Deep-Sea Research Part 1 (*in press*)

Title: Discovery of a recent, natural whale fall on the continental slope off Anvers Island, western Antarctic Peninsula

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Abstract

Whale falls provide a substantial, nutrient-rich resource for species in areas of the ocean that may otherwise be largely devoid of food. We report the discovery of a natural whale fall at 1430 m depth in the cold waters of the continental slope off the western Antarctic Peninsula. This is the highest latitude whale fall reported to date. The section of the carcass we observed—the tail fluke—was more complete than any previously reported natural whale fall from the deep sea and in the early stages of decomposition. We estimate the entire cetacean to measure 5 to 8 m in length. The flesh remained almost intact on the carcass but the skin was missing from the entire section except for the end of the fluke, clearly exposing blubber and soft tissue. The absence of skin indicates rapid and homogenous loss. The dominant macrofauna present were crustaceans, including most prominently the lithodid crab *Paralomis birsteini*, and zoarcid fish typical of the 'mobile-scavenger' successional stage. The density of mobile macrofauna was greatest on the carcass and declined to background levels within 100 m, indicating that they were attracted to the whale fall. This whale fall offers an important opportunity to examine the decomposition of a carcass under deep-sea conditions at polar latitudes.

Keywords:

Polar; Deep Sea; Food Fall; Cetacean; Mobile-Scavenger; *Paralomis birsteini*, Whale Fall

1. Introduction

When a whale carcass falls to the seafloor it delivers a sudden and enormous input of organic carbon. Such food falls constitute an important source of energy and nutrients to otherwise oligotrophic environments, which include large areas of the deep sea (Baco and Smith, 2003; Smith and Baco, 2003; Glover et al., 2010; Amon et al., 2013). The longevity of a whale fall may vary from less than 10 years in oxygen-rich environments to 50 years or more in oxygen-poor environments (Smith and Baco, 2003; Fujiwara et al., 2007; Glover et al., 2010; Lundsten et al., 2010b). During its lifetime, the food, habitat, and shelter that a whale fall provides attract a diverse and dense faunal assemblage which changes through succession over time. The species richness on a single whale fall can exceed 200 species across the various successional stages of decay; the diversity of associated taxa may include food-fall specialists, and species associated with hydrothermal-vent and cold-seep environments (Smith et al., 1989; Bennett et al., 1994; Baco and Smith, 2003; Smith and Baco, 2003; Lundsten et al., 2010a; Amon et al., 2013).

The decomposition of a whale fall varies substantially between carcasses and is affected by factors including carcass size, associated faunal assemblage, water depth and water temperature (Allison et al., 1991; Smith and Baco 2003; Fujiwara et al. 2007; Lundsten et al., 2010b). Four successional stages have been proposed: (1) a ‘mobile-scavenger’ stage usually lasting approximately four months to two years, in which scavengers remove the soft tissue from the carcass; (2) an ‘enrichment-opportunist’ stage, also typically lasting months to years, in which opportunistic polychaetes and crustaceans densely colonize organically enriched sediments and exposed bones; (3) a ‘sulfophilic’ stage typically lasting decades, in which a species-rich, sulfur-loving assemblage thrives on the skeleton as sulfide is produced from the anaerobic breakdown of bone lipids; and (4) a ‘reef’ stage in which suspension feeders opportunistically settle on the remaining hard substrate after nutrients have been depleted (Smith et al., 1989; Smith and Baco, 2003; Goffredi et al., 2004; Lundsten et al., 2010a, 2010b). The presence and duration of each successional stage is case-dependent; under some conditions each stage can progress slowly, while under other conditions, the rate of decomposition can be so rapid that particular stages are short or absent (Smith et al., 2002; Goffredi et al., 2004; Braby et al., 2007; Lundsten et al., 2010a, b).

Today, more than 850,000 whale carcasses are estimated to be scattered on the seafloor globally at various stages of decomposition (Smith and Baco, 2003). Despite their abundance, their discovery is rare and only six natural whale falls have been studied *in situ* (Table 1). Of these, five were discovered in the sulphofilic stage (Smith et al., 1989, Fujioka et al., 1993; Smith and Baco, 2003; Lundsten et al., 2010a; Amon et al., 2013) and one predominantly in the enrichment-opportunist stage (Goffredi et al., 2004).

In this paper, we report the discovery of a seventh natural whale fall, located off the western Antarctic Peninsula (WAP), close to the United States Antarctic Program's Palmer Station. We describe the condition of this largely intact carcass and the associated faunal assemblage. The carcass is the southernmost (and highest-latitude) natural whale fall reported to date and is also in an earlier stage of decomposition than any other natural whale fall previously described.

2. Methods and Study Site

The whale fall was discovered on the continental slope off Anvers Island, Antarctica, on 24 November, 2013, during cruise NBP13-10 of the *RV Nathaniel B. Palmer*. The carcass is located at 64°07.09' S, 66°34.94' W, lying in a north-south orientation perpendicular to the shallow gradient of the continental slope at a depth of 1430 m (Fig. 1). Water temperature at the observation site was 0.82 °C. In this area the continental slope is relatively uniform and the gullies caused by post-glacial ice retreat, which characterize some shelf areas along the WAP, are absent. The substrate consists of fine sediment scattered with occasional glacial dropstones (Fig. 2a).

Images of the whale fall were obtained using SeaSled, a towed-camera vehicle (see Singh et al., 2007 and Eastman et al., 2013 for descriptions) during photography of a 10-km transect of the seafloor running north-to-south along the continental slope in a depth range of 1300 to 1470 m. Images were taken every 6 sec, providing an imaged corridor 2 m wide along the sea floor. SeaSled was equipped with two cameras (both 1.4-megapixel, or 1360 x 1024 pixels), two strobes (150 w-s), an acoustic-doppler current profiler (ADCP; 1200 kHz Teledyne RD Instruments), a Paroscientific depth sensor, and a CTD (Seabird SBE-49 Fast CAT 16-Hz CTD).

All mobile macrofauna visible on the whale fall, and 10 m north and south of its location along the imaged corridor, were recorded and identified to the lowest possible taxonomic level. Densities were established for macrofauna in direct contact with the carcass, within 2 m of the carcass, and 2 – 10 m from the carcass. Fish and crustaceans were also recorded at 50-m intervals, extending 300 m north and south of the whale fall, in order to calculate densities.

3. Results

3. 1. Description of carcass

The image mosaic shows a 2.25 m tail-section of a small cetacean (Fig. 2a). The section observed appears to be roughly one third of the whole carcass, and from this we estimate the entire animal to measure 5 to 8 m in length. The carcass was in the early stages of decomposition and in the 'mobile-scavenger' successional stage. The skin was missing from the entire section, clearly exposing the blubber and soft tissue, except at the very end of the fluke (Fig. 2a, d). The flesh remained almost intact with the exception of the fluke, and the right side of the tail-section where the tissue appears to have been torn into strips (Fig. 2a). Small pieces of flesh also appeared to be scattered on the sediment surrounding the carcass.

3.2. Species assemblage at whale fall

The whale-fall assemblage was dominated by crustaceans and fish. The lithodid *Paralomis birsteini* Macpherson, 1988 (= *P. spectabilis* Birstein and Vinogradov, 1967, not Hansen, 1908) and an unidentified zoarcid were present in the highest densities (Fig. 2; Table 2). Unidentified species of amphipods, the nemertean worm *Parborlasia corrugatus*, and the macrourid fish *Macrourus whitsoni* were also present on or near the whale fall. Benthic invertebrates typical of the Antarctic continental slope, such as sessile anthozoans and mobile holothurians, echinoids, and ophiuroids dominated the surrounding area (Table 2). These taxa were not observed on the carcass. The density of crustaceans and fish was greatest on the whale fall and decreased to background levels within 100 m of the carcass (Fig. 3; Table 2).

4. Discussion

The whale fall reported here was in an earlier stage of decomposition than any natural whale fall reported to date, in addition to being located at higher latitude and in colder water than any natural or implanted whale fall previously studied. Given the location, the species is most likely a juvenile or adult minke whale, *Balaenoptera bonaerensis*.

The macrofauna associated with the carcass were primarily crustaceans and fish, which are typical of the 'mobile-scavenger' successional stage. Amphipods (Jones et al., 1998; Dahlgren et al., 2006; Fujiwara et al., 2007; Lundsten et al., 2010a), lithodid crabs (Williams et al., 2000; Lundsten et al., 2010a, 2010b), and zoarcid and macrourid fish (Jones et al., 1998; Goffredi et al., 2004) have previously been observed in association with both natural and implanted whale falls globally. These taxa are inferred to be attracted to the enriched food-source by its odor plume. In the present study, attraction to the site is evident from the increase in macrofaunal densities with proximity to the whale fall, as observed in other cases (Smith and Baco, 2003). Other invertebrate macrofauna observed in the vicinity of the whale fall were invertebrates that are typical of the Antarctic slope environment, the densities of which did not appear to increase with proximity to the carcass.

The intact condition of the whale fall indicates that it was very recent; implantation experiments have previously shown that flesh is removed in significant quantities within two weeks (Jones et al., 1998; Smith and Baco, 2003; Dahlgren et al., 2006; Glover et al., 2010). In the present example, the flesh was almost entirely intact and the only obvious damage was the shredding of tissue on the side of the carcass, which we propose was the result of feeding by *P. birsteini* (Fig. 2b), or possibly *M. whitsoni*. The intact state of the whale fall suggests that it likely occurred during Austral Spring 2013 and had been on the seabed for a short period prior to observation. In contrast to the intact state of the flesh, however, the skin was missing almost entirely, suggesting rapid and homogenous loss. Mobile-scavengers are typically non-selective, consuming flesh and skin simultaneously (Glover et al. 2010), and to our knowledge the loss of skin without a concurrent loss of flesh has not previously been reported on a whale fall. Our images are reminiscent of a whale fall observed in the North Atlantic (Dahlgren et al., 2006) and a second observed in the North Pacific (Smith et al., 2006), in which the loss of skin is likewise evident in images of a relatively complete carcass.

The independent loss of skin observed here suggests it might have been targeted by a selective scavenger. We regard the lithodid crabs on and adjacent to the fluke as unlikely candidates because they showed no preference for the remaining skin and instead were targeting the flesh. The zoarcids adjacent to the remaining skin on the fluke could have been consuming it, but this preference also seems unlikely considering to the number of zoarcids apparently consuming flesh at other points on the carcass. Amphipods or macrourid fish, or, less likely, nemertean worms could have been responsible for the skin removal; it is possible that the densities of these species we observed were underestimated by the resolution of the images and that they were actually present in greater numbers. Although notothenioid fish, including the Antarctic toothfish *Dissostichus mawsoni*, are found in high densities in waters around the WAP (Eastman et al., 2013), no notothenioids were observed on the carcass. They generally possess weak jaw muscles that are unlikely to be capable of piercing and specifically removing whale skin. An alternative explanation for the lack of skin is spontaneous sloughing during early decomposition. It is unlikely that sloughing would have resulted in the complete and uniform loss of skin we observed here, but such splitting and shedding would have facilitated skin fragmentation. Sloughing may promote rapid removal of skin by scavengers by increasing the ease with which it can be manipulated.

During the decomposition of a whale fall some successional stages may be lacking, or they may overlap in the timing of their occurrence (Smith et al., 2002; Goffredi et al., 2004; Braby et al., 2007; Lundsten et al., 2010a, b). The duration of each successional stage varies among carcasses, although earlier stages, which occur over relatively short periods, may be difficult to distinguish.

The whale fall reported here is located relatively deep and in colder water than has been reported for any previous whale fall, natural or implanted. Low temperature and great depth increase preservation (Allison et al., 1991) and may decrease the rate at which scavengers consume tissue. The comprehensive removal of skin from the carcass, without visible degradation of flesh, suggests the possibility of an additional early successional stage during which the skin is removed by scavengers, probably aided by skin sloughing during decomposition. It is entirely possible that this stage has previously been masked by the rapid onset of the mobile-scavenger stage. This also suggests that the whale fall may be older than estimated based on the timescales of previously proposed successional stages; although certainly recent, the complete loss of skin suggests it may be months-old rather than weeks-old.

Lithodid crabs are generalized predators that feed on a mixture of benthic invertebrates and carrion (Jewett and Feder, 1982; Comoglio and Amin, 1999; Williams et al., 2000; Jørgensen 2005; Lundsten et al., 2010b; Smith et al. 2011). They have been observed to feed at whale falls for many years, across multiple generations and successional stages, initially thriving on the available soft tissue and then for decades after on the small invertebrates that the whale fall continues to attract (Smith et al., 1989; Williams et al., 2000; Baco and Smith, 2003; Smith and Baco, 2003; Goffredi et al., 2004; Glover et al., 2010; Lundsten et al., 2010b; Amon et al., 2013). Despite their broad spatial distribution along the WAP, however (Arana and Retamal, 1999; Thatje and Arntz, 2004; Thatje et al., 2005, 2008), lithodids are absent from waters below 0 °C and are rarely observed at temperatures below 0.5 °C (Griffiths et al. 2013; for discussion on physiological limits, see Thatje et al. 2005). Because feeding is typically impaired at a species' thermal limits, our observation of active feeding by *P. birsteini* at 0.82 °C is important to ongoing discussion about the lower thermal limits of this king crab in particular and lithodids in general (Hall and Thatje 2011).

The whale fall reported here offers an important opportunity to examine the decomposition of a carcass in a unique environment. The rate of decay is likely to be slow due to the low temperature and great depth. This whale fall may provide the opportunity to study the long-term effects of a large food fall on a unique and fragile environment.

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Tables and Figures

Table 1: Natural whale falls reported in literature. NR indicates information not reported in study.

Depth (m)	Geographic region	Latitude	Longitude	Temperature	Dominant stage at discovery	Estimated age at discovery	Reference
1444	Southern Ocean	59°41' S	28°21' W	NR	Sulfophilic	4 – 64 yr	Amon et al., 2013
960	Northeast Pacific Ocean	33°20' N	119°59' W	NR	Sulfophilic	5 – 15 yr	Smith and Baco, 2003
1240	Northeast Pacific Ocean	33°12' N	118°30' W	4.1 °C	Sulfophilic	3 – 34 yr	Smith et al., 1989
1288	Northeast Pacific Ocean	48°40' N	126°50' W	NR	Sulfophilic	< 10 yr	Lundsten et al., 2010a
4037	Northwestern Pacific Ocean	30°55' N	141°49' E	NR	Sulfophilic	NR	Fujioka et al., 1993
2891	Northeast Pacific Ocean	36°36' N	122°26' W	1.67 °C	Enrichment-opportunist	< 1 yr	Goffredi et al., 2004
1430	**Southern Ocean**	**64°07' S**	**66°35' W**	**0.8 °C**	**Mobile-scavenger**	**< 2 mo**	**Present study**

Table 2: Mobile animal taxa observed on or around the whale fall, identified to the highest taxonomic level possible through high-resolution images.

Taxon	Density (ind/m^2) On whale fall	< 2 m from fall	2-10 m from fall
Arthropoda	(25.9)	(0.1)	
Malacostraca			
Amphipoda (unidentified)	9.7	-[1]	-[1]
Decapoda			
Lithodidae, 1sp. (*Paralomis birsteini*)	16.2	0.1	(0.03)
Chordata			
Actinopterygii	(22.6)	(0.6)	(0.3)[2]
Perciformes			
Zoarcidae, 1 sp. (unidentified)	22.6	0.3	-
Gadiformes			
Macrouridae, 1 sp. (*Macrourus whitsoni*)	0	0.3	-
Echinodermata			
Echinoidea, 1 sp. (unidentified)	0	1.25	0.44
Ophiuroidea, 2 sp. (unidentified)	0	3.5	0.69
Holothuroidea, 1 sp. (unidentified)	0	0.25	0.03
Nemertea,			
Anopla			
Lineidae, 1 sp. (*Parborlasia corrugatus*)	-[3]	0.5	0.03
Mollusca			
Gastropoda, 1 sp. (unidentified)	0	0	0.03

[1]Amphipods were only counted on the whale fall as image quality did not allow them to be observed clearly in the surrounding area. [2]Individuals were identified to superclass only. [3]Nemerteans were not observed on the whale fall but it is likely this is due to similarity in color to the whale tissue.

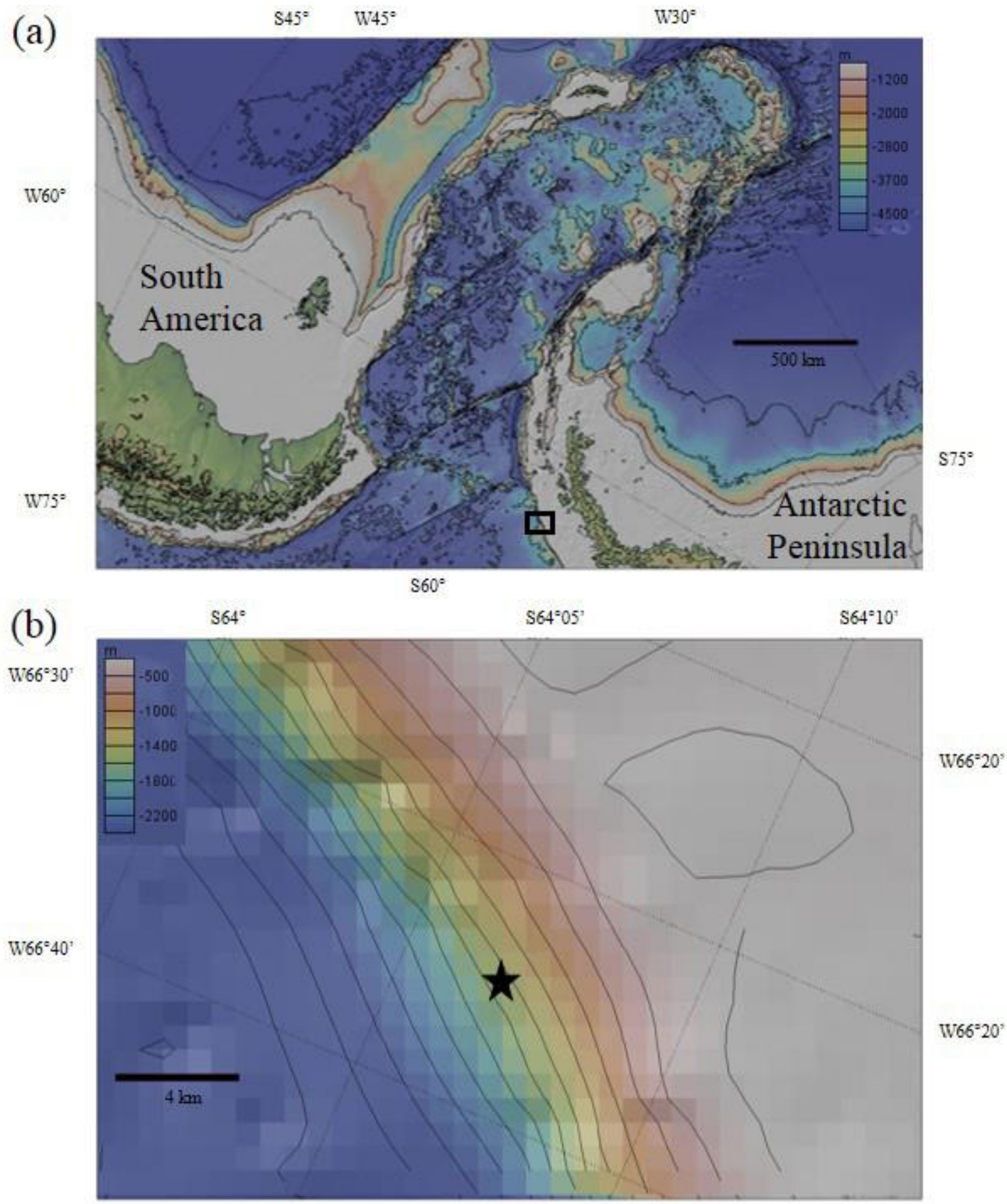

Figure 1. Location of whale fall. (a) Bathymetry of the surrounding region. Contour lines are 1000 m. (b) Local bathymetry of the area surrounding the whale fall. Exact location of whale fall denoted by ★. Contour lines are 200 m. Location of (b) is marked in (a) by open black rectangle. Bathymetry constructed in GeoMapApp. Bathymetry data from Smith and Sandwell (1997).

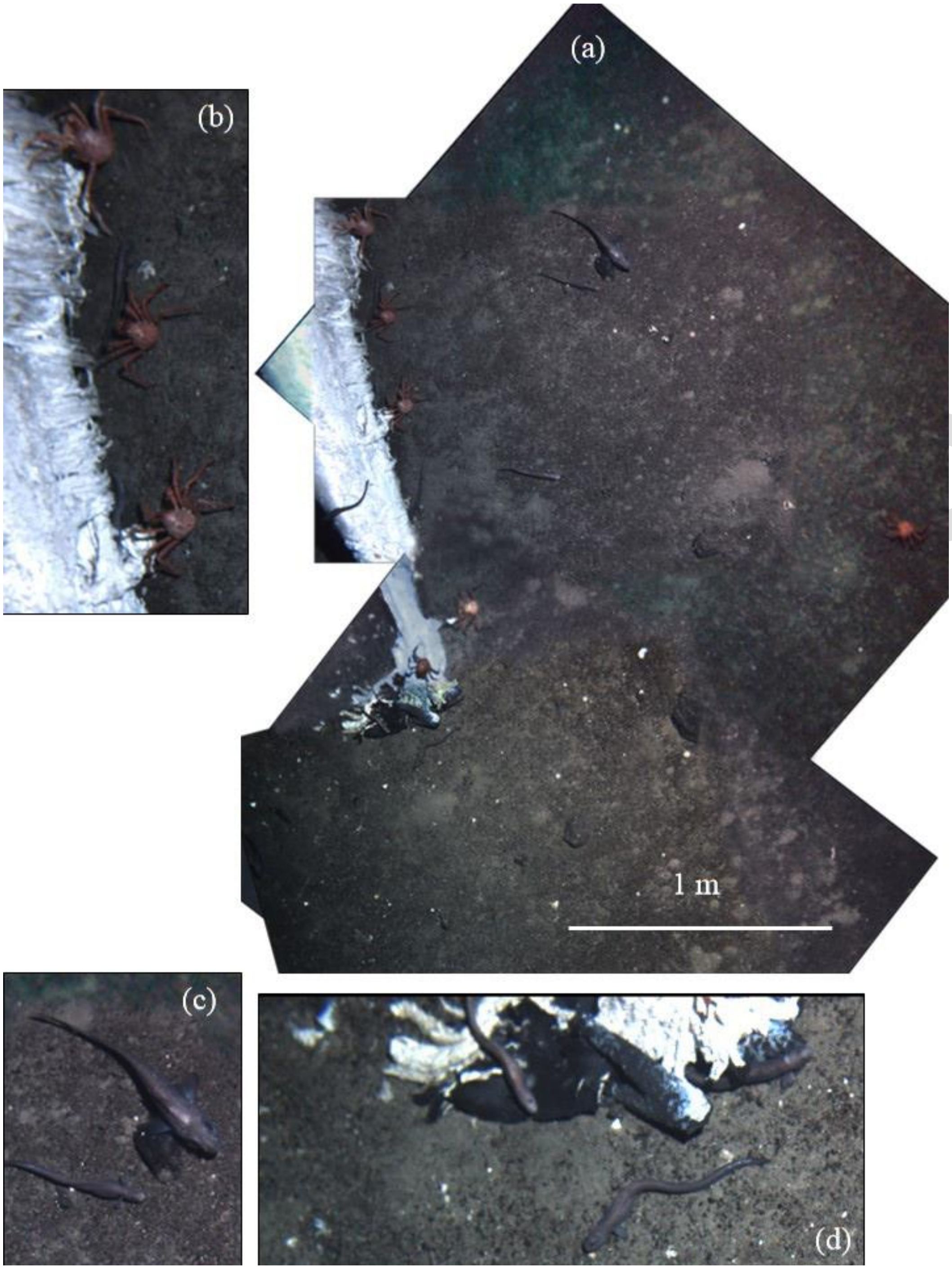

Figure 2. (a) Photo-mosaic of whale fall from images collected by SeaSled. Area shown is approximately 7 m^2. (b) Three individuals of *Paralomis birsteini* feeding on carcass. (c) *Macrourus whitsoni* (top) and unidentified zoarcid (bottom). (d) Fluke of carcass showing remaining skin (dark section at bottom of fluke).

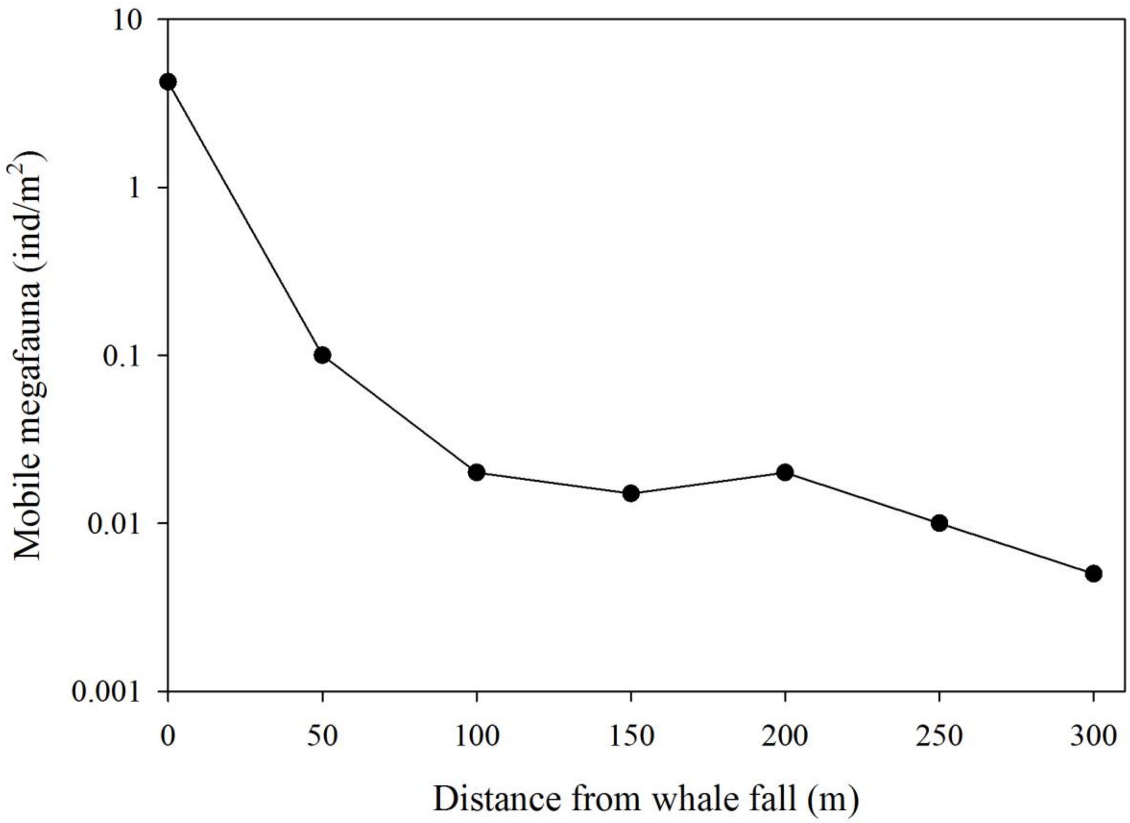

Figure 3. Density of crustaceans and fish with distance from the whale fall.