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The discovery of a natural whale fall in the Antarctic deep sea



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ABSTRACT

Large cetacean carcasses at the deep-sea floor, known as 'whale falls', provide a resource for generalist-scavenging species, chemosynthetic fauna related to those from hydrothermal vents and cold seeps, and remarkable bone-specialist species such as *Osedax* worms. Here we report the serendipitous discovery of a late-stage natural whale fall at a depth of 1444 m in the South Sandwich Arc. This discovery represents the first natural whale fall to be encountered in the Southern Ocean, where cetaceans are abundant. The skeleton was situated within a seafloor caldera, in close proximity (< 250 m) to active hydrothermal vents. We used a DNA barcoding approach to identify the skeleton as that of an Antarctic minke whale (*Balaenoptera bonaerensis*). The carcass was in an advanced state of decomposition, and its exposed bones were occupied by a diverse assemblage of fauna including nine undescribed species. These bone fauna included an undescribed species of *Lepetodrilus* limpet that was also present at the nearby hydrothermal vents, suggesting the use of whale-fall habitats as stepping stones between chemosynthetic ecosystems. Using Remotely Operated Vehicle (ROV) videography, we have quantified the composition and abundance of fauna on the whale bones, and tested a hypothesis that varying concentrations of lipids in the bones of whales may influence the microdistribution of sulfophilic whale-fall fauna. Our data supported the hypothesis that more lipid-rich bones support a greater abundance of sulfophilic bacterial mats, which are also correlated with the abundance of grazing limpets (*Pyropelta* sp.). The abundance of *Osedax* sp. on bones however, showed a negative correlation with the bacterial-mat percentage cover, and hence greatest abundance on bones predicted to have lowest lipid content.

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1. Introduction

Recent studies of both natural and experimentally-implanted whale skeletons have provided a remarkable insight into the fate of the planet's largest creatures after their death. Whale remains on the seabed, termed 'whale falls', provide a large amount of organic enrichment, shelter and substrate to the deep-sea floor and thus produce a habitat that is distinct from that of the surrounding benthic community (Smith et al., 1989, 2002; Jones et al., 1998; Smith and Baco, 2003; Smith, 2006). Such carcasses can be consumed by a diverse community of both generalist-scavenging species such as fish and crustacea, and highly specialised feeders such as 'bone-boring' *Osedax* worms (Baco and Smith, 2003; Smith and Baco, 2003; Rouse et al., 2004).

Faunal assemblages occupying whale falls vary in species diversity and community structure, which may reflect stages of decomposition on the seafloor (Bennett et al., 1994; Smith and Baco, 2003; Smith, 2006), although such stages may be difficult to distinguish for some carcasses (Lundsten et al., 2010b). The first recognised stage, known as the mobile-scavenger stage, is characterised by the removal of soft tissue from the carcass by organisms such as hagfish, sharks, and crustaceans and is thought to last from 4 to at least 24 months (Smith et al., 1989; Smith and Baco, 2003). The second stage is the enrichment-opportunist stage, during which organically-enriched sediments and exposed bones are colonised by dense assemblages of heterotrophic fauna exploiting the remaining soft tissue and bones for months to years depending on the size of the carcass (Levin et al., 1994; Smith and Baco, 2003). During the third stage, sulphide derived from the anaerobic breakdown of bone lipids by microbes fuels a species-rich assemblage on and around the bones; this stage may last for decades (Smith, 1992, 2006; Bennett et al., 1994; Deming et al., 1997; Smith and Baco, 2003). A significant component of

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the fauna found during this stage derives nutrition from this sulphide-based chemoautotrophy, via microbial endosymbiosis or direct bacterial grazing (Bennett et al., 1994; Smith et al., 2002; Smith and Baco, 2003; Smith, 2006). This third stage may also facilitate the dispersal of some faunal species between other chemosynthetic environments by providing 'stepping stones' between ephemeral, sulphide-rich habitats (Smith et al., 1989; Bennett et al., 1994; Naganuma et al., 1996; Smith and Baco, 2003; Lorion et al., 2009; Lundsten et al., 2010a). The final stage is thought to be a 'reef stage', where the remains of bones form a hard-substrate habitat for suspension feeders such as anemones, although to date, it has not been recorded in the scientific literature (C. Smith, personal communication). The enrichment-opportunist, sulfophilic and reef stages are thought to overlap to some extent (Smith et al., 2002; Goffredi et al., 2004; Braby et al., 2007). Estimates of the duration of each stage and whale falls in their entirety are still poor as so few carcasses have been studied in any detail, but it is estimated that the entire decomposition process can take anywhere from years to > 100 years depending on the size of the carcass, the fauna present and the ecological setting (Smith et al., 2002; Smith and Baco, 2003; Schuller et al., 2004; Braby et al., 2007; Fujiwara et al., 2007; Lundsten et al., 2010b).

The discovery of natural whale falls on the seafloor is extremely rare. To date, only six natural whale falls have been discovered through chance encounters and studied with ROVs or submersibles in depths ranging from 150 to 4037 m (Smith et al., 1989; Fujioka et al., 1993; Smith and Baco, 2003; Goffredi et al., 2004; Lundsten et al., 2010a), although considerably more have been observed in photo-surveys but remain unsampled (C. Smith, personal communication). In addition to these, there are a number of records of whale bones unexpectedly trawled up from depth with attached fauna (Tebble, 1966; Dell, 1987, 1995; Marshall, 1987, 1994; Waren, 1989; McLean, 1992; Bolotin et al., 2005). Discovering natural whale falls is important to deep-sea science because they provide a unique view into the natural processes of the taphonomy of large cetaceans on the seafloor: i.e. their settlement, decomposition and ultimately fossilisation (Allison et al., 1991). Natural whale falls are also important as the majority of whale falls studied have been implanted within the last twenty years and as a result, are relatively young. With natural whale falls, it is possible that carcasses have been decomposing on the seafloor for longer periods (Schuller et al., 2004).

One important aspect of whale-fall ecology that has hitherto not received attention is the variation in community structure along a whale skeleton in the sulfophilic stage. A summary of data has recently emerged on the specific composition of whale bones possibly influencing faunal communities (Higgs et al., 2011b). Whale bones are thought to be composed of 10% lipid and 25% protein on average, but lipid content can be as high as 80% by weight (Allison et al., 1991; Gage, 2003; Higgs et al., 2011b). A 40-ton whale carcass may carry 2000–3000 kg of lipids in its skeleton (Lundsten et al., 2010b). Organisms living on the whale skeleton are likely to be dependent on the lipid–protein matrix of the bone, either directly or indirectly via chemoautotrophic bacteria (Bennett et al., 1994; Deming et al., 1997; Smith et al., 2002; Smith and Baco, 2003). The 'oil-gradient hypothesis' states that the abundance of sulfophilic organisms in late-stage whale falls will correspond to changes in oil throughout the whale skeleton over time (Higgs et al., 2011b). In older whale-fall communities, the majority of fauna is expected to be found on the humerus and lower vertebrae (lumbar and caudal), as these are the most oil-rich and therefore, sulfidic of bones. One of the most prevalent types of sulfophilic fauna at whale falls is sulfur-oxidising bacterial mats which cover the bones (Smith and Baco, 2003). Higgs et al. (2011b) hypothesised that these bacterial mats may act as a useful proxy for the sulphide output and therefore lipid

content of the bones, as these are the basis of the grazing food chain during this stage of whale falls (Treude et al., 2009).

During both the enrichment-opportunist and the sulfophilic stage of whale falls, a unique genus of siboglinid polychaetes, *Osedax*, consume the bones of the skeleton heterotrophically (Rouse et al., 2004; Glover et al., 2005b). It was initially speculated that *Osedax* relied for nutrition on hydrocarbon degradation (Rouse et al., 2004), then collagen and cholesterol (Goffredi et al., 2005), and finally primarily on collagen alone (Goffredi et al., 2007; Higgs et al., 2011a). These worms are thought to use acid-secreting enzymes on the surface of a root-like structure to bore into the bones (Higgs et al., 2011a). It has only been realized recently how this genus affects the taphonomy of whale skeletons, contributing to their rapid degradation by boring into the bones at high densities (Braby et al., 2007; Higgs et al., 2011c). There are limited data however, on whether the genus *Osedax* has a preference for certain bone types or positions on whale skeletons, or even the role of *Osedax* in different successional stages (Goffredi et al., 2005; Fujikura et al., 2006, 2007; Braby et al., 2007). Questions still to be addressed include whether *Osedax* colonise early and persist through to the sulfophilic stage, and whether degradation by *Osedax* inhibits the progression of whale skeletons into the reef stage.

The aims of this paper were to investigate the ecology of a late-stage natural whale fall, determine the successional stage and likely age of the carcass, analyse the whale-fall community structure, and test the 'oil-gradient hypothesis'. DNA barcoding of the bones was used to determine the whale species. All organisms found growing on the bones and in the immediate vicinity of the skeleton were identified, including a range of species undescribed to science. Using a high-definition refinement of ROV videography, we also examined the 'intra' whale-fall variations in community composition allowing us to test the 'oil-gradient hypothesis' for the first time. This included the examination of the distribution of bacterial mats along the bones of differing lipid content. The hypothesis was also extended to species that depend on the bacterial mats and the bone-specialist *Osedax*.

2. Methods

2.1. Observation and sample collection at the whale fall

The skeleton was found in the South Sandwich Arc, which is part of a complex tectonic system located south of the Polar Front in the East Scotia Sea at 59°41.671'S, 28°21.089'W, at a depth of 1444–1447 m (Fig. 1). The vicinity of the whale fall contained several chemosynthetic environments such as white-smoker vent fields and areas of diffuse flow, currently being investigated as part of the UK-funded ChESOs (Chemosynthetic Ecosystems of the Southern Ocean) project. The whale fall was encountered serendipitously in a video survey of the area during Dive #148 of the *Isis* ROV on February 7th 2010, as part of Voyage 42 of the *RRS James Cook*.

The ROV followed a grid of survey lines at an altitude of 3.5 m above the seafloor to obtain overlapping video images of the whale skeleton from its downward-looking 3-chip CCD video camera during *Isis* Dives #148 (February 7th 2010) and #151 (February 10th 2010). The Doppler control facility of the ROV enabled precise movements of the vehicle relative to the seafloor during video surveys, and a gyrocompass was used to maintain constant vehicle heading. Two parallel lasers mounted 0.1 m apart provided a scale in images. Frames from the downward-looking video camera were extracted and compiled into an overall digital mosaic image of the whale skeleton (Fig. 2). A high-definition video camera and digital-stills camera on separate adjustable pan-and-tilt mounts were also used to obtain

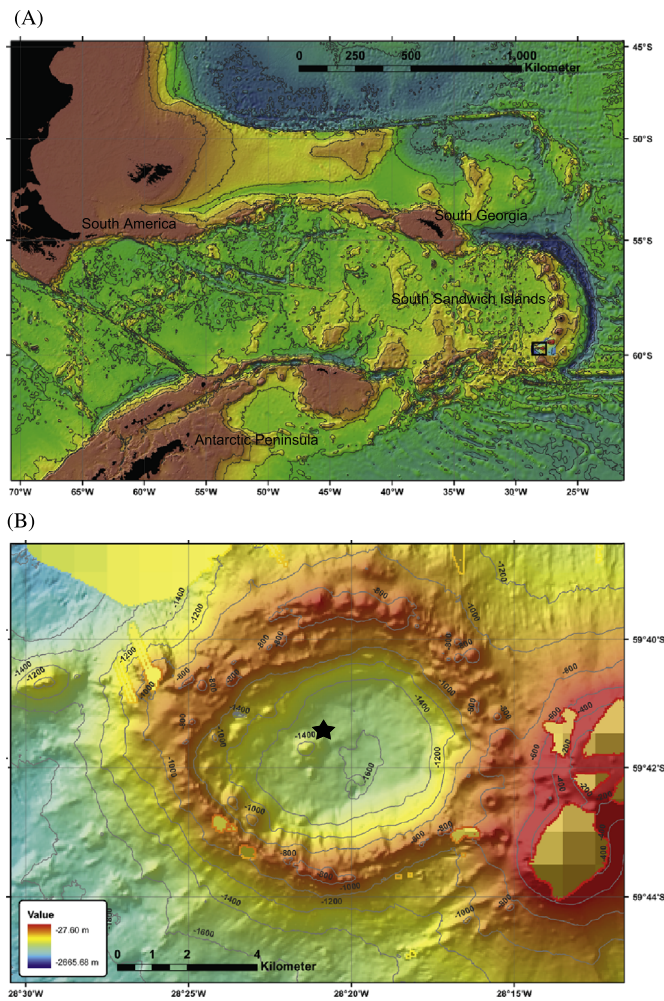


Fig. 1. Location of the whale fall. (a) Bathymetry of the Scotia Sea and surrounding region. Contour lines are 1000 m with land above sea level indicated in black. (b) Bathymetry of the Kemp Caldera with the specific location of the whale fall denoted by ★. Contour lines are 200 m. Bathymetry data for (a) is from Smith and Sandwell (1997). (b) was constructed from unpublished ship-based bathymetry data from the British Antarctic Survey.

supplementary close-up observations of bones and fauna. Three bone samples were retrieved from the skeleton with the ROV manipulators (Fig. 2). These bones were placed in individual bioboxes on the ROV until recovery on the deck of the ship, thereby preventing unnecessary washing of the bone samples.

Video footage from the ROV cameras was analysed as follows: (1) each bone in the skeleton was numbered and where possible, its anatomical type identified from bone morphology; (2) fauna visible on bones in video images was identified to the lowest taxon possible; (3) abundances of organisms were quantified on bones from digital still and video images, using four groups to classify organisms present: (i) bacterial mats; (ii) *Osedax*; (iii) peracarids (Amphipoda and Isopoda); and (iv) gastropods (*Pyropelta*). Only bone-encrusting fauna that could be resolved were quantified. Amphipoda and Isopoda were grouped into peracarids because the two orders could not be distinguished from each other on the footage. Visible bone surface areas were calculated using the scaling lasers in the ROV imagery and 3D-geometric models of bone shape, to provide numbers of individuals per m² for each faunal group and percentage coverage for bacterial mats.

2.2. DNA barcoding of the whale fall

DNA was isolated from the caldera whale bone using liquid nitrogen to freeze the bone so that it could be ground into powder. Approximately 0.1 g of bone powder was placed in each of three vials. Extraction was done using Qiagen DNeasy Blood and Tissue Extraction Kit following the protocol: Purification of Total DNA from Animal Tissue. Qiagen extractions were stored at -20 °C. The primers used were made for a segment approximately 873 bp in length, containing the complete cytochrome b gene and part of the tRNA of the *Orcinus orca* complete mitochondrion genome: Whale892F and Whale892R (Foote et al., 2011) (NC_014682). The primer sequences were as follows: 5'-GTTATAGCCACCGCATTCGT-3' and 5'-AATTCCAGCTTTG-GGTGTG-3'. The DNA extracted from one vial of bone material (0.1 g) was used for PCR using PureTaq Ready-To-Go PCR beads (GE Healthcare). The PCR was performed in 25 µL reactions, consisting of 1 µL of each primer, 2 µL DNA template and 21 µL dH₂O. The PCR amplification profile consisted of initial denaturation at 95 °C for 5 min, 35 cycles of denaturation at 94 °C for 45 s, annealing at 55 °C for 45 s, extension at 72 °C for 2 min and a final extension at 72 °C for

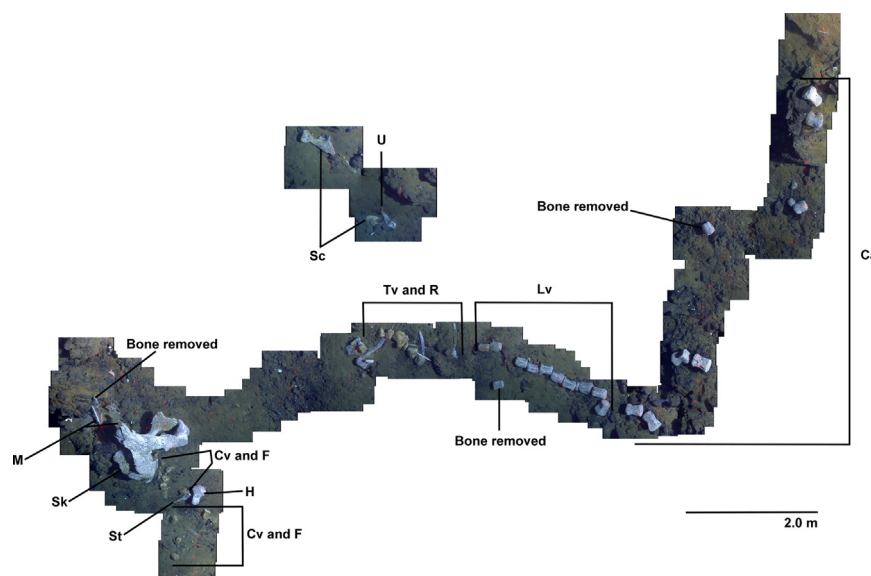


Fig. 2. Photo mosaic of the whale fall. The three bones removed by the ROV for further analysis are indicated, as well as the anatomical bone types within the skeleton. M—mandible, Sk—skull, F—small unidentified fragment, H—humerus, U—ulna, Sc—scapula, St—sternum, R—rib, Cv—cervical vertebra, Tv—thoracic vertebra, Lv—lumbar vertebra, Ca—caudal vertebra.

10 min. Products of the PCR were confirmed by electrophoresis in a 1.5% agarose gel. Purification of the PCR products was achieved using a Qiagen PCR Purification Kit. Sequencing was performed on an ABI 3730XL DNA Analyser (Applied Biosystems) at the Natural History Museum London Sequencing Facility using the primers described above.

Overlapping sequence fragments were merged into consensus sequences using Geneious (Drummond et al., 2011) and aligned using MUSCLE (Edgar, 2004) provided as a plug-in in Geneious with default settings. The mtDNA sequences for all of the whales used in the phylogenetic analysis were obtained from GenBank. Bayesian phylogenetic analyses (BA) were conducted with MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003). Analyses were run three times with the combined dataset with four chains for 2,000,000 generations, with 400,000 generations discarded as burn-in. The evolutionary models used for the molecular data in BA were obtained by running the two separate datasets in MrModelTest (Nylander, 2004), and for tRNA the optional model was K80+G. For cytochrome b, the data were partitioned into codon positions with position 1 following K80+G, position 2 following HKY, while HKY+G was used for position 3. In the combined BA, the data were partitioned into the two parts (cytochrome b and tRNA) and the evolutionary models mentioned above were applied to each partition and corresponding codon position respectively.

2.3. $^{210}\text{Pb}/^{226}\text{Ra}$ analysis of the whale fall

The isotopic pair ($^{210}\text{Pb}/^{226}\text{Ra}$) has been used previously to establish the time since cetacean death and deposition on the seafloor by Schuller et al. (2004). We tried to analyse the age since death of the caldera skeleton using this method but were unsuccessful after two attempts. Seven other bones from skeletons of known varying ages were also analysed during this study to show the degree of error with the methodology. Despite taking great care to avoid contamination, ratios of the isotopic pair $^{210}\text{Pb}/^{226}\text{Ra}$ were greater than unity on both occasions. Attempts are however, ongoing. As a result, only the state of decomposition of the bones could be used to gauge the age of the skeleton.

3. Results

3.1. Location and initial observations of the whale fall

The skeleton was found in a seafloor caldera west of Kemp Seamount on the southern tip of the South Sandwich Island

arc (Fig. 1). The whale fall was on the northeast slope of a small sub-cone in the centre of the caldera at 1444–1447 m (Fig. 1). The substratum was rocky with a thin layer of sedimentation. Sediment underneath the whale bones was black in colour.

The whale fall was approximately 10.7 m long and completely skeletonised, lying in a disjointed line with the skull downslope (Fig. 2). The dorsal surface of the skeleton was uppermost (evidenced by the positions of the skull and mandibles) (Fig. 2). The vertebral column had been displaced from the skull but remained with most bones in order (Fig. 2). Some lumbar and caudal vertebrae were spread upslope in a haphazard manner (Fig. 2). Several bones appeared to be missing, including many smaller bones such as the pelvic bones, ear complexes, some ribs, chevrons, vertebral and pectoral epiphyses, radii, vorners, hyoid bones, carpals and metacarpals (Fig. 2). However, there were several unidentified fragments and these may have constituted some of the missing bones (Fig. 2). Most of the bones were highly-degraded, although the degree of damage was variable (Fig. 2). Spongy bone was exposed on many of the bones following the removal of compact bone and some bones, such as the mandibles, were fragmented in several places. There was no evidence of any of the vertebral processes, with the cervical and thoracic vertebrae the most badly-eroded regions of bones (Fig. 2). Despite the high degree of erosion on many of the bones, they did still have lipid present. Sawing through sections of the collected bones revealed visual and olfactory confirmation of large amounts of oil (D. Amon, personal observation). The smaller bones (unidentified fragments and cervical vertebrae) that were present were observed to be almost completely covered with sediment, but the majority of bones were, however, still projecting above the sediment.

3.2. DNA barcoding of the whale fall

The DNA sequence was run in BLAST through Geneious (Drummond et al., 2011) and the analysis (MrBayes) of 13 mysticete sequences (using *Physeter catodon*, *Orcinus orca* and *Hippopotamus amphibius* as outgroups) identified the species of whale as an Antarctic minke whale (*Balaenoptera bonaerensis*) by 97% DNA sequence similarity of the cytochrome b gene (745 bp) and a segment of the tRNA gene (746–873 bp). The genetic result was in concordance with the examination of some remaining morphological features of the skull region, and the overall size of the carcass; however, the morphology on its own would not have been enough to confirm identification to species level.

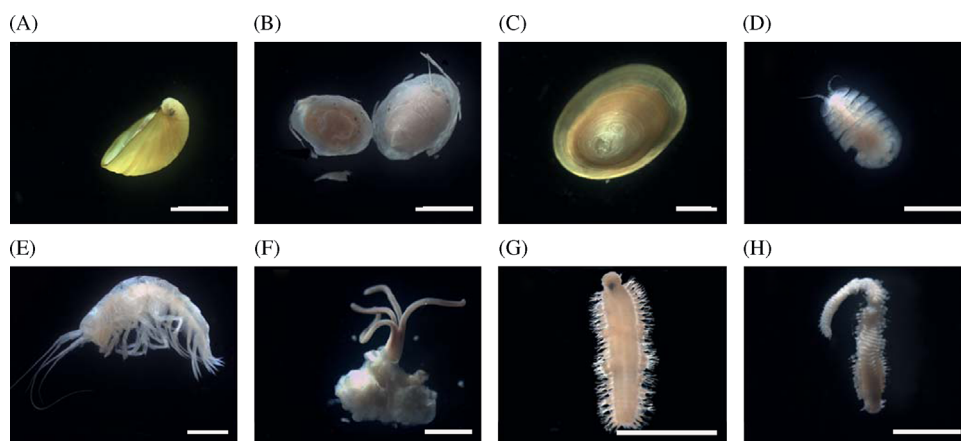


Fig. 3. Fauna found on the whale bones. (a) *Lepetodrilus* sp., (b) *Osteopeltidae* sp., (c) *Pyropelta* sp., (d) *Jaera* sp., (e) *Lysianassidae* sp., (f) *Osedax* sp., (g) *Ophryotrocha* sp. P, (h) *Ophryotrocha* sp. X. There was also *Capitellidae* sp. (not shown). Scale for (a–h) is 2000 μm .

Table 1Megafaunal and macrofaunal taxa with their respective locations with regard to the whale skeleton as observed by the ROV *Isis*.

Phylum	Class	Order	Family	Genus		Location
Porifera	indet.	indet.	indet.	indet.	2 spp.	Surrounding
Cnidaria	Anthozoa	Actinaria	indet.	indet.	4 spp.	Surrounding
Nemertea	Anopla		Cerabratulidae	<i>Parbolasia</i>	1 sp.	Surrounding
		indet.	indet.	indet.	1 sp.	Surrounding
Mollusca	Cephalopoda	Teuthida	indet.	indet.	2 spp.	Surrounding
	Bivalvia	indet.	indet.	indet.	1 sp.	Surrounding
	Gastropoda		Lepetodrilidae	<i>Lepetodrilus</i>	1 sp.	Bone epifaunal
			Osteopeltidae	indet.	1 sp.	Bone epifaunal
			Pyropeltidae	<i>Pyropelta</i>	1 sp.	Bone epifaunal
Sipuncula	indet.	indet.	indet.	indet.	1 sp.	Surrounding
Annelida	Polychaeta	Sabellida	indet.	indet.	1 sp.	Surrounding
			Siboglinidae	<i>Osedax</i>	1 sp.	Bone infaunal
		Eunicida	Dorvilleidae	<i>Ophryotrocha</i>	2 spp.	Bone epifaunal
			Capitellidae	indet.	1 sp.	Bone epifaunal
Arthropoda	Malacostraca	Decapoda	Nematocarcinidae	<i>Nematocarcinus</i>	1 sp.	Surrounding
		Isopoda	Munnopsidae	<i>Ilyarachna</i>	1 sp.	Surrounding
			Janiridae	<i>Jaera</i>	1 sp.	Bone epifaunal
		Amphipoda	Lysianassidae	indet.	1 sp.	Bone epifaunal
	Pycnogonida	Pantopoda	Ammotheidae	<i>Sericosura</i>	1 sp.	Surrounding
Echinodermata	Asteroidea	Forcipulatida	Stichasteridae	indet.	1 sp.	Surrounding
	Opiuroidea	indet.	indet.	indet.	1 sp.	Surrounding
	Echinoidea	Camarodonta	Echinidae	<i>Sterechinus</i>	1 sp.	Surrounding
Chordata	Actinopterygii	Gadiformes	Macrouridae	indet.	1 sp.	Surrounding
		Perciformes	Nototheniidae	<i>Dissostichus</i>	1 sp.	Surrounding

3.3. Whale-fall successional stage and community composition

The bones provided a substratum for nine taxa of abundant encrusting macrofauna (Fig. 3 and Table 1). Gastropods included an undescribed species of *Lepetodrilus*, an undescribed species of Osteopeltidae, and an undescribed species of *Pyropelta* (Fig. 3 and Table 1). The bones also harboured an undescribed species of amphipod (Lysianassidae sp.) and an undescribed species of isopod (*Jaera* sp.) (Fig. 3 and Table 1). There were also four undescribed species of polychaetes on the whale skeleton: two *Ophryotrocha* (sp. X and sp. P), an *Osedax* sp. and a Capitellidae sp. (Fig. 3 and Table 1). White and pink microbial mats covered much of the bone surface. We also observed 21 morphospecies of fauna in the immediate vicinity (< 2 m) of the bones including several species of nemerteans, actinarians, echinoderms, poriferans, an unidentified polychaete tubeworm, and unidentified bivalves (Table 1). Bivalves were found within 0.2 m of the skeleton and were completely buried, only visible from their siphons. These were not sampled and so could not be positively identified.

3.4. Variation in community composition along the skeleton

Many of the bone epifauna were distributed differentially along the skeleton (Fig. 4). Mean bacterial-mat cover was less than 5% of surveyed bone surface area on the cervical and thoracic vertebrae (Fig. 4). Bacterial mats were also absent on some of the heavily-sedimented small unidentified fragments of bone (Fig. 4). The highest mean bacterial-mat percentage cover was on the humerus, with 72% of the surveyed bone surface area covered (Fig. 4). The lumbar- and caudal-vertebral region of the skeleton also had high mean bacterial-mat percentage cover (54% and 55% respectively) (Fig. 4). The bacterial mats appeared to be thickest on the anterior and posterior ends of these vertebrae.

Pyropelta sp. were most dense on the sternum (1034 m^{-2}), the mandibles (mean 803 m^{-2}) and the ulna (858 m^{-2}) (Fig. 4). The humerus (445 m^{-2}), skull (322.21 m^{-2}), lumbar vertebrae (mean 282 m^{-2}) and caudal vertebrae (mean 288 m^{-2}) also had high densities of *Pyropelta* sp. (Fig. 4). *Pyropelta* sp. had the lowest

mean densities on the cervical and thoracic vertebrae (20 and 60 m^{-2} respectively), and the small unidentified fragments of bone (62 m^{-2}) (Fig. 4). These low mean densities may have been due to the fact that *Pyropelta* sp. were absent from some of the individual bones of these anatomical types (Fig. 4). *Osedax* sp. were most dense on the mandibles and the thoracic vertebrae (mean 1176 m^{-2} and 765 m^{-2} respectively) (Fig. 4). *Osedax* sp. were least prevalent on the ribs, sternum, humerus, lumbar vertebrae, and caudal vertebrae with all those bone regions having less than mean 220 m^{-2} (Fig. 4). Peracarids were most dense on the mandibles (mean $13,427 \text{ m}^{-2}$) and skull (7338 m^{-2}) (Fig. 4). They were least abundant on the cervical vertebrae (mean 693 m^{-2}) (Fig. 4). Otherwise the peracarids showed a fairly uniform mean presence on surveyed bones with between 1497 m^{-2} and 3652 m^{-2} (Fig. 4). *Jaera* sp. was frequently observed on the trunk or palps of specimens of *Osedax* sp.

The densities of bacterial mats ($p=0.001$), *Pyropelta* sp. ($p<0.0006$) and *Osedax* sp. ($p<0.003$) did differ significantly between the twelve anatomical types of bones. There was however no significant difference for peracarid densities between different anatomical types of bones. The densities of *Pyropelta* sp. and the percentage covers of bacterial mats were strongly positively correlated on surveyed bones ($r=0.579$, $p<0.00001$). Peracarid and *Pyropelta* sp. densities were also strongly positively correlated ($r=0.713$, $p<0.0002$). *Osedax* sp. showed the opposite trend, decreasing in densities with increasing coverage of bacterial mats ($r=-0.508$, $p<0.0002$). On closer inspection of this trend, it appeared that *Osedax* sp. was found only growing on areas of bone devoid of white bacterial mats (Fig. 5).

4. Discussion

4.1. Species, age and successional processes of the whale skeleton

The large size (approximately 10.7 m) of the spread-out skeleton suggested that this was an adult, possibly female, specimen. Average adult lengths for Antarctic minke whales are 8.5 m

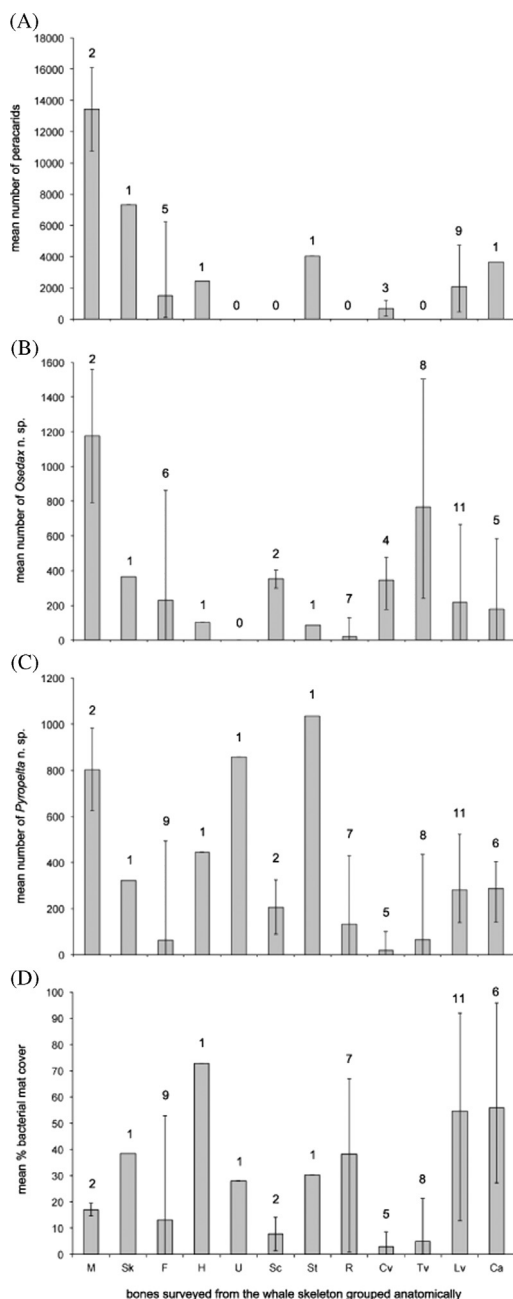


Fig. 4. The microdistribution of fauna on the bones on the whale fall. (a) The mean number of peracarids (amphipods—Lysianassidae sp., and isopods—*Jaera* sp.) per metre squared exposed surface area of bone (b) the mean number of *Osedax* sp. per metre squared exposed surface area of bone (c) the mean number of *Pyropelta* sp. per metre squared exposed surface area of bone (d) the mean percentage of bacterial-mat cover of exposed surface area of bone. Bones were grouped together according to their anatomical types as follows: M—mandible, Sk—skull, F—small unidentified fragment, H—humerus, U—ulna, Sc—scapula, St—sternum, R—rib, Cv—cervical vertebra, Tv—thoracic vertebra, Lv—lumbar vertebra, Ca—caudal vertebra. Numbers above each column are the number (*n*) of bones of that anatomical type where that type of fauna could be quantified. Means $\pm$ SD are indicated by bars on each column.

for males and 9.0 m for females, with a maximum size given as 10.7 m (R. Sabin, personal communication). The size of this whale resulted in the organic enrichment of the sediment and the subsequent creation of anoxic conditions from high microbial oxygen consumption, denoted by blackened sediments below the whale bones and as seen previously at other natural whale falls and emplacement experiments (Allison et al., 1991; Bennett et al.,

1994; Naganuma et al., 1996; Jones et al., 1998; Smith et al., 1998; Smith and Baco, 2003; Glover et al., 2005b, 2008; Braby et al., 2007; Fujiwara et al., 2007; Treude et al., 2009; Lundsten et al., 2010a).

No mobile scavengers were observed at the remains, and all soft tissue had been consumed. The whale fall was thus in either the enrichment-opportunist or sulfophilic stage of decomposition (Smith and Baco, 2003). The sulfophilic stage has been observed to last from six years to several decades, and is typified by the presence of chemosynthetic sulphide-oxidising microorganisms (e.g. *Beggiatoa* spp.) covering the bones (Smith et al., 1989; Allison et al., 1991; Bennett et al., 1994; Deming et al., 1997; Baco and Smith, 2003; Smith and Baco, 2003; Schuller et al., 2004).

Thin long bones, like the mandibles, were fragmented in several places and the cervical and thoracic vertebrae were the most badly-eroded regions of bone. The missing bones tended to be smaller bones, which may have been carried away by currents, or scavenging animals, or these bones may have become completely buried in the sediment or eroded.

The whale fall, despite the advanced successional stage, was still inhabited by a diverse assemblage of organisms, including many species that we have confirmed are as of yet, undescribed to science (being formally described elsewhere). The abundance of undescribed species at this whale fall was not surprising given a historical lack of deep-sea exploration in the region, and the high endemism of fauna in the Southern Ocean resulting from hydrographic isolation by the Polar Front (Orsi et al., 1995; Rogers, 2012; Rogers et al., 2012).

Many of the bone-encrusting fauna observed at this whale fall, however, were from families or genera known to inhabit whale falls and other chemosynthetic environments. The sulfidic conditions found at whale falls can be similar to those found at other chemosynthetic environments such as hydrothermal vents and cold seeps, and consequently some clades and even some species show overlap between these habitats (Tunnicliffe et al., 1996, 2003; Sibuet and Olu, 1998; Smith and Baco, 2003; Treude et al., 2009). For example, *Lepetodrilus* sp. from our whale-fall site, was also found on a variety of substrates at the nearby hydrothermal vents, both within the caldera where the whale fall was found (J. Copley, K. Linse, Marsh, Rogers, personal observation) and at newly-discovered vent fields on the East Scotia Ridge during this research voyage (Rogers et al., 2012). Rogers et al. (2012) observed that this limpet was grazing epizooic microbes at the vent sites, which allows speculation that these limpets were consuming microbes on the whale bones here. *Lepetodrilus* spp. have been found previously at vents, seeps, and whale falls (Desbruyeres et al., 2006; Johnson et al., 2008). The genus *Pyropelta* has also been found previously at vents, seeps and whale falls, and is a known bacterial grazer, while the family Osteopeltidae is comprised of whale-fall specialists (Marshall, 1987; Bennett et al., 1994; Smith et al., 2002; Desbruyeres et al., 2006).

The dorvilleid genus *Ophryotrocha* has been observed in abundance at reducing environments (Bennett et al., 1994; Naganuma et al., 1996; Deming et al., 1997; Baco et al., 1999; Van Dover, 2000; Smith et al., 2002; Baco and Smith, 2003; Smith and Baco, 2003; Rouse et al., 2004; Glover et al., 2005a; Dahlgren et al., 2006; Pleijel et al., 2008; Wiklund et al., 2009; Lundsten et al., 2010a). Wiklund et al. (2009) noted that they depend on the bacterial mats covering the whale bones rather than the whale bones themselves, and thus could live at other chemosynthetic environments if bacterial mats are present. Members of the amphipod family Lysianassidae are frequently found at food falls and are known to be opportunistic scavengers (Jones et al., 1998; Smith and Baco, 2003; Lundsten et al., 2010b). The isopod genus *Jaera* has only previously been recorded in estuaries and shallow

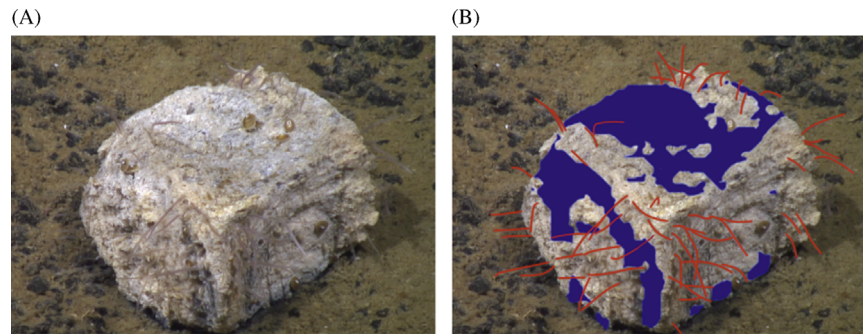


Fig. 5. *Osedax* sp. distribution with regard to bacterial mats. A lumbar vertebra from the whale skeleton showing the surface area of the bone covered by bacterial mats and the location of individuals of *Osedax* sp.

intertidal waters, so its occurrence here in the deep Southern Ocean is remarkable (Linse, personal communication).

The other fauna in the immediate vicinity of the bones could not all be identified to generic level but the clades observed were consistent with those seen at other late-stage whale falls (carideans, bivalves, isopods, actinarians and echinoderms (Marshall, 1987; Bennett et al., 1994; Naganuma et al., 1996; Deming et al., 1997; Baco et al., 1999; Van Dover, 2000; Smith and Baco, 2003; Rouse et al., 2004; Lundsten et al., 2010a). As a result of the lack of positive identifications, it was not clear which of the surrounding fauna were whale-fall specialists or 'background' deep-sea fauna using the whale fall opportunistically as an additional food source (Wiklund et al., 2009). The high species richness during the sulfophilic stage of whale falls is thought to be due to high trophic diversity, with bacterial-mat grazers, species with chemoautotrophic endosymbionts, bone specialists, organic-enrichment respondents, predators and suspension feeders (Bennett et al., 1994; Baco and Smith, 2003).

Fauna with endosymbionts such as bivalve molluscs are typical of the sulfophilic stage in whale-fall ecology (Smith et al., 1989; Bennett et al., 1994; Feldman et al., 1998; Baco et al., 1999; Fujiwara et al., 2009; Lorion et al., 2009; Lundsten et al., 2010a). The unidentified bivalves may have arrived from nearby hydrothermal vents to take advantage of the reducing conditions under the bones. There have, however, been few records of siboglinids other than the bone specialist *Osedax* spp., *Escarpiia spicata* and *Lamellibrachia barhami* at whale falls (Feldman et al., 1998; Rouse et al., 2004; Glover et al., 2005b; Lundsten et al., 2010a). Whale falls, with their combination of sediment, sulphide and hard substratum (bone) may offer an intermediate-habitat type between hard-substratum vents and sedimented-hosted seeps in the evolution of some deep-sea chemosynthetic taxa (Baco et al., 1999; Smith and Baco, 2003).

It can therefore be confidently stated that the caldera whale fall was in the sulfophilic stage of decomposition from several characteristics; (a) there was no evidence of soft tissue present, (b) the bones were significantly eroded with mandibles and ribs fragmented, and vertebral processes missing, (c) there was sustained chemoautotrophic production fuelled by sulphides indicated by abundant bacterial mats growing on the bones and surrounding sediment, (d) the sediments below the bones were black in colour indicating anoxia, and (e) the assemblage of fauna present on and around the skeleton resembled those seen at previous whale falls in the sulfophilic stage (Smith and Baco, 2003).

The caldera-skeleton's condition was compared with other known late-stage whale falls that had sufficient information. Several of the previous whale falls seemed younger than the caldera whale fall based on bone-erosion observations. The carcasses studied by Jones et al. (1998) and Dahlgren et al. (2006) had been on the seafloor for less than a year. Whale-385 and whale-1018 still had vertebral processes after 1.1 years on

the seafloor (Braby et al., 2007), as did whale-382 and whale-633 after 2.4 years and 2.2 years respectively (Lundsten et al., 2010b). The most similarities existed between the Santa Catalina Basin whale fall (Allison et al., 1991; Bennett et al., 1994; Smith and Baco, 2003), the Vancouver whale fall (Lundsten et al., 2010a), the implanted sperm-whale carcasses off Japan (Fujiwara et al., 2007), the Torishima whale fall (Naganuma et al., 1996), whale-2893 (Lundsten et al., 2010b), and the caldera whale fall. All these carcasses shared most of the sulfophilic-stage characteristics (a–e) above. The Vancouver whale fall, the implanted Japanese sperm-whale carcasses and the Torishima whale fall had bones of a similarly-degraded manner but mandibles were intact suggesting that our caldera skeleton may be slightly older (Naganuma et al., 1996; Fujiwara et al., 2007; Lundsten et al., 2010a, 2010b). Bacterial mats were abundant at all six whale-carcass groups and the diverse faunal assemblages were comprised of similar animals e.g. *Ophryotrocha* spp., ophiuroids, amphipods, isopods, *Pyropelta* spp. and other limpets (Bennett et al., 1994; Smith and Baco, 2003; Lundsten et al., 2010a).

The Vancouver whale skeleton was estimated to be at least 6–10 years old and the Torishima whale skeleton, 1–16 years old, based on bivalve-shell size (Naganuma et al., 1996; Lundsten et al., 2010a). The implanted Japanese sperm-whale carcasses had been implanted for three years (Fujiwara et al., 2007) and whale-2893 was on the seafloor for 3.9 years although Lundsten et al. (2010a) had noted that this carcass had degraded extremely rapidly. The Santa Catalina Basin whale fall was aged by Schuller et al. (2004) to 1948 (64 years since death). Therefore, by comparison with other whale-fall observations and data, the caldera whale fall may have been on the deep-sea floor between 4 and 64 years.

4.2. The 'oil-gradient hypothesis'

The estimated age of 4 to 64 years for this whale skeleton allowed for the testing of the 'oil-gradient hypothesis', which proposes that differences in lipid content in different parts of whale skeleton and between different whale species may result in variations in the assemblage structure of whale falls and the rate of degradation of different parts of the skeleton (Higgs et al., 2011b). Although lipid-content data for Antarctic minke whale bones are not available, data from other mysticete whales can be used as a proxy (Higgs et al., 2011b). The most lipid-rich bones in the great whales are the lumbar and caudal vertebrae (40–50% depending on the species), and the humeri (approximately 64%) (Higgs et al., 2011b). The mandibles and skull are estimated to have 20–45%, and the bones of the chest region (scapula, sternum and ribs) 15–30%. The cervical vertebra usually contains less lipid than the lumbar and caudal regions, and the thoracic vertebra contain an even lower lipid content of ~10%.

The bacterial mats on whale bones tend to be sulfophilic (Deming et al., 1997) and are therefore found growing most heavily on the lipid-rich regions of bone. They require sulphide as an energy source for carbon-dioxide fixation and oxygen for the oxidation of the sulphide (Deming et al., 1997). In our study, the mean percentage cover by sulfophilic bacterial mats corresponded to predicted bone–lipid content. The bacterial mats were less prevalent on bones predicted to have lower lipid content, such as the cervical vertebrae, thoracic vertebrae and small unidentified bone fragments. The lumbar and caudal vertebrae, and the humerus (bones with high lipid content) exhibited the highest percentage coverage of bacterial mats, specifically on the anterior and posterior ends of these vertebrae. The skull and mandibles tended to have more bacterial mats than the cervical and thoracic vertebrae, but less than the other bones. Trends such as these have been seen previously: Bennett et al. (1994) reported that bacterial mats were largely absent from buried or highly-degraded ribs and thoracic vertebrae, with heaviest coverage seen on anterior and posterior ends of vertebrae. In addition, regions of the skull and caudal vertebrae were the most covered in bacterial mats (Bennett et al., 1994). Lundsten et al. (2010a) observed bacterial mats covering at least small portions of the lower vertebrae as well as the skull and jaws. Treude et al. (2009) witnessed large changes in bacterial-mat coverage over a one-year period for a six- to seven-year-old carcass. At first, the skull, thoracic vertebrae and ribs were most covered but one year later the skull and ribs showed decreases in bacterial-mat coverage but still retained the most cover. Bones like the thoracic- and caudal-vertebral regions, however, showed large decreases (approximately 30%) in cover.

The genus *Pyropelta* is comprised of bacterial grazers and so it follows that these limpets would be most abundant on the bones with the most bacterial-mat coverage, as was seen at this skeleton. There may have been other bacterial grazers, such as dorvilleids, that were overlooked, as they were too small to be seen in the video footage. The *Osedax* sp. had the greatest abundance on bones with predicted lower lipid content, such as the mandibles, and the cervical and thoracic vertebrae, and was rarest on the high-lipid bones; the lumbar and caudal vertebrae, and the humerus. The densities of *Osedax* sp. on the bones was negatively correlated with the percentage cover by bacterial mats with *Osedax* sp. found only growing on areas of bone devoid of white bacterial mats. This may have been as a result of (1) competition for space with the bacterial mats; (2) ecosystem engineering by the burrowing activity of *Osedax* sp., which may facilitate the influx of oxygen into bones and thus limit the anaerobic decomposition of bone lipids. However, burrowing by *Osedax* may also promote escape of sulphide (Higgs et al., 2011a) or influx of seawater sulphate for increased sulphate reduction (Treude et al., 2009). Conversely, measurements of the micro-environment between individual *Osedax* roots and their bone matrix indicate anoxic conditions (Huusgaard et al., 2012); (3) the anaerobic breakdown of bone lipids creating a high-sulphide environment that is not conducive to *Osedax* sp. growth or settlement; (4) *Osedax* sp. may secrete a substance inhibiting bacterial-mat growth in the immediate vicinity of the worm, although no evidence of this has been found thus far. Overall, a similar trend for macrofauna in general was previously reported by Bennett et al. (1994), where there was a near-total absence of all macrofauna from yellow and white microbial mats occurring on the anterior and posterior ends of vertebrae.

The occurrence of *Osedax* sp. also corresponded with the high levels of erosion seen in the thoracic and cervical vertebrae. *Osedax* bore into bones in high densities contributing to their rapid degradation and this can have huge taphonomic significance (Braby et al., 2007; Higgs et al., 2010, 2011b; Kiel et al.,

2010). Lundsten et al. (2010b) noted that the skulls of whales off California were slow to be colonized by *Osedax* and also took the most time to degrade, highlighting the potential influential effect *Osedax* can have on bones. This bone erosion can be as high as 6% per year and possibly even higher depending on the species and the location (Higgs et al., 2011a). The collagen and proteinaceous areas that the *Osedax* rely on for nutrition via bacterial endosymbionts (Goffredi et al., 2005, 2007; Higgs et al., 2011a) may be more plentiful or easier to access in bones with lower lipid content—the ‘oil-protection theory’ (Higgs et al., 2011b). Higgs et al. (2011b) states “it may be that the bioeroding organisms in the seawater are excluded from the bones by the hydrophobic oils, or that the breakdown of the lipids creates an environment that is not conducive to bioeroding micro-organisms (e.g. high sulphide levels)”. Even though information in the literature regarding differential patterns of erosion at whale falls was sparse, Dominici et al. (2009) observed increased levels of degradation of thoracic vertebrae compared with lumbar and caudal ones in fossil skeletons. This has also been seen at recent whale falls (Bennett et al., 1994; Naganuma et al., 1996; Lundsten et al., 2010a). Allison et al. (1991) and Naganuma et al. (1996) specifically mentioned rib degradation and Bennett et al. (1994) noted vertebrae and rib degradation.

Goffredi et al. (2005) and Braby et al. (2007) noted that *Osedax rubiplumus* were most prevalent on enamel-covered bones like the ribs and mandibles whereas *O. frankpressi*, *O. roseus*, *O.* ‘yellow collar’ and *O.* ‘orange collar’ preferred vertebral processes. *Osedax* ‘spiral’ was observed growing on degraded and sedimented bone fragments (Braby et al., 2007). *O. japonicus* have been observed growing on bone, blubber and spermaceti (Fujikura et al., 2006; Fujiwara et al., 2007). *Osedax* spp. have even been observed growing on quadruped bones (Jones et al., 2008; Vrijenhoek et al., 2008) and teleost vertebrae (Rouse et al., 2011). This evidence suggests that even though *Osedax* spp. does feed on the organic content at whale skeletons, the exact preference of nutritional material taken from the bone may differ between species and so the occurrence of *Osedax* sp. may be as a result of species preference also. There may be other influential factors such as succession of *Osedax* spp. (Braby et al., 2007), competition for resources, and environmental parameters such as sedimentation also (Glover et al., 2008).

5. Conclusions

This was the first natural whale fall to be observed in the Southern Ocean, despite this area harbouring an abundance of large cetaceans. The presence of large amounts of lipids in the bones showed that the carcass was still able to support life on the seafloor even after a considerable time, and the diverse faunal assemblage found on this skeleton included several undescribed species. The study of this whale skeleton has shown that there is evidence for the ‘oil-gradient hypothesis’. Further exploration of the deep sea in this area is necessary for the taxonomy of fauna and the biogeographic patterns of chemosynthetic ecosystems in this ocean to be clarified.

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