

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

2

3 **Title: Discovery of a recent, natural whale fall on the continental slope off**

4 **Anvers Island, western Antarctic Peninsula**

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18 **Abstract**

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

34 **Keywords:**

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

36

37

38 **1. Introduction**

39 When a whale carcass falls to the seafloor it delivers a sudden and enormous input of organic  
40 carbon. Such food falls constitute an important source of energy and nutrients to otherwise  
41 oligotrophic environments, which include large areas of the deep sea (Baco and Smith, 2003;  
42 Smith and Baco, 2003; Glover et al., 2010; Amon et al., 2013). The longevity of a whale fall may  
43 vary from less than 10 years in oxygen-rich environments to 50 years or more in oxygen-poor  
44 environments (Smith and Baco, 2003; Fujiwara et al., 2007; Glover et al., 2010; Lundsten et al.,  
45 2010b). During its lifetime, the food, habitat, and shelter that a whale fall provides attract a  
46 diverse and dense faunal assemblage which changes through succession over time. The species  
47 richness on a single whale fall can exceed 200 species across the various successional stages of  
48 decay; the diversity of associated taxa may include food-fall specialists, and species associated  
49 with hydrothermal-vent and cold-seep environments (Smith et al., 1989; Bennett et al., 1994;  
50 Baco and Smith, 2003; Smith and Baco, 2003; Lundsten et al., 2010a; Amon et al., 2013).

51 The decomposition of a whale fall varies substantially between carcasses and is affected by  
52 factors including carcass size, associated faunal assemblage, water depth and water temperature  
53 (Allison et al., 1991; Smith and Baco 2003; Fujiwara et al. 2007; Lundsten et al., 2010b). Four  
54 successional stages have been proposed: (1) a ‘mobile-scavenger’ stage usually lasting  
55 approximately four months to two years, in which scavengers remove the soft tissue from the  
56 carcass; (2) an ‘enrichment-opportunist’ stage, also typically lasting months to years, in which  
57 opportunistic polychaetes and crustaceans densely colonize organically enriched sediments and  
58 exposed bones; (3) a ‘sulfophilic’ stage typically lasting decades, in which a species-rich, sulfur-  
59 loving assemblage thrives on the skeleton as sulfide is produced from the anaerobic breakdown  
60 of bone lipids; and (4) a ‘reef’ stage in which suspension feeders opportunistically settle on the  
61 remaining hard substrate after nutrients have been depleted (Smith et al., 1989; Smith and Baco,

62 2003; Goffredi et al., 2004; Lundsten et al., 2010a, 2010b). The presence and duration of each  
63 successional stage is case-dependent; under some conditions each stage can progress slowly,  
64 while under other conditions, the rate of decomposition can be so rapid that particular stages are  
65 short or absent (Smith et al., 2002; Goffredi et al., 2004; Braby et al., 2007; Lundsten et al.,  
66 2010a, b).

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

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

78

## 79 **2. Methods and Study Site**

80 The whale fall was discovered on the continental slope off Anvers Island, Antarctica, on 24  
81 November, 2013, during cruise NBP13-10 of the *RV Nathaniel B. Palmer*. The carcass is located  
82 at 64°07.09' S, 66°34.94' W, lying in a north-south orientation perpendicular to the shallow  
83 gradient of the continental slope at a depth of 1430 m (Fig. 1). Water temperature at the

84 observation site was 0.82 °C. In this area the continental slope is relatively uniform and the  
85 gullies caused by post-glacial ice retreat, which characterize some shelf areas along the WAP,  
86 are absent. The substrate consists of fine sediment scattered with occasional glacial dropstones  
87 (Fig. 2a).

88 Images of the whale fall were obtained using SeaSled, a towed-camera vehicle (see Singh et al.,  
89 2007 and Eastman et al., 2013 for descriptions) during photography of a 10-km transect of the  
90 seafloor running north-to-south along the continental slope in a depth range of 1300 to 1470 m.  
91 Images were taken every 6 sec, providing an imaged corridor 2 m wide along the sea floor.  
92 SeaSled was equipped with two cameras (both 1.4-megapixel, or 1360 x 1024 pixels), two  
93 strobes (150 w-s), an acoustic-doppler current profiler (ADCP; 1200 kHz Teledyne RD  
94 Instruments), a Paroscientific depth sensor, and a CTD (Seabird SBE-49 Fast CAT 16-Hz CTD).

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

100

### 101 **3. Results**

#### 102 ***3. 1. Description of carcass***

103 The image mosaic shows a 2.25 m tail-section of a small cetacean (Fig. 2a). The section  
104 observed appears to be roughly one third of the whole carcass, and from this we estimate the

105 entire animal to measure 5 to 8 m in length. The carcass was in the early stages of decomposition  
106 and in the ‘mobile-scavenger’ successional stage. The skin was missing from the entire section,  
107 clearly exposing the blubber and soft tissue, except at the very end of the fluke (Fig. 2a, d). The  
108 flesh remained almost intact with the exception of the fluke, and the right side of the tail-section  
109 where the tissue appears to have been torn into strips (Fig. 2a). Small pieces of flesh also  
110 appeared to be scattered on the sediment surrounding the carcass.

### 111 **3.2. Species assemblage at whale fall**

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

121

## 122 **4. Discussion**

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

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

138 The intact condition of the whale fall indicates that it was very recent; implantation experiments  
139 have previously shown that flesh is removed in significant quantities within two weeks (Jones et  
140 al., 1998; Smith and Baco, 2003; Dahlgren et al., 2006; Glover et al., 2010). In the present  
141 example, the flesh was almost entirely intact and the only obvious damage was the shredding of  
142 tissue on the side of the carcass, which we propose was the result of feeding by *P. birsteini* (Fig.  
143 2b), or possibly *M. whitsoni*. The intact state of the whale fall suggests that it likely occurred  
144 during Austral Spring 2013 and had been on the seabed for a short period prior to observation. In  
145 contrast to the intact state of the flesh, however, the skin was missing almost entirely, suggesting  
146 rapid and homogenous loss. Mobile-scavengers are typically non-selective, consuming flesh and  
147 skin simultaneously (Glover et al. 2010), and to our knowledge the loss of skin without a  
148 concurrent loss of flesh has not previously been reported on a whale fall. Our images are  
149 reminiscent of a whale fall observed in the North Atlantic (Dahlgren et al., 2006) and a second

150 observed in the North Pacific (Smith et al., 2006), in which the loss of skin is likewise evident in  
151 images of a relatively complete carcass.

152 The independent loss of skin observed here suggests it might have been targeted by a selective  
153 scavenger. We regard the lithodid crabs on and adjacent to the fluke as unlikely candidates  
154 because they showed no preference for the remaining skin and instead were targeting the flesh.  
155 The zoarcids adjacent to the remaining skin on the fluke could have been consuming it, but this  
156 preference also seems unlikely considering to the number of zoarcids apparently consuming flesh  
157 at other points on the carcass. Amphipods or macrourid fish, or, less likely, nemertean worms  
158 could have been responsible for the skin removal; it is possible that the densities of these species  
159 we observed were underestimated by the resolution of the images and that they were actually  
160 present in greater numbers. Although notothenioid fish, including the Antarctic toothfish  
161 *Dissostichus mawsoni*, are found in high densities in waters around the WAP (Eastman et al.,  
162 2013), no notothenioids were observed on the carcass. They generally possess weak jaw muscles  
163 that are unlikely to be capable of piercing and specifically removing whale skin. An alternative  
164 explanation for the lack of skin is spontaneous sloughing during early decomposition. It is  
165 unlikely that sloughing would have resulted in the complete and uniform loss of skin we  
166 observed here, but such splitting and shedding would have facilitated skin fragmentation.  
167 Sloughing may promote rapid removal of skin by scavengers by increasing the ease with which it  
168 can be manipulated.

169 During the decomposition of a whale fall some successional stages may be lacking, or they may  
170 overlap in the timing of their occurrence (Smith et al., 2002; Goffredi et al., 2004; Braby et al.,  
171 2007; Lundsten et al., 2010a, b). The duration of each successional stage varies among carcasses,  
172 although earlier stages, which occur over relatively short periods, may be difficult to distinguish.



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

183 Lithodid crabs are generalized predators that feed on a mixture of benthic invertebrates and  
184 carrion (Jewett and Feder, 1982; Comoglio and Amin, 1999; Williams et al., 2000; Jørgensen  
185 2005; Lundsten et al., 2010b; Smith et al. 2011). They have been observed to feed at whale falls  
186 for many years, across multiple generations and successional stages, initially thriving on the  
187 available soft tissue and then for decades after on the small invertebrates that the whale fall  
188 continues to attract (Smith et al., 1989; Williams et al., 2000; Baco and Smith, 2003; Smith and  
189 Baco, 2003; Goffredi et al., 2004; Glover et al., 2010; Lundsten et al., 2010b; Amon et al., 2013).  
190 Despite their broad spatial distribution along the WAP, however (Arana and Retamal, 1999;  
191 Thatje and Arntz, 2004; Thatje et al., 2005, 2008), lithodids are absent from waters below 0 °C  
192 and are rarely observed at temperatures below 0.5 °C (Griffiths et al. 2013; for discussion on  
193 physiological limits, see Thatje et al. 2005). Because feeding is typically impaired at a species'  
194 thermal limits, our observation of active feeding by *P. birsteini* at 0.82 °C is important to

195 ongoing discussion about the lower thermal limits of this king crab in particular and lithodids in  
196 general (Hall and Thatje 2011).

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

201

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210

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In press

## 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
<b>1430</b>	<b>Southern Ocean</b>	<b>64°07' S</b>	<b>66°35' W</b>	<b>0.8 °C</b>	<b>Mobile-scavenger</b>	<b>&lt; 2 mo</b>	<b>Present study</b>

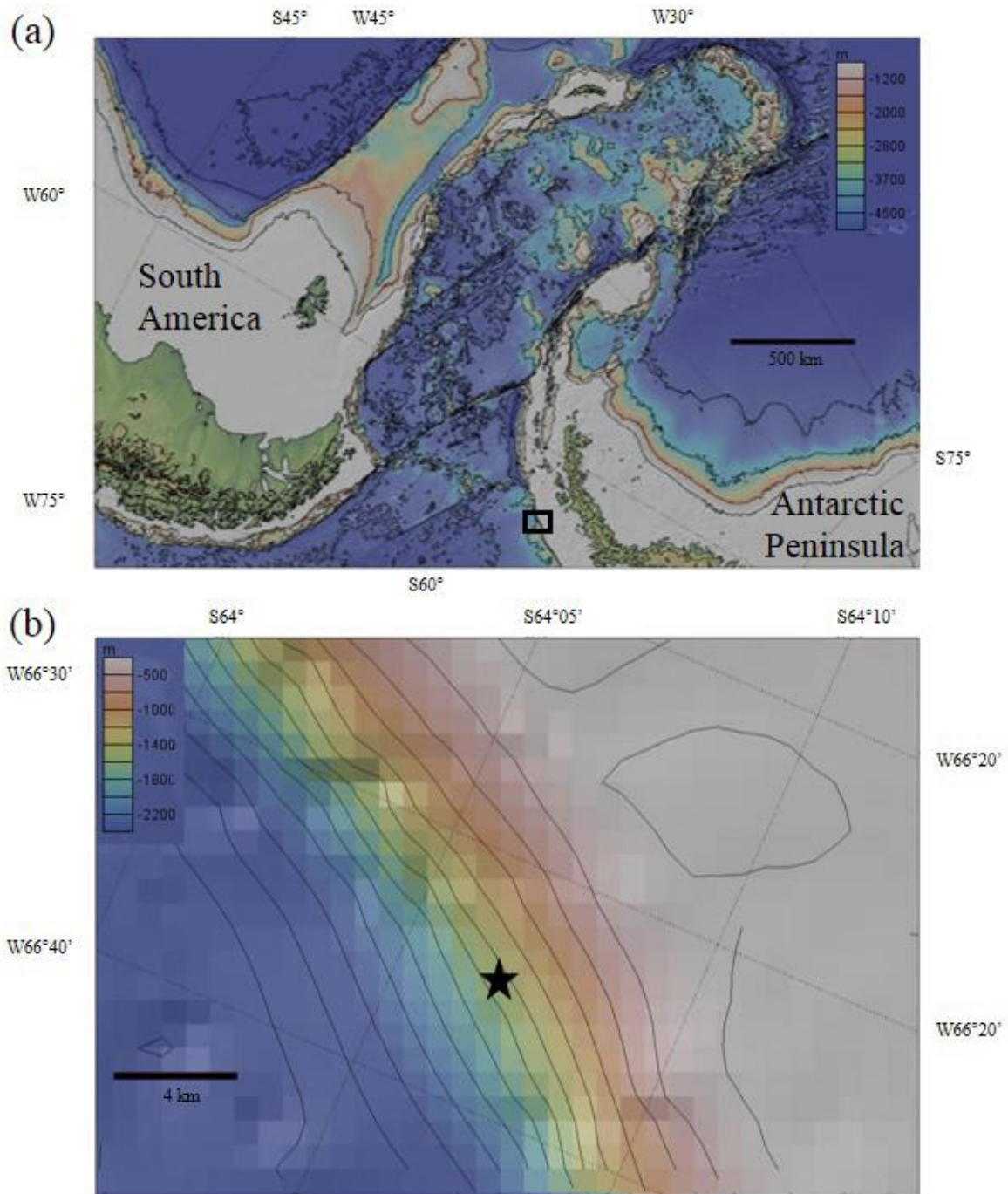


**Table 2:** Mobile animal taxa observed on or around the whale fall, identified to the highest taxonomic level possible through high-resolution images.

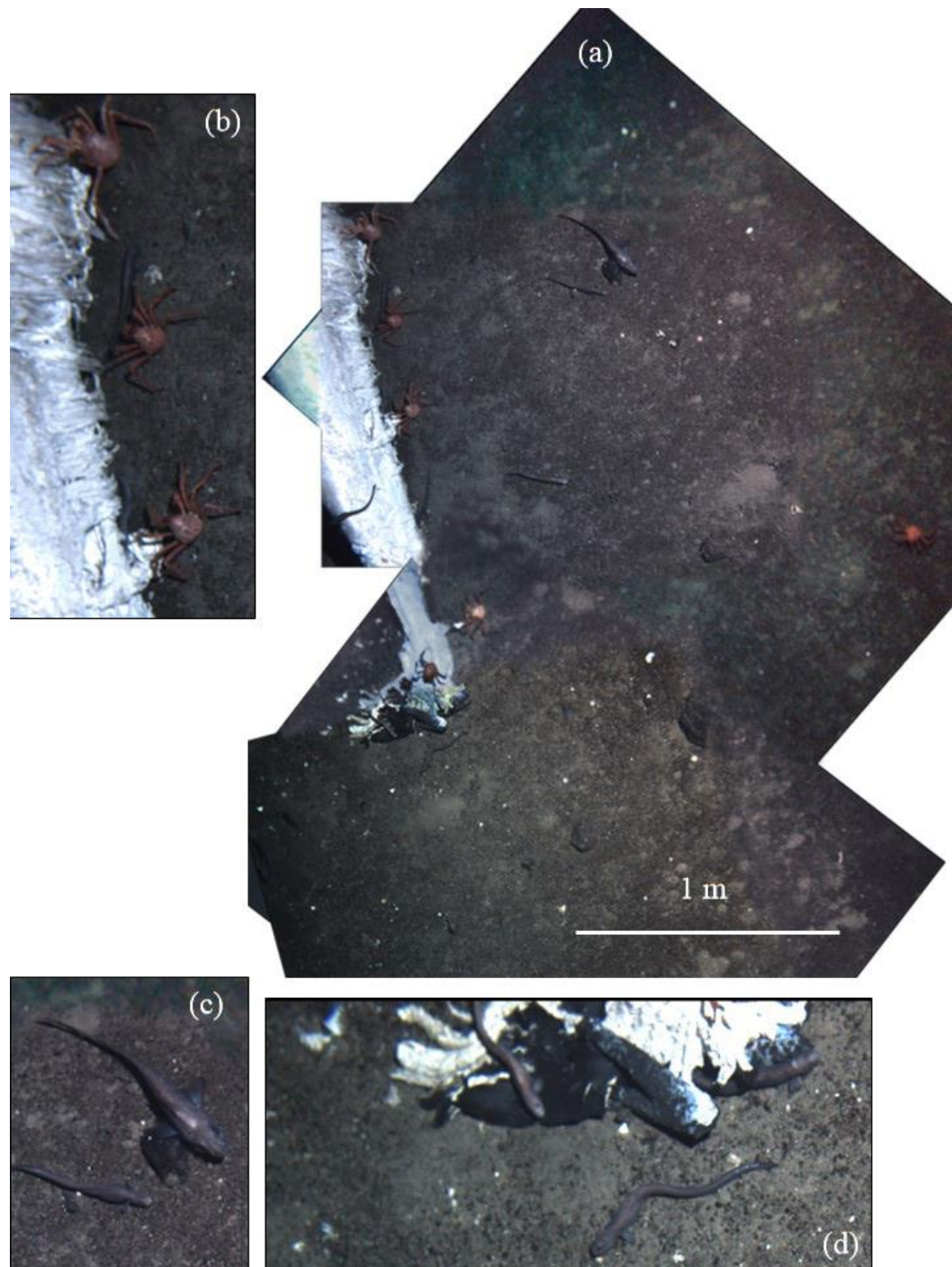
Taxon	Density (ind/m <sup>2</sup> )		
	On whale fall	< 2 m from fall	2-10 m from fall
Arthropoda	(25.9)	(0.1)	
Malacostraca			
Amphipoda (unidentified)	9.7	<sup>1</sup>	<sup>1</sup>
Decapoda			
Lithodidae, 1 sp. ( <i>Paralomis birsteini</i> )	16.2	0.1	(0.03)
Chordata			
Actinopterygii	(22.6)	(0.6)	(0.3) <sup>2</sup>
Perciformes			
Zoarcidae, 1 sp. (unidentified)	22.6	0.3	-
Gadiformes			
Macrouridae, 1 sp. ( <i>Macrourus whitsoni</i> )	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. ( <i>Parborlasia corrugatus</i> )	<sup>3</sup>	0.5	0.03
Mollusca			
Gastropoda, 1 sp. (unidentified)	0	0	0.03

<sup>1</sup>Amphipods were only counted on the whale fall as image quality did not allow them to be observed clearly in the surrounding area. <sup>2</sup>Individuals were identified to superclass only.

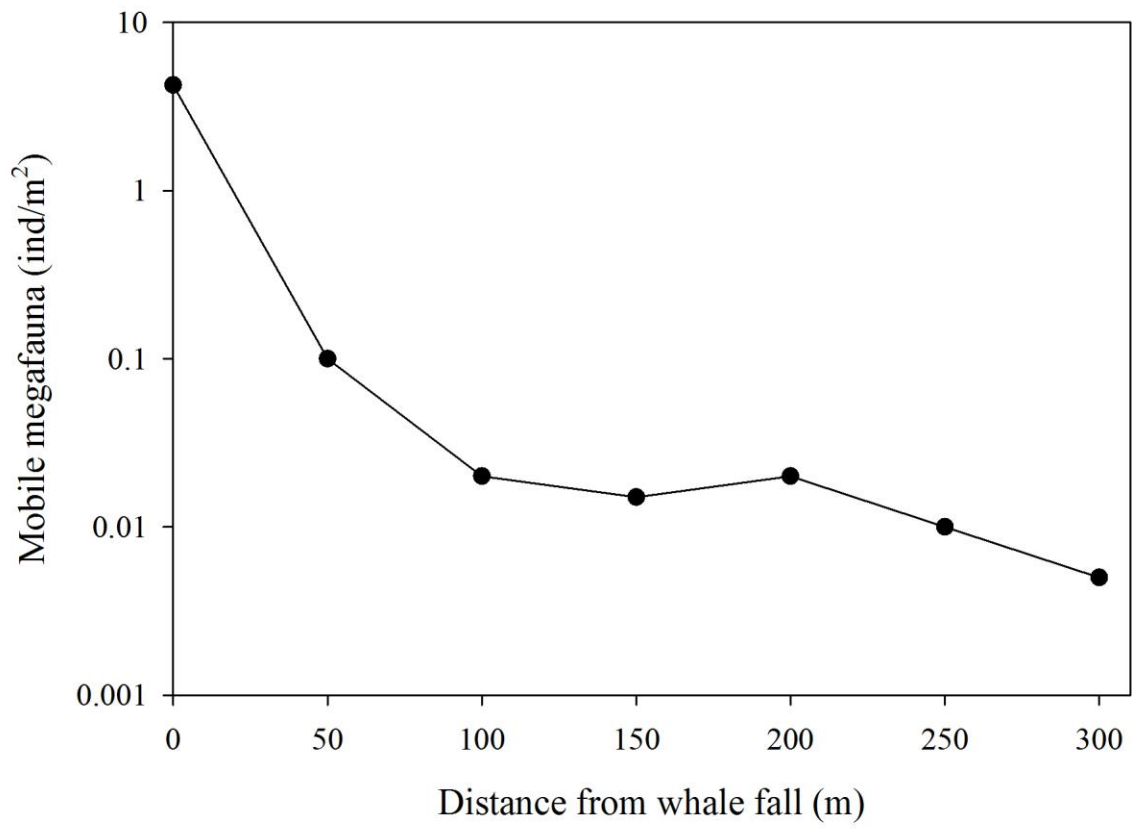
<sup>3</sup>Nemertean was not observed on the whale fall but it is likely this is due to similarity in color to the whale tissue.



**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<sup>2</sup>. (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.