1   **Molluscs from a shallow-water whale-fall in the North Atlantic**

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17   ABSTRACT: We conducted a species-level study of molluscs associated with a 5 m long
18   carcass of a minke whale at a depth of 125 m in the Kosterfjord (North Sea, Sweden). The
19   whale fall community was quantitatively compared with the community commonly living in
20   the surrounding soft-bottom sediments. Five years after the deployment of the dead whale at
21   the sea floor, the sediments around the whale carcass were dominated by the bivalve *Thyasira*
22   *sarsi* (Philippi), which is known to contain endosymbiotic sulphur-oxidizing bacteria, whilst
23   the background sediments were dominated by another thyasirid, *T. equalis* (Verril & Bush),
24   less dependent on chemosynthesis for its nutrition. The Kosterfjord samples were further
25   compared at the species level with mollusc abundance data derived from the literature and
26   including samples from different marine settings of the west coast of Sweden (active methane
27   seep, fjords, coastal and open marine environments). The results show high similarity

28 between the Kosterfjord whale-fall community and the community developed in one of the

29 Swedish fjords (Gullmar Fjord) during hypoxic conditions. This study indicates that at

30 shallow-water whale falls, the sulphophilic stage of the ecological succession is characterized

31 by generalist chemosynthetic bivalves commonly living in organic-rich, sulphidic

32 environments.

33 **INTRODUCTION**

34 In the deep sea, the arrival of a whale carcass generates an organic-rich "island" in an

35 otherwise food-poor deep-sea, supporting a highly specialized and diverse assemblage of

36 animals that exhibit a series of successional stages (Smith & Baco 2003). Sharks, hagfish and

37 other scavenging organisms remove flesh and soft tissues (the mobile scavenger stage),

38 polychaetes, crustaceans and other opportunistic small-sized animals thrive on organic

39 remains (the enrichment opportunist stage), whilst a long-lasting and complex community

40 relies on the hydrogen sulphide and other chemical compounds produced by microbial

41 consumption of the lipid-rich bones (the sulphophilic stage: Smith & Baco 2003). During the

42 sulphophilic stage chemosynthetic bacteria - free living or in symbiosis within vesicomyid

43 clams, bathymodiolin mussels and siboglinid tube worms – are at the base of a food web

44 where organic matter is primarily produced by the oxidation of inorganic compounds. Some

45 of these animals are restricted to vertebrate carcasses, such as the gutless (although

46 heterotrophic) bone-eating worm *Osedax* (Rouse et al. 2004, 2011), whilst chemosynthetic

47 taxa are often found at other deep-sea reducing habitats, including hydrothermal vents and

48 hydrocarbon seeps (Smith & Baco 2003, Dubilier et al. 2008).

49 As they are not restricted to a specific geological setting, whale falls may have played a key-

50 role in the dispersal of chemosynthetic fauna among these habitats (the stepping stone

51 hypothesis: Smith et al. 1989). Evidence consistent with this hypothesis includes molecular

52 studies suggesting that some obligate taxa, specialist at deep-water extreme habitats,

53 originated from shallow-water ancestors living on organic falls (Distel et al. 2000, Jones et al.

54 2006, Duperron 2010). However, natural whale falls from shallow waters, commonly defined

55 as less than 200 m deep (see Dubilier et al. 2008, Dando 2010), are poorly documented in

56 modern settings (see Smith 2006), and their faunal composition as well as the course of the

57 ecological succession poorly known. The shelf-depth sea floor has much higher organic

58 carbon content and hence the organic input from a whale carcass may represent a less

59 significant contribution to nutrient budgets in comparison with the deep sea (Smith 2006).

60 The only report of a fully developed natural (i.e not artificially sunk) whale-fall community

61 in shallow waters comes from the fossil record, where the discovery of a late Pliocene (about

62 3 Ma old) baleen-whale with large lucinid clams testifying for the sulphophilic stage, gave

63 some insights with regard ecological succession at shelf depths (Dominici et al. 2009, Danise

64 et a. 2010).

65 As natural whale falls are rarely encountered on the sea floor, the artificial sinking of whale

66 carcasses and the subsequent monitoring of ecological succession is an extremely useful tool

67 to analyse how community structure changes over time and to understand the relationships

68 with other shallow and deep-water reducing environments. Time-series studies carried out so

69 far on modern shallow-water whale falls in the North Sea show the presence on the shelf of

70 some obligate taxa, such as the siboglinid *Osedax mucofloris* (Glover et al. 2005, Dahlgren et

71 al. 2006). Several species of dorvilleid and chrysopetalid polychaetes documented at shallow

72 whale falls are also present at other shallow sites characterized by high levels of organic

73 carbon flux, such as fish farms (Dahlgren et al. 2004, Wiklund et al. 2009a, 2009b).

74 Studies of temporal processes at very shallow (<40 m) whale falls in the Gullmar Fjord,

75 Sweden, show that decomposition of small cetacean carcasses at shelf-depth settings is

76 initially considerably slower than at deep-sea sites, and that the carcasses are consumed by

77 generalist mobile scavengers already known from the same area (Glover et al. 2010). The

78 monitoring of a minke whale sunken at 30 m depth in the Sea of Japan reports the exclusive

79 presence of non-selective deposit feeders associated with the carcass (Pavlyuk et al. 2009).

80 With regard to molluscs, time-series studies have not yet been conducted in shallow waters,

81 although isolated reports indicate the presence of the bathymodiolin mussel *Idas simpsoni* at

82 0-300 m depth in the North Sea living attached to whale bones (Marshall 1900, Tebble 1966,

83 Warén 1991). Artificial whale falls sunk just below the 200 m depth threshold in the

84 northwest Pacific (219–254 m: Fujiwara et al. 2007) show a general composition of the fauna

85 similar to that of deep-water reducing habitats, with a chemosynthesis-based fauna mainly

86 represented by the bathymodiolin mussel *Adipicola pacifica*. In contrast to this finding no

87 evidence for a sulphophilic stage was found at a whale carcass artificially sunk at 385 m

88 depth in the Monterey Submarine Canyon, north-eastern Pacific (Braby et al. 2007).

89 Here we present a species-level study of molluscs associated with a 5 m long minke whale

90 (*Balaenoptera acutorostrata*) experimentally implanted in October 2003 at a depth of 125 m

91 in the Kosterfjord (Skagerrak, Sweden). Time-series studies previously carried on the

92   same site have shown that the Atlantic hagfish (*Myxine glutinosa*), sharks and other

93   scavenging organisms consumed the flesh and exposed the bones within 5 weeks of

94   implantation, and that the carcass was completely skeletonised after 6 months on the sea floor

95   (Dahlgren et al. 2006). Nine months after sinking the carcass was colonized by *Osedax*

96   *mucofloris*, the first species of *Osedax* known from a shelf-depth whale-fall, and the first

97   from the Atlantic Ocean (Glover et al. 2005, Dahlgren et al. 2006). Our sampling was

98   performed 5 years after the sinking of the carcass. Sediment samples were collected at the

99   whale fall sites and at the surrounding soft bottom sediments in order to compare the whale

100 fall mollusc fauna with the organisms commonly living in the area. Our primary objective

101 was to analyse the community structure of the benthic mollusc fauna associated with a

102 shallow-water whale-fall. Our second aim was to evaluate the differences in taxonomic

103 composition and community structure between the whale fall community, the surrounding

104 background community and the macrofaunal community related to other ephemeral,

105 sulphide-rich habitat of the same area. For this reason the Kosterfjord samples were merged

106 into a larger dataset built from literature data on mollusc relative abundances at a regional

107 scale. The set includes data from one large pockmark in the North Sea (150–168 m: Dando et

108 al. 1991), from soft sediment samples collected in the Gullmar Fjord at 115 m depth at times

109 of hypoxic bottom water conditions (Josefson 1986, 1987, 1988), and from soft sediment

110 samples of the west coast of Sweden (21–106 m: Agrenius 2001, 2002, 2003, 2005).

111 **STUDY AREA**

112 The Kosterfjord is situated in the north eastern part of the Skagerrak, the major gateway

113 between the north Atlantic and the Baltic Sea. It is a 250m deep, 62km long submarine trench

114 parallel to the coastline of Sweden to the east and sheltered by the Koster islands to the west

115 (Figure 1). The trench is a fault fissure connected in the north-west to the Norwegian Trough

116 which in turn is connected to the deep North Atlantic. As a consequence of its connection

117 with the North Atlantic and the prevailing open-ocean marine conditions (including high

118 salinity) the Kosterfjord is not a typical fjord (Palm et al. 2004).

119 The Skagerrak bottom is characterized by muddy sediments and a high content of organic

120 material (about 2% of organic carbon), with sedimentation rates of 0.20 cm/year in the

121 Northern sector (Josefson 1985, Van Weering et al. 1987). The overall oceanographic regime

122 is driven by a counter clockwise circulation pattern, where dense, saline (30–35 psu) and

123 oxygenated oceanic water underflows the more brackish (8–30 psu) surface water outflow of

124   the Baltic Sea. The main surface currents entering the area are the Jutland Current from the

125   North Sea (south-west) and the Baltic Current from south-east. The mixing between these

126   two currents forms the Norwegian Coastal Current, with a predominating northern heading,

127   which flows out of the Skagerrak on the Norwegian side. This surface circulation is

128   compensated by a deep counter current that brings the saline Atlantic water through the 700

129   m deep Norwegian Trench into the Skagerrak (Wisshak et al. 2005). However, the

130   temperature and salinity of the surface waters are subject to strong seasonal fluctuations; in

131   deeper waters the fluctuation is present with lower amplitude. Measurements of bottom water

132   temperature at 125 m depth in the Kosterfjord indicate only small variations during the year

133   of 4.8–7.5 °C, with salinity 34.3–34.7 psu (Dahlgren pers. obs.).

134   The Gullmar Fjord is a 27 km long fjord on the west coast of Sweden, about 70km south of

135   the Kosterfjord. It has a sill at 42 m water depth which restricts water flow to the deep basin

136   of 115 m water depth. Periodically the water in the bottom of the basin has low oxygen

137   levels. During the 1979-1980 winter the bottom of the basin became azoic, due to oxygen

138   deficiency (Josefson & Widbom 1988).

139   **MATERIALS AND METHODS**

140   **Sampling.** For the present study four sediment samples were collected and analysed for their

141   mollusc composition. Sample W1 was collected in May 2008 from the minke whale skeleton

142   at 125 m depth, samples B1, B2 and B3 (background samples) were collected in January

143   2009 at a distance from whale bones, respectively 18 m south, 13 and 55 m north from the

144   whale, at 125-126 m depth. The sampling at the whale fall was conducted with a small

145   Speere ROV (Remotely Operated Vehicle) equipped with a forward-mounted sampling scoop

146   16 cm long with a diameter of 8,4 cm. 4420 cm^3 of sediments were collected with three ROV

147   scoops close to the whale bones (W1), stored in a sample basket (size 34x26.5x25 cm) and

148   retrieved. Due to its size and shape the scoop was able to collect only surface sediments (max

149   sampled depth ~5 cm). Each of the three background sediment samples (B1, B2, B3) was

150   collected using a Van Veen grab with a sampling area of 0.1 m^2 and that would have

151   penetrated to on average of 7-10 cm, and up to a maximum of 20 cm. The total volume of

152   collected sediments was about 15000 cm^3 for each background sample (Table 1).

153   The sediment samples were wet sieved through a 0.5 mm screen and preserved in ethanol

154   (≈80%) before identification. No attempt was made to separate live from dead individuals.

155   The residue was washed with hydrogen peroxide and sorted under a binocular microscope for

156   all recognizable hard shelled biogenic components. The latter include molluscs, serpulids,

157   echinoids, bryozoans, decapods, ostracods, brachiopods, fishes and whale bone fragments.

158   Molluscs were determined at the species level and used for quantitative comparisons. Both

159   live and dead specimens were counted. The total number of bivalve individuals was counted

160   as the highest number of right or left valves and half of the remaining, the latter roughly

161   corresponding to the number of unmatchable valves (i.e., 50 left and 48 right valves:

162   50+(48/2)=74 individuals). Gastropods were equated to the number of apices. Nomenclature

163   used follows Hansson (1998).

164   **Data analyses.** The Kosterfjord dataset, including 1575 specimens belonging to 45 mollusc

165   species, formed the basis for the analyses of sample diversity and trophic structure.

166   Rarefaction curves (Hurlbert 1971) were calculated to compare mollusc sample species

167   richness of the whale fall sample (W1) with species richness of the background samples (B1,

168   B2, B3). The height of a rarefaction curve is a function of community species richness, and

169   its curve steepness is a function of species evenness, allowing a comparison of diversity in

170   samples of different sizes (Hayek & Buzas 1997, Gray 2000). Diversity indices were also

171   calculated for each sample, each influenced to some degree by community structure. The

172   Simpson index is affected by the 2-3 most abundant species and represents the probability

173   that 2 individuals chosen at random from a sample belong to the same species (Hayek &

174   Buzas 1997). Shannon's index (H) provides a measure of uncertainty in the identity of an

175   individual pulled randomly from a sample (Hayek & Buzas 1997), with low H indicating a

176   fairly high certainty of outcome (i.e. low diversity). H is thus insensitive to rare (especially

177   singleton) species. Fisher's α is a number close to that of species expected to be represented

178   by only a single (i.e. rare) individual (Hayek & Buzas 1997). The four Kosterfjord samples

179   (n=1575) were also used for trophic analysis. Seven trophic categories were distinguished

180   consistently following the Molluscan Life Habits Databases (Todd 2000). Abbreviations

181   appropriate for the present study were used: chemosymbiotic deposit feeders (DC),

182   suspension feeders (SU), subsurface deposit feeders (DU), surface deposit feeder (DS),

183   herbivores, including herbivores on fine-grained substrates, herbivores on rock, rubble or

184   coral substrates and herbivores on plant or algal substrates (HE) and predatory carnivores,

185   including scavengers (CP). Comparisons were expressed through percent of number of

186   specimens (n, abundance) and number of species (S, richness) for each category.

187   The larger dataset, made by merging the Kosterfjord data with literature data (Appendix 1),

188   includes five samples form a North Sea pockmark with active methane seeps and three from

189   the surrounding sediments at 150-166 m depth (Dando et al. 1991), three samples collected in

190   the Gullmar Fjord during periods of low oxygen conditions (Josefson 1986, 1987, 1988), and

191   82 samples from the west coast of Sweden ranging from 26 to 106 m depth (Agrenius 2001,

192   2002, 2003, 2005). The latter were collected in the Kattegat and the Skagerrak and are

193   subdivided in samples from fjords (25), coastal areas (35) and open sea settings (22). The

194   samples from the North Sea pockmark were collected with a Smith-McIntyre grab sampling

195   0.1 m^2, a gravity corer or a multiple corer (S1 to S6), and with a box corer sampling 0.085 m^2

196   (R1, R5, R8) (Dando et al. 1991) (Appendix 2). The samples from the Gullmar Fjords were

197   taken with a modified Smith-McIntyre grab, covering a bottom area of 0.1 m^2 and taking a

198   sediment volume of 15.5 l (Appendix 2). Each sample (GF1, GF2, GF3) is the mean of 5

199   replicate grabs (Josefson 1986, 1987, 1988). Each of the Kattegat and the Skagerrak samples

200   derives from the sum of four replicate sub-samples collected with a 0.1m^2 Smith-McIntyre

201   grab (Agrenius 2001, 2002, 2003, 2005) (Appendix 2). Macrofauna was collected by washing

202   the sediment through a 0.5mm mesh sieve for the North Sea pockmark samples, and through

203   a or 1mm mesh sieve for all the others. The total dataset is made of 97 samples, for a total of

204   105 mollusc species (gastropods, bivalves, scaphopods) and 26.298 individuals. None of the

205   previous studies specify if live specimens or both live and dead shells were counted, so that it

206   is assumed that the whole dataset is inclusive of both dead and live specimens. If only live

207   specimens were included, the merging of live and live/dead assemblages in the same dataset

208   (e.g. the Kosterfjord dataset and the data derived from the literature) would not alter

209   significantly the results of our analysis. It is shown by a previous analysis of 85 habitat-level

210   live dead molluscan data sets that a strong correlation exists between live and death

211   assemblages, with species dominant in a single live census also dominating the local death

212   assemblage, and species rare or unsampled alive being also rare dead (Kidwell, 2002).

213   Furthermore death assemblages are known to capture environmental gradients as much as

214   living assemblages (Tomašových & Kidwell 2009, Albano & Sabelli 2011, Weber & Zuschin

215   submitted) and comparisons of evenness based on many collections provide reasonably

216   accurate estimates of differences in average large-scale community structure (Olszewski &

217   Kidwell 2007), so that a study based on both live and death assemblages is considered as

218   informative as one based solely on live specimens. In addition, variation in life span is known

219   to yield little bias of proportional abundances when passing from the live to the death

220   assemblage (Kidwell & Rothfus 2010).

221 After removing species occurring only in one sample (singletons), multivariate analysis was

222 performed on a dataset with 68 species and 26.174 individuals (99.5% of the original

223 dataset). To overcome problems connected with comparing samples of different size,

224 abundances were transformed into percentages. Percentages were then square-root

225 transformed to de-emphasize the influence of the most abundant taxa and increase the effect

226 of rare species (Clarke & Warwick 2001), allowing for a stronger correspondence with

227 known environmental gradients (see Tomašových & Kidwell 2009). Hierarchical

228 agglomerative cluster analysis was performed using the paired group method and the Bray–

229 Curtis algorithm (Q mode cluster). Data were elaborated through detrended correspondence

230 analysis (DCA), a multivariate statistical technique widely used with ecological data to

231 ordinate taxa along underlying ecological gradients (Hill & Gauch 1980). In a DCA plot, axis

232 1 reflects the primary source of ecological variation in the composition of fauna and axes 2

233 the additional sources of variation beyond the principal gradient. A similarity percentage

234 analysis (SIMPER, see Clarke & Warwick 2001) was performed to determine which species

235 were responsible for similarity within groups of samples. Those species for which the ratio of

236 mean similarity to standard deviation of similarity is >1 typify the sample group, and were

237 listed in the comparisons. Diversity indices, cluster analysis and DCA analysis were

238 performed with the software PAST (Hammer et al. 2001). SIMPER analysis was performed

239 with the software PRIMER (Clarke & Warwick 2001). To avoid ambiguities in the final

240 interpretation, the results of the multivariate analyses were evaluated considering possible

241 effects of sampling methods on one side, and of taphonomic processes on species abundances

242 in time-averaged death assemblages on another (Tomašových & Kidwell 2011).

243

244 **RESULTS**

245 **Whale fall and background community structure.** During sampling at the whale fall site

246 the skull, one mandible and some ribs were still visible on the sea floor. Exposed bones were

247 covered in a mixture of bacterial mats (associated with blackened bone regions, indicative of

248 sulphide release) and muddy sediments. No molluscs were seen lying directly over or around

249 the bones during the survey (nor in more than 20 bones brought to the laboratory and

250 analysed over the years). Algal debris was trapped within the bones (e.g. *Fucus serratus*) and

251 the decapod *Hyas araneus* was frequently observed close to the skeleton (Figure 2). Bones

252   were highly bioeroded and specimens of the bone eating worm *Osedax mucofloris* were

253   recorded living on collected bone samples, five years after carcass deployment.

254   The sieving residue included molluscs, regular and irregular echinoids (*Brissopsis lyrifera*

255   and *Spatangus purpureus*), brachiopods (*Crania* sp. and terebratulids), benthic foraminifers,

256   ostracods, serpulids, bryozoans, decapods, fish fragments and teeth and myxinid dental

257   plates. Sample W1 was dominated by the bivalve *Thyasira sarsi* (51% of the total), followed

258   by *Abra nitida* (16.2%), *Tellimya ferruginosa* (8%), *Mytilus edulis* (4.9%) and the nuculanid

259   *Ennucula tenuis* (4.7%) (Figure 3). Among the gastropods the most abundant were *Pusillina*

260   *sarsii* (3.7%), *Cylichna cylindracea* (2.5%) and *Alvania punctura* (2%). Specimens of

261   *Thyasira sarsi* (Figure 4A) and *Abra nitida* (Figure 4B) were observed alive during sieving

262   operations. *Thyasira equalis* was the most abundant species in B1, B2 and B3 samples,

263   accounting respectively for the 43.1%, 22.9% and 27.8% of the total. Besides *T. equalis*, the

264   background samples contained many protobranchiate bivalves, such as *Ennucula tenuis*,

265   *Yoldiella philippiana*, *Nucula sulcata*, *Nuculana minuta* and *N. pernula* (Figure 3). Also the

266   semelid *Abra nitida* and the cardiid *Parvicardium minimum* were represented in significant

267   quantities in the background sediments.

268   The background samples B2 and B3 exhibit higher species richness and a more even

269   distribution than W1, that is, W1 is dominated by fewer species (Figure 5). Although W1

270   derives from a smaller volume of sediments compared with the background samples (see

271   Table 1), it contains a larger number of individuals, and its rarefaction curve reaches an

272   asymptotic shape. This indicates that if a larger volume of similar sediments had been

273   collected from the whale fall, no further taxa would have been added. The diversity indices

274   help to interpret results from rarefaction curves (Table 2). W1 has the highest value of D, the

275   Simpson index of Dominance, being dominated by a few species, and the lowest value of H,

276   the Shannon's index. The Shannon's index is more affected by species in the middle of the

277   species rank sequence which are rare at the whale fall but are abundant in the background

278   samples. The background sediments are in fact characterized by a higher number of rare

279   species than W1, as also highlighted by their high values of the Fisher's α index. B1, the

280   sample with the lower number of individuals, has intermediate values.

281   **Trophism**. The two predominant thyasirids, *Thyasira sarsi* (dominant at W1) and *Thyasira*

282   *equalis* (dominant at B1, B2, and B3), are infaunal chemosymbiotic deposit feeders

283   containing symbiotic sulphur-oxidizing bacteria in their gill tissue (Southward 1986). Both of

them are mixotrophic and can derive part of their nutrition heterotrophically by particulate feeding (Dufour & Feldbeck 2006). In particular, studies on the nutritional dependence of the two bivalves on chemoautotrophic symbiotic bacteria show that *T. equalis* has fewer symbiotic bacteria in its gills compared to *T. sarsi*, indicating that the nutritional importance of carbon fixed by the bacteria is less in *T. equalis* (Dando & Spiro 1993, Dufour 2005). *T. sarsi* instead derives 50-100 % of its tissue carbon from carbon fixed by bacteria (Spiro et al. 1986, Schmaljohann et al. 1990). The chemosymbiotic trophic group has the highest abundance in all the four samples, but the lowest species richness (Figure 6). Like chemosymbiotic deposit feeders, surface deposit feeders have a high overall abundance but low species richness, being represented only by the semelid *Abra nitida*, more abundant in W1 than in the background community. Subsurface deposit feeders (nuculids, nuculanids, yoldiids and dentaliids) have both high abundance and high diversity in B1, B2 and B3 (38%, 46% and 47.9% respectively). The same subsurface deposit feeders are present in all samples but their abundance in W1 is the lowest (8.4%). Suspension feeders have a high species richness, both in whale fall and background fauna. The mytilids *Mytilus edulis* and *Musculus discors* and the montacutid *Tellymia ferugginosa* characterise sample W1, whereas pectinids, anomiids and cardiids are typical of B1, B2 and B3. Herbivores are diverse but rare in all samples. Those associated with the whale fall, such as the rissoids *Rissoa lilacina* and *Pusillina sarsi*, are typical of shallower settings where they are associated to algae (*Laminaria spp.*) or seagrass (*Zostera marina*) (Warén 1996). The rissoid species *Onoba* cf. *tumidula* was recently found also at relatively shallow water vents (557-713 m) in the North Atlantic (Schander et al. 2010), suggesting a rather wide environmental range for the whole family. Carnivores are the least represented among the trophic categories, only the burrowing *Cylichna cylindracea* was present in the whale fall sample.

Extreme vs normal benthic environments. The samples collected at the Kosterfjord whale fall and in the surrounding sediments were compared with samples from a shallow water North Sea methane seep area, from soft sediment samples collected in the Gullmar Fjord at 115 m depth at times of hypoxic bottom water conditions and with samples collected in normal marine bottoms along the Swedish west coast. The cluster agglomerative diagram shows that samples form four main clusters at rather high value of similarity (around 0.4: Figure 7). Cluster 1 groups samples from "organic-rich sediments", i.e., the whale fall sample (W1) and the three samples from the Gullmar Fjord (GLF1, 2, 3). Cluster 2 groups samples from the methane seep area and comprises all samples related to the North Sea pockmark

317   with active methane seepage, whether they were collected from the side of the pockmark (R5,

318   R8, S1, R1, S2) or from the surrounding bottom sediments not directly related to methane

319   seepage (S4, S5, S6). Cluster 3 contains samples from the Swedish west coast with average

320   depth < 50 m, comprising those from fjords and those from onshore settings. Cluster 4 groups

321   all offshore soft bottom samples, i.e., with an average depth > 50 m. The Kosterfjord

322   background samples (B1, B2, B3) became included in the latter group, in particular with

323   samples collected in the same area at 91-102 m depth (SK13 and SK14: Figure 7, Appendix

324   2). This result confirms that the distribution of species abundances in samples is relatively

325   unaffected by sampling and processing methods. Consistently with the cluster analysis, in the

326   DCA diagram the four main sample clusters show practically no overlap (Figure 8). The first

327   two axes of the ordination, DC1 and DC2, are representative of the full distribution of data,

328   explaining 90.7 % of the variance (DC1 = 65.7%, DC2 = 25%). A small overlap occurs

329   between onshore and offshore samples, consistently with a gradual depth-related transition

330   between samples. If in the dendrogram fjords and onshore samples were grouped together, in

331   the DCA they are well separated, forming two distinct sub-clusters, fjord samples at low DC2

332   values and onshore samples at high DC2 values. The ordination of samples along DC1

333   follows a depth gradient (see Appendix 3). Onshore and fjord samples score the lowest DC1,

334   onshore samples ranging 28-59 m depth, fjord samples 21-47 m. Offshore samples have

335   intermediate DC1 values, their depth gradually shifting from 50 to 125 m with increasing

336   DC1 scores. Consistently, W1 and samples from the Gullmar Fjord, collected at a depth of

337   115 m, have intermediate DC1 values. Samples from the methane seep area, collected

338   between 150 and -166 m, rest on the right part of the diagram. Samples are also widely

339   scattered along DC2. Gullmar Fjord samples have the lowest DC2 values, followed by W1,

340   fjord samples and some of the samples from the methane seep area, merging with onshore

341   and offshore samples at high DC2 scores. Concerning the possible occurrence of both dead

342   and live assemblages in our dataset, when samples are pooled, we can expect that variation in

343   species composition among samples will be higher when living or death assemblages are

344   ordinated separately. The centroid of such pooled assemblages should be located between the

345   centroids of living and death assemblages (Tomašových & Kidwell 2011). Given the

346   distribution of environmentally separable groups of sample in the multidimensional space, at

347   clearly separable DC2 values (Figure 8), an eventual separation of live and dead assemblages

348   within each cluster would not alter the significance of the difference between clusters.

349 SIMPER analysis allowed us to highlight which taxa are responsible for the similarity within

350 samples forming the five main groups (Table 3). The whale fall and the Gullmar Fjord

351 samples have the highest similarity among the five groups. In particular, their similarity is

352 given by the occurrence in all of them of the bivalves *T. sarsi* and *A. nitida*, with a

353 cumulative contribution of the 76.7%. Even if *T. sarsi* occurs in two of the samples collected

354 inside of the North Sea pockmark (R8 and S1), the largest contribution to the similarity

355 between samples from the methane seep area is given by the thyasirids *T. equalis* and *T.*

356 *obsoleta*. Onshore, offshore and fjord samples are dominated by the bivalves *Kurtiella*

357 *bidentata*, *Abra nitida*, nuculanids like *Ennucula tenuis* and *Nucula nitidosa* and the

358 gastropods *Hyla vitrea*, which contribute with different percentage within each group.

359 **DISCUSSION**

360 **The Kosterfjord whale fall.** The quantitative analysis of the Kosterfjord samples shows that

361 the presence of a minke whale carcass on the sea floor at shelf depths still influences the

362 composition and structure of the benthic community five years after its implantation.

363 Although some species are shared between the whale fall and the background community, the

364 whale-fall community clearly shows a lower diversity in its species composition, a different

365 ranking of species, and dominance of the chemosymbiotic bivalve *Thyasira sarsi*. The

366 Kosterfjord whale fall is similar to sites with high organic input in shallow water

367 environments (see Pearson & Rosenberg 1978). Rarefaction curves and diversity indices

368 show a markedly lower diversity in the area close to the source of organic matter with respect

369 to the background sediments. The high abundance of *T. sarsi* in the sediments closely

370 associated with the skeleton suggests that the decay of the whale organic matter created an

371 ephemeral habitat with high sulphate reduction rates, i.e. a certain degree of reliance on

372 chemosynthesis. The density of *T. sarsi* is in fact dependent upon the sulphate reduction rate

373 in the sediment (Dando et al. 2004). Sulphide conditions could have been further favored by

374 the presence of macroalgae trapped within the bones, which can alone introduce reduced

375 compounds in the sediments (Dando et al. 1993). The species *T. sarsi* is widely distributed in

376 the NE Atlantic and is generally found in association with organic-rich sediments with high

377 total sulphide concentrations (Dando & Southward 1986). In the North Sea and in the

378 Skagerrak *T. sarsi* is associated with sewage-polluted fjords, anoxic fjords, fish farms and

379 active methane seeps (Dando et al. 1991, Dando & Spiro 1993, Dando et. al. 1994,

380 Rosenberg et al. 2002, Kutti et al. 2007), with a depth range of 50-340 m (Dufour 2005).

381 Conversely, the dominant species in the background sediments and absent in the whale fall

382   collection, *T. equalis*, is the most common thyasirid on the North European continental shelf,

383   preferring sediments with less-organics with respect to *T. sarsi*, possibly avoiding hydrogen

384   sulphide rich sediments (Dando & Southward 1986).

385   The opportunist species *Abra nitida*, common along the northern part of the Swedish west

386   coast, is a density-dependent species unaffected by turbid conditions (Josefson 1982). Its high

387   abundance at the whale-fall site could be linked to the presence of high organic content, as

388   observed in fish farm areas with increased food supply (Kutti et al. 2007). The abundance of

389   *Tellymia ferugginosa* in the whale-fall sample, a small bivalve living symbiotically in the

390   burrow of the echinoid *Echinocardium cordatum* (Gillan & De Ridder 1997), is indicative of

391   the occurrence of the echinoid itself. *Echinocardium cordatum,* a deep burrower, may not

392   have been directly collected due to the shallow depth of our sampling. The species hosts

393   ectosymbiotic sulphide-oxidizing bacteria, *Thyothrix* like, in its intestinal caecum and is

394   known to burrow below or at the level of the oxidized-reduced interface, ingesting both

395   surface and deep reduced sediments. This symbiosis opens an access for *E. cordatum* to

396   sulphide-rich habitats (Temara et al. 1993, Brigmon & De Ridder 1998) and adds further

397   evidence for the presence of a chemosynthetic ecological niche at this shallow-water whale

398   fall site (Bromely et al. 1995). As with *E. cordatum*, the presence of other deeper burrowers

399   may have been overlooked because of the shallow sampling depth within the sediment.

400   Among these missing taxa may be the lucinid bivalves, chemosymbiotically hosting sulphur-

401   oxidizing bacteria in their gill tissue and living in burrows of up to 20 cm depth (Dando et al.

402   1986).

403   Both the whale fall and the surrounding sediment communities record the presence of coastal

404   species, such as the mytilids *Mytilus edulis* and *Musculus cf. discors* and littorinid

405   gastropods, which were probably transported down-slope by bottom currents. Most of the

406   gastropods found at the whale fall site, including the rissoids, are known to dwell on sea

407   weeds, and were possibly transported by drifting algae, as shown by algal debris around

408   whale bones (Figure 2). Because alive and dead specimens were not distinguished during our

409   sampling procedures, it is not possible here to support the hypothesis that some rissoid

410   species could be adapted to live also in reducing environments, as recently found in some

411   North Atlantic vents (Schander et al. 2010).

412   **Environmental gradients on the Swedish shelf**. The species level, multivariate comparison

413   of the Kosterfjord samples with samples collected from soft-bottom sediments across the

414   west Swedish coast allowed a better interpretation of environmental parameters controlling

415   the faunal composition at the Kosterfjord whale fall. In this study, the ordination of samples

416   along the principal axis of the DCA is controlled by water depth. The faunal composition

417   changes continuously along a depth gradient, with shallower samples on the left side of the

418   diagram and deeper on the right side. This result is in accordance with the interpretation that

419   in marine environments water depth is the single most important factor controlling the

420   distribution of benthic organisms (see Gauch 1982), and as amply proven in other case

421   studies (Scarponi & Kowaleski 2004, Dominici et al. 2008, Danise 2010).

422   The significance of the DC2 ordination is generally more difficult to interpret, because

423   variations in water depth sum up continuously changing values of other parameters that

424   directly affect the distribution of benthic species, such as food availability, water energy,

425   substrate texture, seasonality, oxygen content and salinity. Samples from reducing soft

426   bottoms are mainly distributed at low DC2 scores, particularly those from the Gullmar Fjord,

427   where bottom waters are periodically affected by low oxygen conditions (Josefson 1987,

428   Josefson & Wibdon 1988, Dando & Spiro 1993). The three samples included in this study

429   were collected between 1985 and 1987, at a time of re-colonization of the sediments by *T.*

430   *sarsi* after a period of oxygen depletion resulting in the death of the bottom fauna. Dando &

431   Spiro (1993) report high concentrations of total reduced sulphur in the Gullmar Fjord

432   sediments in 1986, together with negative $\delta^{13}C$ values in the gills of collected specimens of *T.*

433   *sarsi*, indicating a significant carbon input from autotrophic endosymbiotic bacteria. In

434   addition, samples from the large North Sea pockmark are characterized by the presence of

435   high total sulphide concentrations in the surface layers, as compared to surrounding areas

436   (Dando et al. 1991). In particular, both samples R8 and S1 which have low DC2 values, host

437   the bivalve *T. sarsi* with negative $\delta^{13}C$ values (Dando et al. 1991). Since macrobenthic

438   communities associated with fjords, organic enriched sediments and high sulphide methane

439   seeps all occur in the lower part of the diagram and communities from open marine,

440   oxygenated, environments in the upper part, the DC2 score may be a direct measure of the

441   degree of sulphide concentration and an indirect measure of oxygen level of soft bottom

442   sediments.

443   The general picture that can be drawn from our study of north European shelf molluscs shows

444   that the benthic community structure at the Kosterfjord whale fall is similar to that of

445   communities developed in other organic-rich, sulphide environments. In particular, among

446   the secondary colonisers of the enriched sediments at the whale fall are the symbiont-

447 containing thyasirids, suggesting an ecological succession similar to that of other organic

448 rich-sediments (Pearson & Rosenberg 1978, Dando et al. 2004). A global comparison of

449 whale-fall communities is hampered by the lack of relevant studies at comparable

450 environmental conditions. In comparison with 219-254 m whale-fall communities in the

451 northwest Pacific (Fujiwara et al. 2007), the Kosterfjord whale fall lacks molluscs typical of

452 deep water, such as the mytilid mussels (*Adipicola pacifica*) and the cocculinid limpets.

453 Among the bathymodiolin mussels, *Idas simpsoni* has been described from trawled bones on

454 the North Sea shelf (Marshall 1900, Warén 1991, Tebble 1996) and in oil-polluted areas

455 (Hartley & Watson 1993, Southward 2008), but was not found at the Kosterfjord whale fall

456 during the ROV survey, careful examination of multiple recovered bones or in sediment

457 samples. In a time-series study of oil-polluted sediments around North Sea wells and

458 platforms, the benthic community responded to high levels of oil contamination with the

459 appearance of the bathymodiolin *I. simpsoni*, followed by *T. sarsi* when oil concentrations

460 gradually lowered (Hartley & Watson 1993).

461 **Conclusion**

462 Our evidence suggests that the Kosterfjord whale-fall mollusc community is structured

463 around species that exploit a variety of food sources on the continental shelf, including

464 heterotrophs and chemoautotrophs. This result is similar to that recorded from a fossil analog

465 from the Pliocene of Italy (Dominici et al. 2009, Danise et al. 2010). However, it is in

466 contrast with the data on the polychaete fauna. To date a total of 7 new species of polychaete

467 have been recorded from the Kosterfjord whale fall, of which just 3 are present at other

468 organic-rich settings such as fish-farms (Glover et al. 2005, Wiklund et al. 2009a, 2009b,

469 Wiklund pers. comm.). This may well be partly because the polychaete fauna of organic-rich

470 habitats is less well studied than the mollusc fauna, but the presence of specialists such as

471 *Osedax mucofloris* at Kosterfjord is in contrast with the pattern for Mollusca. From an

472 ecological perspective, our data suggest that shelf-depth whale-falls are a natural analog to

473 areas of organic pollution, such as oil spillages and fish farms, and as such may well offer

474 interesting insights into natural bioremediation at these habitats. From an evolutionary

475 perspective, small carcasses at shelf-depths may provide an avenue for speciation in

476 polychaetes, but not necessarily in molluscs.

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FIGURE CAPTIONS

Figure 1. Map showing the North Sea, the Skagerrak and Kattegat basins. The location of the methane seep area studied by Dando et al. (1991) and the experimental whale-fall site, next to the Sven Lovén Centre for Marine Sciences, Tjärnö, are highlighted. Modified from Palm et al 2004.

Figure 2. Remotely operated vehicle video stills showing the minke whale skeleton 5 years after implantation. A. Minke whale skull covered by muddy sediment and sulphides. B. Minke whale ribs partially covered by sediments and sulphides, showing intense bioerosion. The decapod *Hyas araneus* in the upper part of the figure, algal debris (*Fucus serratus* on the right) trapped within whale bones.

Figure 3. Percentage abundance of the quantitatively important species (>2%) for each of the four Kosterfjord samples.

Figure 4. Live bivalves collected at the Kosterfjord whale fall. A. Specimen of *Thyasira sarsi* collected from the sediments besides whale bones. B. Specimen of *Abra nitida*.

Figure 5. Rarefaction curves with 95% confidence intervals (vertical bars) or the whale fall (W1) and the background samples (B1, B2, B3).

Figure 6. Trophic analysis expressed through percent of number of individuals (abundance) and number of species (richness). Trophic categories: chemosymbiotic deposit feeders (DC), suspension feeders (SU), subsurface deposit feeders (DU), surface deposit feeder (DS), herbivores (HE) and predatory carnivores, including scavengers (CP).

Figure 7. Hierarchical agglomerative cluster (paired group method) based on the Bray-Curtis algorithm. For similarity values of 0.3-0.4 samples group in four main clusters.

Figure 8. DCA q-mode diagram. Each point in the diagram correspond to one sample of the dataset (n=97). Samples are grouped according to the clusters recognized after the hierarchical agglomerative cluster analysis. Onshore and fjord samples can be grouped in two distinct sub-clusters.

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TABLE CAPTIONS

Table 1. Site and sampling information.

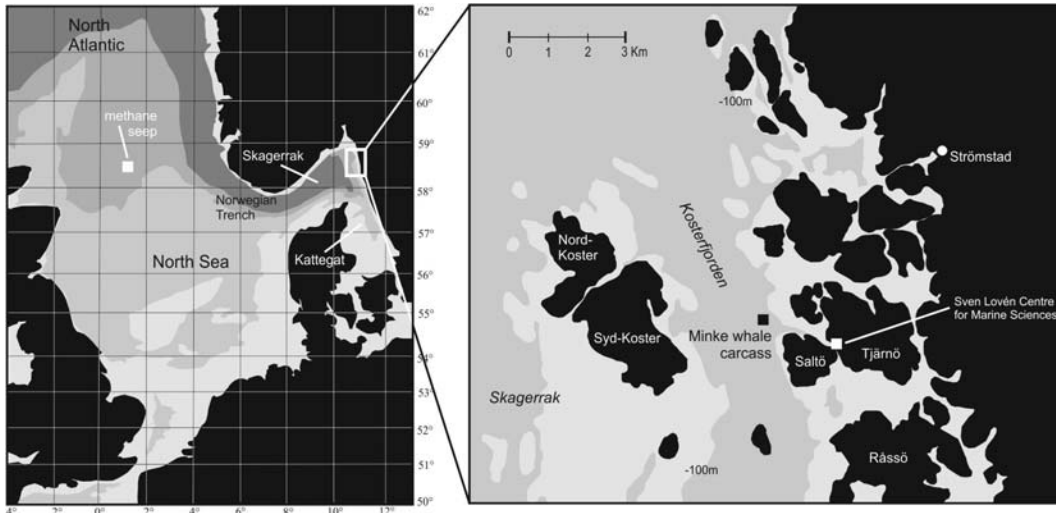**Table 2**. Species abundance, number of individuals and diversity indices of the studied
samples.

Table 3. Characteristic species of each group of samples calculated for standardized data set
and square-root transformed abundances using similarity percentage analysis (SIMPER,
Clarke & Warwick 2001).

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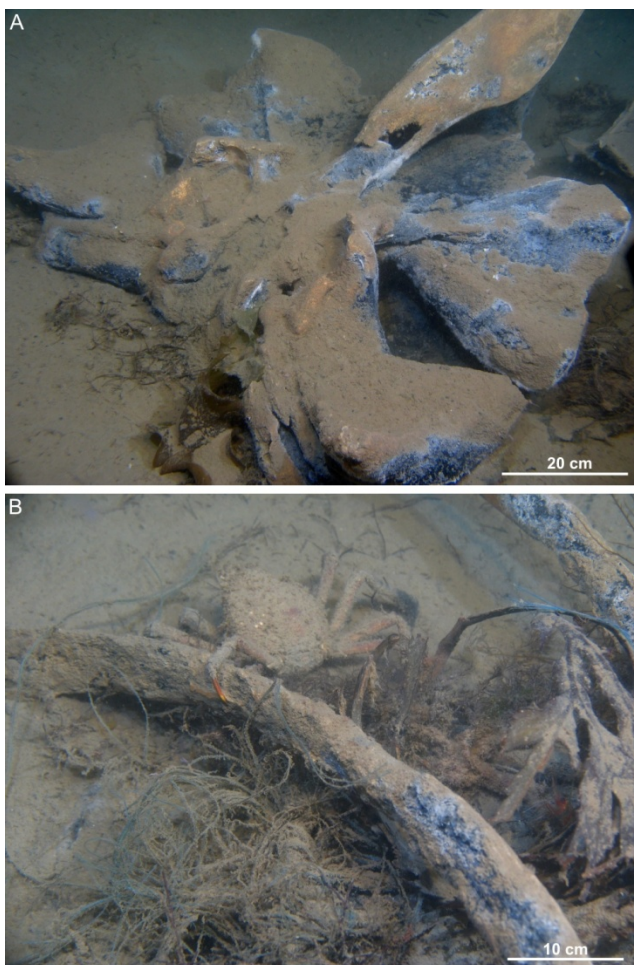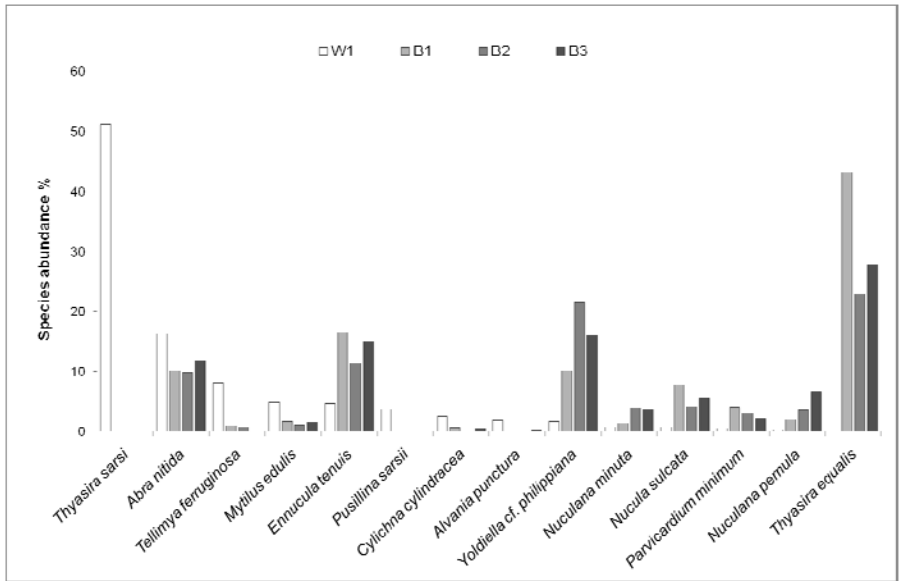
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724   **FIGURES**

725   **Figure 1**
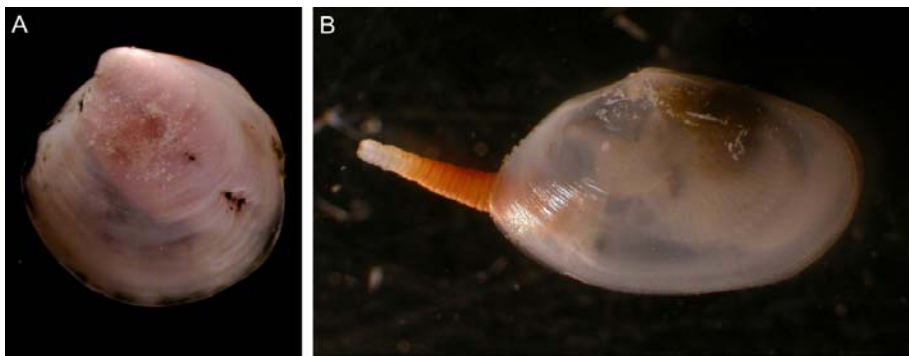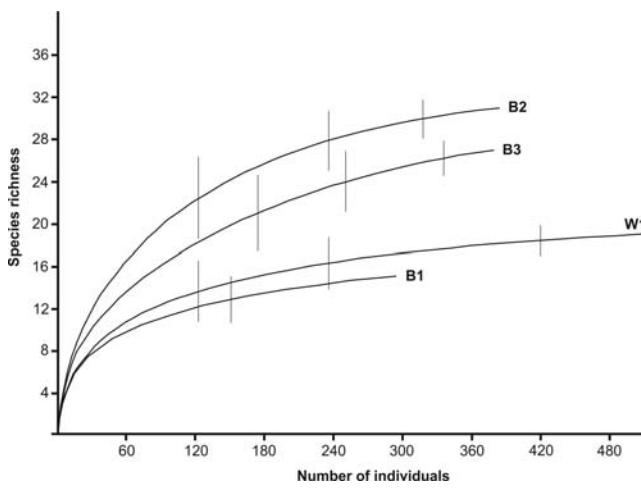

726   **Figure 2**

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728 **Figure 3**

729 **Figure 4**

730 **Figure 5**
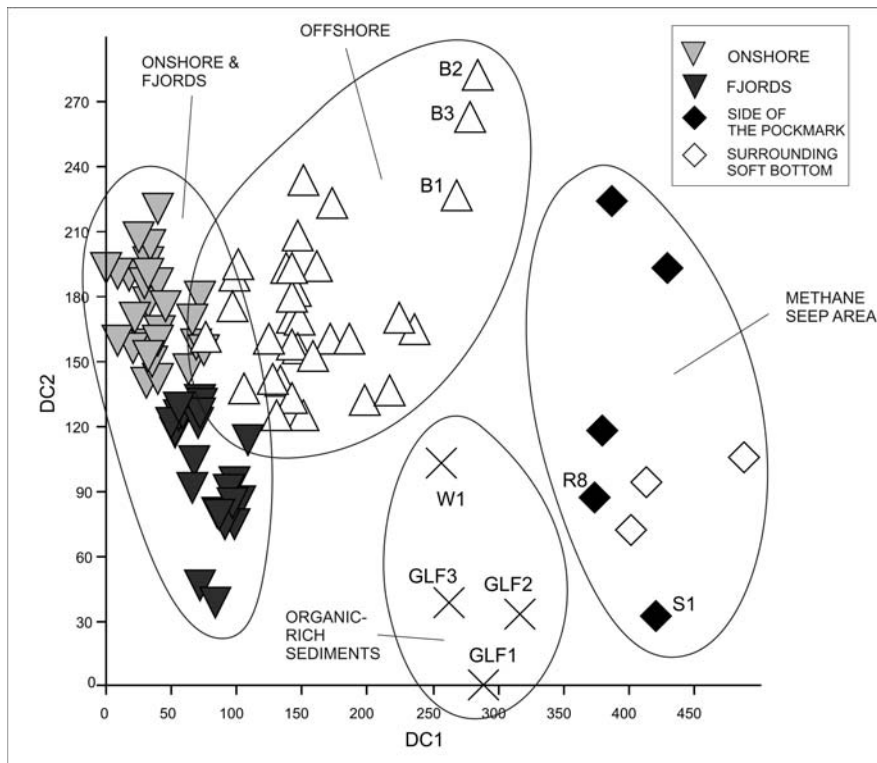
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Figure 6

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733   **Figure 7**

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Figure 8

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737 **TABLES**

Sample	Name	Volume	Sampling methods	Depth	Latitude	Longitude	Distance from the whale	Sampling date
		(cm³)		(m)	(N)	(E)	(m)	
Kosterfjord whale fall	W1	4420	ROV scoop	125	58° 52,968'	11° 05,728'	0	May 2008
Kost. backgorund sediments	B1	15500	0.1 mq Van Veen grab	125	58° 52,963'	11° 05,719'	18	January 2009
Kost. backgorund sediments	B2	15500	0.1 mq Van Veen grab	125	58° 52,973'	11° 05,725'	13	January 2009
Kost. backgorund sediments	B3	15500	0.1 mq Van Veen grab	126	58° 52,991'	11° 05,705'	55	January 2009

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739 **Table 1**

Sample	N° of species	N° of individuals	Simpson index of Dominance	Shannon index	Fisher's α index
			(D)	(H)	(α)
W1	19	512	0.3022	1.755	3.887
B1	15	297	0.2421	1.828	3.332
B2	31	385	0.1297	2.516	7.947
B3	27	381	0.1495	2.297	6.638

740 **Table 2**

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Species	Av. abund.	Av. similarity	Sim/SD	Contribution	Cumulative %
"Organic-rich sediment" samples					
Average similarity = 64.89					
Thyasira sarsi	6.83	30.26	7.47	46.63	46.63
Abra nitida	4.67	19.52	4.19	30.08	76.72
"Onshore" samples					
Average similarity = 60.38					
Kurtiella bidentata	7.31	30.04	3.18	49.76	49.76
Hyala vitrea	4.43	15.09	1.61	25	74.75
Varicorbula gibba	1.5	4.27	1.3	7.07	81.83
Abra nitida	1.75	4	1.02	6.63	88.46
"Fjord" samples					
Average similarity = 57.38					
Abra nitida	5.94	19.59	2.9	34.14	34.14
Kurtiella bidentata	3.96	8.99	1.11	15.67	49.81
Nucula nitidosa	2.21	6.41	2.77	11.18	60.99
Hyala vitrea	2.65	6.37	1.48	11.1	72.09
Thyasira flexuosa	2.15	6.14	1.82	10.7	82.79
Varicorbula gibba	1.26	3.01	1.3	5.24	88.03
"Offshore" samples					
Average similarity =48.91					
Abra nitida	4.45	12.49	2.26	25.53	25.53
Ennucula tenuis	3.43	8.44	1.98	17.25	42.78
Hyala vitrea	2.63	5.67	1.16	11.59	54.38
Thyasira equalis	2.56	5.34	1.3	10.92	65.29
Tellymia tenella	1.79	3.72	1.03	7.61	72.9
Parvicardium minimum	1.76	3.7	1.09	7.56	80.46
"Methane seep area" samples					
Average similarity =48.91					
Thyasira equalis	6.16	25.82	2.87	47.9	47.9
Thyasira obsoleta	4.44	15.06	1.52	27.94	75.84

742 **Table 3**