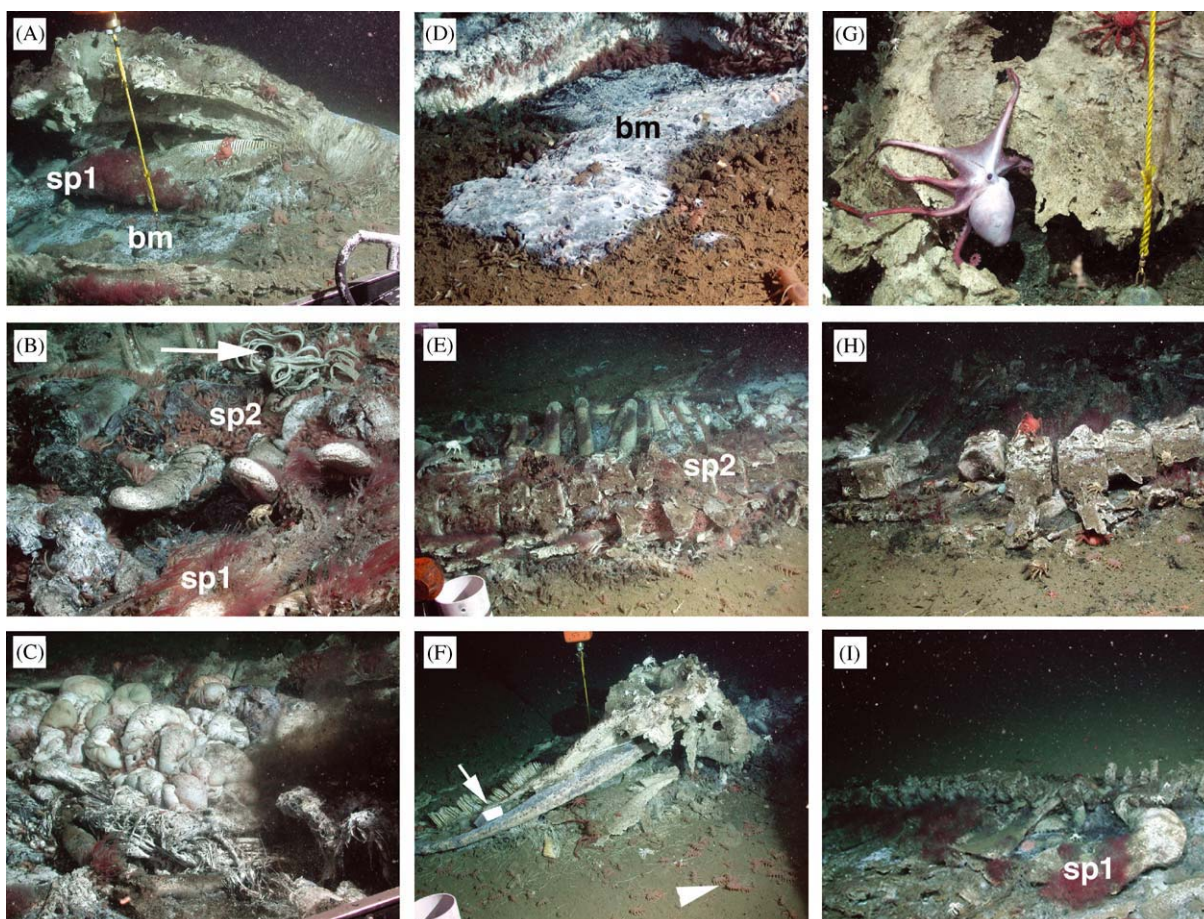


Fig. 2. Digital still images of the Monterey whale fall community: panels A–C at time 1 (dive # T391, February 6, 2002); panels D–F at time 2 (dive # T406, March 10, 2002); and panels G–I at time 3 (dive # T486, October 9, 2002). (A) Skull showing bacterial mat (bm), and abundant annelid A (sp1), along with the yellow cord of the homer beacon. (B) Rib bones, with abundant annelids A and B (sp2), along with whale tracheal rings (arrow). (C) Inflated intestines. (D) Thick bacterial mat along the right side of the carcass. (E) Mid-section of the carcass showing exposed bones and abundant annelid B. (F) Skull showing dense assemblages of *S. clarki* (arrowhead) and pieces of trash (short arrow) with homer beacon in the distance. (G) Skull with resident octopus (probably *Graneledone* sp.). (H) Mid-tail section of carcass showing highly degraded bones. (I) Thoracic section of carcass showing dominance of annelid A.

Phylogenetic analyses revealed that annelid A occupies a basal position among members of this family (parsimony and neighbor-joining bootstrap values of 89 and 91, respectively) with only 85–88% 18S rDNA sequence similarity to other siboglinid genera including the frenulates *Siboglinum* and *Spirobrachia*, the monoliferan *Sclerolinum*, and the vestimentiferans *Ridgeia* and *Lamellibrachia*. The 12–15% difference between annelid A and other members of the group provides good support for the novelty of this

polychaete species (Halanych et al., 2001). Morphological criteria support this conclusion and a formal identification, including a full taxonomic and morphological description is in progress (G. Rouse, South Australian Museum, pers. comm.).

The second dominant species, annelid B, was pink in color, had numerous modified parapodia, and a pair of long palps (Figs. 2B/E and 3F). Phylogenetic analyses of ribosomal 18S sequences revealed that annelid B (GenBank accession

Table 1
Animal taxa associated with the Monterey Canyon whale fall

Cnidaria	Nemertea
Anthozoa	Unidentified, 1 sp.
Unidentified, 1 sp.	
<i>Liponema brevicornis</i> ^a	
Scyphozoa	Mollusca
<i>Benthocodon</i> sp. ^a	Cephalopoda
	<i>Graneledone</i> sp. ^a
Annelida	Arthropoda
Polychaeta	Malacostraca
Siboglinidae, 1 sp.	Galatheidae, 1 sp.
(annelid A)	<i>Munidopsis</i> sp.
Spionidae, 2 spp.	<i>Paralomis verrilli</i> ^a
(inc. annelid B)	Lysianassidae, 1 sp.
Ampharetidae, 3 spp.	
Polynoidae, 2 spp.	Echinodermata
Chaetopteridae, 1 sp.	Holothuroidea
Hesionidae, 1 sp.	<i>Scotoplanes</i> sp.
Dorvilleidae, 1 sp.	<i>Paelopatides</i> sp. ^a
Cirratulidae, 1 sp.	Ophiuroidea, various spp. ^a
Onuphidae, 1 sp.	
Unidentified, 2 spp.	Chordata
	Osteichthyes
Sipuncula	<i>Coryphaenoides</i> sp. ^a
Unidentified, 2 spp.	Zoarcidae, 1 sp. ^a
	Macrouridae, 2 spp. ^a

Note: All species were collected unless otherwise noted.

^aIdentified from high-resolution video.

#AY240928) exhibited 86% similarity to two selected genera of the family Spionidae (*Polydora* and *Pygospio* spp.). Judging by its unusual morphology and difference in ribosomal 18S sequence from known taxa it is likely a new species, or even a new genus, within the family Spionidae (G. Rouse, pers. comm.; Rouse and Pleijel, 2001). Spionids are important among the deep-sea benthos and some respond to seafloor enrichment (Kihlsinger and Woodin, 2000). These animals are known to hold their palps erect to entrap particles (Taghon et al., 1980) and this is the position in which we observed annelid B. For all individuals collected ($n = 28$), we observed a size range of 1.9–5.4 cm in length.

Ten additional polychaete species were collected from the whale fall (Table 1). Large green tube-dwelling ampharetids (~6 cm in length), thought to be bacterial grazers on whale falls (Smith and Baco, 2003), dominated the adjacent sediment community (Fig. 3E). It is worth noting that many

of these polychaetes, including the green ampharetid, a hesionid, and two unidentified annelids, have also been examined by taxonomists and are thought to be new taxa (G. Rouse and F. Pleijel, pers. comm.). Decapod crustaceans, including galatheids and lithodids, were present on the carcass itself and appeared to dominate the scavenging component of this whale fall community. Echinoderms including *Scotoplanes clarki*, a variety of ophiuroids, and sea urchins were present in large numbers in adjacent sediments. Abundance of *S. clarki* in particular was estimated to be 60–90 individuals m^{-2} . The pom pom anemone, *Liponema brevicornis*, also occurred in adjacent sediments, and a variety of unidentified anemones occurred on the bones. Grazing limpets and snails were absent. Though we observed a small number of macrourid fish in the periphery, none were observed foraging directly on the whale carcass.

3.4. Whale fall community at time 2 (March 10, 2002)

One month after the initial discovery, the whale skull was still easily recognized, however, ribs and other skeletal parts had collapsed to the substrate (Fig. 4A). Flesh and intestines were not as prominent as at time 1 (Fig. 2E, compared to 2C). Many bones appeared to be clean and the single caudal vertebra that was collected was highly degraded. Associated fauna at time 2 was very similar to time 1, including a dominance of annelids A and B, large aggregations of *S. clarki* (Fig. 2F; abundance estimated at 40–60 individuals m^{-2}), and the presence of a few peripheral octopus. The area covered with filamentous bacterial mat had increased from time 1 both on the sediment surface near the skull and in a new area along the posterior right side of the carcass (Fig. 2D; area of bacterial mat coverage was estimated to be ~6 m^2).

3.5. Whale fall community at time 3 (October 9, 2002)

Very little soft tissue remained 8 months after the initial discovery (although baleen was still

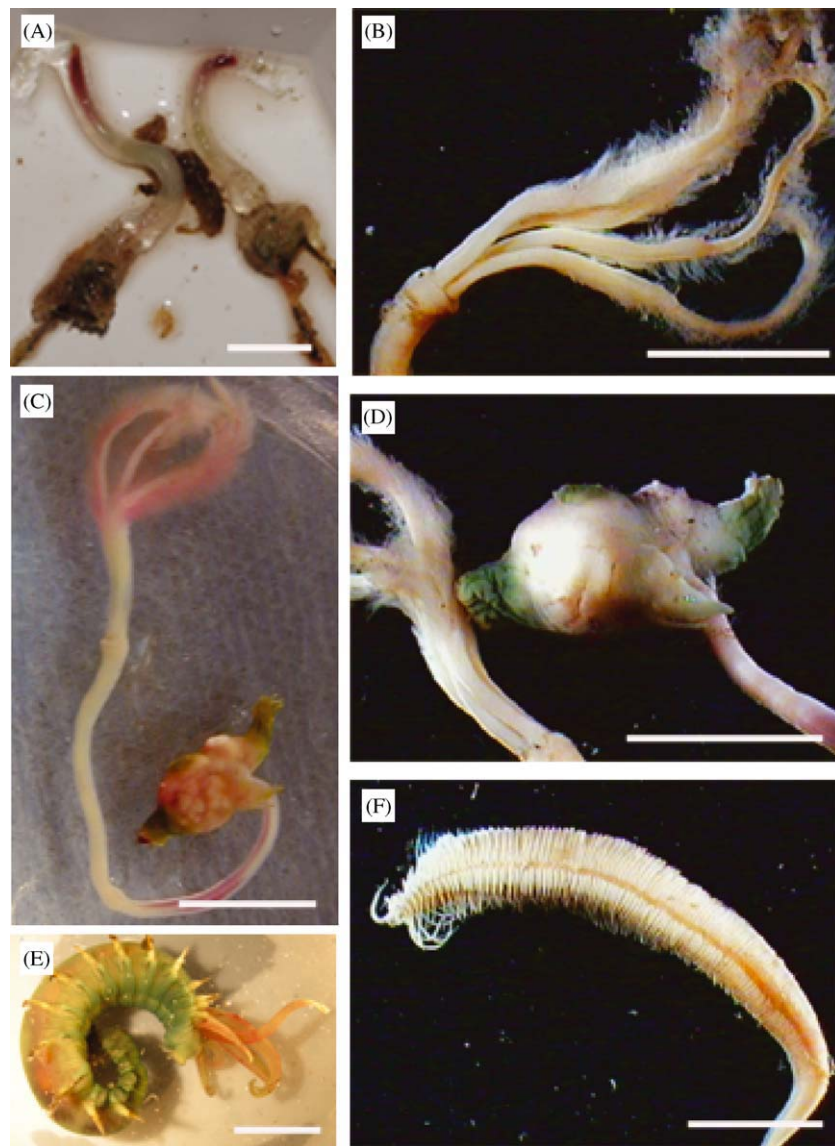


Fig. 3. The three dominant worm species associated with the whale fall. Annelid A was found exclusively on bones. Annelid B was in tissues and surrounding sediments. The large green ampharetid occurred only in surrounding sediments: (A) annelid A in mucous tubes; (B) annelid A showing anterior plume; (C) annelid A dissected from its mucous tube; (D) annelid A showing the posterior brood sac and proximal portions of green roots; (E) an ampharetid worm; and (F) annelid B showing highly modified parapodia with setae. Scale bars = 1 cm.

present), and many bones were exposed and noticeably degraded (Figs. 2G–H, 4B).

Coverage by bacterial mats had greatly expanded and was heaviest in sediments immediately adjacent to the carcass (Fig. 4B; area of bacterial

mat coverage was estimated to be $\sim 15 \text{ m}^2$). Underlying and adjacent sediments were black in color and core samples smelled strongly of sulfide. We collected several bones for radiometric dating, lipid measurements, and faunal composition,

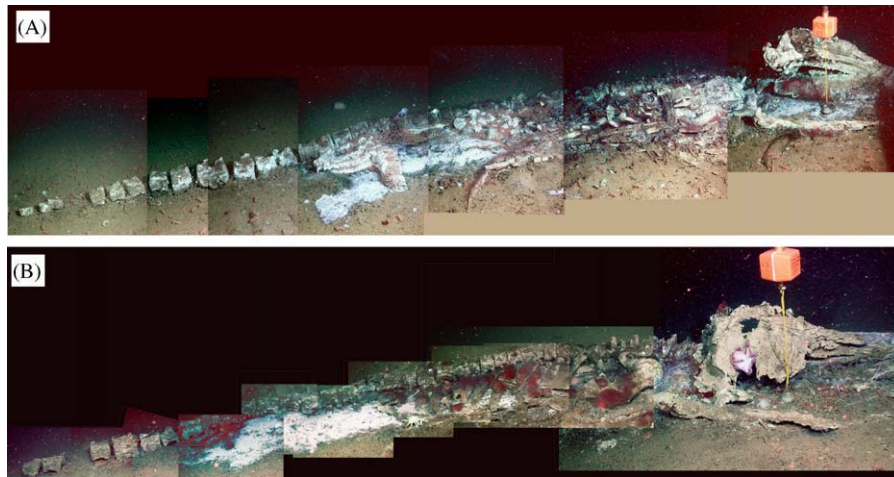


Fig. 4. Photo mosaics of digital still images: (A) time 2 (dive #T406, March 10, 2002) and (B) time 3 (dive # T486, October 9, 2002).

including one large rib, two small ribs, and a large thoracic vertebra. Bone samples appeared oily and less heavily calcified than bones collected from larger whales (C. Smith, University of Hawaii at Manoa, pers. comm.), which is expected for a juvenile whale (Rice et al., 1984).

Covering the exposed surfaces of many bones, annelid A still appeared to be the dominant animal (Fig. 4B). The worms penetrated the marrow cavity of bones with “roots” that extended from a posterior brood sac (Fig. 3D). Individuals of annelid A on the collected bones ranged from 0.5 to 7.0 cm in length from plume to brood sac. Their density on one portion of a rib bone was 3–20 individuals cm^{-2} , which rivals, if not surpasses, previous estimates of single species (dorvilleids at 1 worm cm^{-2} ; Van Dover, 2000) and multiple species (4 worms cm^{-2} ; Smith and Baco, 2003) densities on whale carcasses. Annelid B, which was abundant on previous visits, was nearly absent (a few were observed in video surveillance and one individual was collected). New animal species, not observed at time points 1 and 2, included large polynoid polychaetes (6–7 cm in length), small but dense aggregations of three species of sipunculids, and a large nemertean. Lithodid crab debris was found directly below an octopus living in the occipital bone of the whale skull (Fig. 2G). Galatheid crabs and large ampharetid polychaetes dominated the surrounding sediments, along with

S. clarki and various ophiuroids, which were in much lower abundance than at times 1 and 2. A zoarcid fish (*Pachycara* sp.) appeared to be closely associated with the fall, in contrast to the few other fish, mostly macrourids and possibly liparids, observed in the periphery at times 1 and 2 (J. Drazen, Monterey Bay Aquarium Research Institute, pers. comm.).

4. Discussion

4.1. Whale fall community

Community dynamics at large food falls, including whales, probably rely as much on specific dispersal capabilities, spatial distributions, and bathymetric ranges of the associated organisms, as they do on facilitation between stages, as the succession model suggests. Thus, individual whale fall communities may differ greatly depending on the location and depth of the whale fall, on the pool of available colonizers, and on chance. Shortly after deposition on the seafloor, the Monterey Bay whale fall exhibited components of all three successional stages described by Smith and Baco (2003). For other known whale falls, a mobile scavenger stage exists for 4–12 months in duration, dominated by hagfish and macrourids, sleeper sharks, crabs, ophiuroids, and amphipods

(Smith and Baco, 2003). Although no large vertebrate scavengers were observed feeding on the Monterey carcass during our visits, amphipods and a few fish were observed. The scavenger stage is typically followed by an enrichment opportunist stage (for 1–2 years in duration) dominated by polychaete worms and crustaceans (Smith and Baco, 2003). This appeared to be the primary stage of the Monterey whale fall as opportunistic polychaetes and crustaceans were dominant. Thick bacterial mats were contained within the outline of the skull and jawbones and along the perimeter of several large fins suggesting the presence of hydrogen sulfide. The ‘sulfophilic stage’ is thought to last up to 50 years in duration and is dominated by sulfide-tolerant and sulfide-dependent invertebrates and bacterial mats (Smith and Baco, 2003).

We hypothesize that the delayed degradation of the Monterey whale fall community results from its depth (2891 m), which is greater than previously studied falls off of California (1000–2000 m depth; Smith et al., 1989; Allison et al., 1991; Smith, 1992; Smith and Baco, 2003) and New Zealand (800–955 m depth; Marshall, 1987). Increased hydrostatic pressure (and low temperatures) may promote organic preservation (Allison et al., 1991). Microbial processes are reduced 1–3 orders of magnitude (relative to processes at 1 atm), especially at depths greater than 2000 m (Allison et al., 1991; Deming et al., 1997). Also, the mobile scavengers may be limited by depth. Two common species of hagfish found in Monterey Bay, *Eptatretus stouli* and *E. deanii*, have depth limits of 600 and 1900 m, respectively (Wisner and McMillan, 1990), and Pacific sleeper sharks (*Somniosus pacificus*) have only been observed above 2000 m (Isaacs and Schwartzlose, 1975; Ebert et al., 1987). However, rattails (*Coryphaenoides armatus*, *C. filifer*, and *C. leptolepis*), flatnose codling (*Antimora rostrata*, *Spectrunculus grandis*), and a variety of small ophidids and liparids known to prey on amphipods near bait falls occur at depths up to 3000 m in Monterey Bay (J. Drazen, Monterey Bay Aquarium Research Institute, pers. comm.). Nevertheless, only a few large potential scavengers (several *C. armatus* and one liparid) were observed during visits to the whale.

Invertebrates that characterize the enrichment opportunist stage at shallower whale falls primarily dominated the Monterey whale fall. Polychaetes make up 50–60% of species richness at previously studied natural and implanted whale falls (Bennett et al., 1994). Some polychaetes are tolerant of high sulfide and low oxygen, both of which occur during pulses of organic enrichment, potentially explaining their common occurrence at whale falls. Two undescribed annelids at the Monterey whale fall (annelids A and B) appear to be whale fall specialists. At least 21 of the 200 species previously documented at whale falls are known only from this environment and appear to be whale fall specialists (Smith and Baco, 2003). Exclusive use of such transient habitats would require rapid growth, early maturity, high reproductive rates, and great dispersal capabilities (Turner, 1973), characteristics that are typically attributed to terrestrial “weedy species” (Baker, 1965). Both worms were highly abundant at the whale fall, increasing in numbers from February to March, and exhibited a size range indicative of continuous recruitment. Although molecular analyses placed both of these undescribed worm species within the phylum Annelida, both annelids A and B exhibited very unusual morphologies and significant divergences within the 18S ribosome to warrant consideration as new species (G. Rouse, pers. comm.; Rouse et al., submitted).

Remnants of annelid A were previously observed on a whale fall in the Santa Catalina Basin (C. Smith, pers. comm.). Our molecular analysis suggests that this worm is related to frenulate and vestimentiferan tubeworms, found at deep-sea hydrothermal vents, cold-water sulfide/hydrocarbon seeps and other reducing environments. Vestimentiferan worms are known only to exist in strict obligate relationships with bacterial endosymbionts (Jones, 1985; Feldman et al., 1997). We are currently investigating the possibility that annelid A depends on endosymbionts for nutrition, as it does not appear to possess a functional gut.

The relatively fresh Monterey whale fall also exhibited thick bacterial mats (covering adjacent sediments and long bones (ribs, jaws, etc.) that typically appear later in shallower whale falls

within the sulfophilic stage. Although the sulfophilic stage is estimated to last up to 50 years on large whale falls (Smith and Baco, 2003), the persistence of adequate sulfide levels may be shorter for smaller whale species and juveniles (Baco-Taylor, 2002; Smith and Baco, 2003). Vertebrae of the Monterey whale fall showed no evidence of large lipid reserves, and they were already porous and degraded at our 8-month visit. Elevated sulfide and methane levels due to lipid decomposition during the sulfophilic stage create an environment analogous to that found at deep-sea hydrothermal vents and cold-water sulfide/hydrocarbon seeps (Smith et al., 1989; Deming et al., 1997; Van Dover, 2000). Smith and Baco (2003) have noted significant associations, especially at higher taxonomic levels, between whale fall species and species found at deep-sea vents and seeps, including polynoids, dorvilleids, bivalves, and a variety of gastropods. The Monterey whale fall, however, had no animal species shared with vent and seep communities. The vesicomyid clam, *Ectenagena extenta*, occurs at nearby cold-seeps 300 m to the southwest, but not in the sediments surrounding the Monterey whale fall. Vesicomyids, which depend on thiotrophic endosymbionts for nutrition, are common at shallower whale falls in the Santa Catalina Basin and off of San Nicolas Island, California (Baco et al., 1999), but these clams have been identified only as *C. elongata* or members of the *Vesicomya gigas/kilmeri* species complex. Vesicomyid species appear to be stratified by bathymetry (Goffredi and Barry, 2002), and it is possible that the deep-dwelling *E. extenta* species of Monterey Bay is incapable of utilizing a whale fall for nutrition. Alternatively, the whale fall may be too recent to allow sufficient time for vesicomyid colonization. Thus, if the sulfophilic stage of the Monterey whale fall lasts long enough, we might expect that adult movement or larval dispersal will eventually bring vesicomyids to this sulfide-rich fall.

4.2. Local seafloor enrichment

The intense organic enrichment associated with whale falls is also exploited by a number of deep-sea generalists. We observed dense aggregations of

the sea cucumber *S. clarki*, brittlestars, and sea urchins on sediments adjacent to the carcass. Echinoderms, in particular, are prevalent suspension and deposit feeders in the deep sea and probably utilize fresh organic carbon material resulting from the breakdown of a whale carcass (Lauerman and Kaufmann, 1998).

Monterey Canyon is an active sediment transport conduit that facilitates the rapid movement of recent sediments and other material into the deep sea (Paull et al., 2002). Organic enrichment of the benthos along the California margin typically involves macrophytic algae and terrestrial plant debris (e.g., trees), especially in the channels of active submarine canyons. For example, kelp debris (*Phyllospadix* spp. and *Macrocystis pyrifera*) can account for 20–80% of the total particulate organic carbon reaching the seafloor in Carmel and Monterey Canyons (Harrold et al., 1998). We observed relatively fresh *Phyllospadix* debris at the Monterey fall site during all three time points. The density of trash near the whale fall site supports the idea of frequent and intense flow events, resulting in the accumulation of materials within the canyon axes.

During the past 10 years of Monterey Canyon exploration, we have discovered the remains of eight marine mammals (three whales, two seals, one elephant seal, and two of unknown identity) at separate locations within ~180 km² of the seafloor (Fig. 1). Six out of eight of these remains were found in axes of canyons. Thus, the deposition of large animal remains in these material transport conduits has the potential to dramatically affect the diversity and structure of benthic communities, especially under primary migration corridors for whales. Continuing studies of the diverse invertebrate fauna associated with the Monterey whale fall can help us understand the complicated dynamics of community change in patchy deep-sea environments.

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