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

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13 Running head: Molluscs from a shallow whale-fall

14 Key words: whale fall, Bivalvia, chemosynthetic, *Thyasira sarsi*, North Atlantic, organic-
15 enriched sediments, minke whale

16

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* (Verrill & 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 vesicomid
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 out 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 cm³ 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 m² 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 cm³ 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 unmatched 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 from 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 0.1 m^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 axis 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

284 them are mixotrophic and can derive part of their nutrition heterotrophically by particulate
285 feeding (Dufour & Feldbeck 2006). In particular, studies on the nutritional dependence of the
286 two bivalves on chemoautotrophic symbiotic bacteria show that *T. equalis* has fewer
287 symbiotic bacteria in its gills compared to *T. sarsi*, indicating that the nutritional importance
288 of carbon fixed by the bacteria is less in *T. equalis* (Dando & Spiro 1993, Dufour 2005). *T.*
289 *sarsi* instead derives 50-100 % of its tissue carbon from carbon fixed by bacteria (Spiro et al.
290 1986, Schmaljohann et al. 1990). The chemosymbiotic trophic group has the highest
291 abundance in all the four samples, but the lowest species richness (Figure 6). Like
292 chemosymbiotic deposit feeders, surface deposit feeders have a high overall abundance but
293 low species richness, being represented only by the semelid *Abra nitida*, more abundant in
294 W1 than in the background community. Subsurface deposit feeders (nuculids, nuculanids,
295 yoldiids and dentaliids) have both high abundance and high diversity in B1, B2 and B3 (38%,
296 46% and 47.9% respectively). The same subsurface deposit feeders are present in all samples
297 but their abundance in W1 is the lowest (8.4%). Suspension feeders have a high species
298 richness, both in whale fall and background fauna. The mytilids *Mytilus edulis* and *Musculus*
299 *discors* and the montacutid *Tellymia ferugginosa* characterise sample W1, whereas pectinids,
300 anomiiids and cardiids are typical of B1, B2 and B3. Herbivores are diverse but rare in all
301 samples. Those associated with the whale fall, such as the rissoids *Rissoa lilacina* and
302 *Pusillina sarsi*, are typical of shallower settings where they are associated to algae
303 (*Laminaria spp.*) or seagrass (*Zostera marina*) (Warén 1996). The rissoid species *Onoba cf.*
304 *tumidula* was recently found also at relatively shallow water vents (557-713 m) in the North
305 Atlantic (Schander et al. 2010), suggesting a rather wide environmental range for the whole
306 family. Carnivores are the least represented among the trophic categories, only the burrowing
307 *Cylichna cylindracea* was present in the whale fall sample.

308 **Extreme vs normal benthic environments.** The samples collected at the Kosterfjord whale
309 fall and in the surrounding sediments were compared with samples from a shallow water
310 North Sea methane seep area, from soft sediment samples collected in the Gullmar Fjord at
311 115 m depth at times of hypoxic bottom water conditions and with samples collected in
312 normal marine bottoms along the Swedish west coast. The cluster agglomerative diagram
313 shows that samples form four main clusters at rather high value of similarity (around 0.4:
314 Figure 7). Cluster 1 groups samples from “organic-rich sediments”, i.e., the whale fall sample
315 (W1) and the three samples from the Gullmar Fjord (GLF1, 2, 3). Cluster 2 groups samples
316 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 feruginosa* 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 $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ 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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684

685 **FIGURE CAPTIONS**

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

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

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

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

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

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

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

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

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713

714 **TABLE CAPTIONS**

715 **Table 1.** Site and sampling information.

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

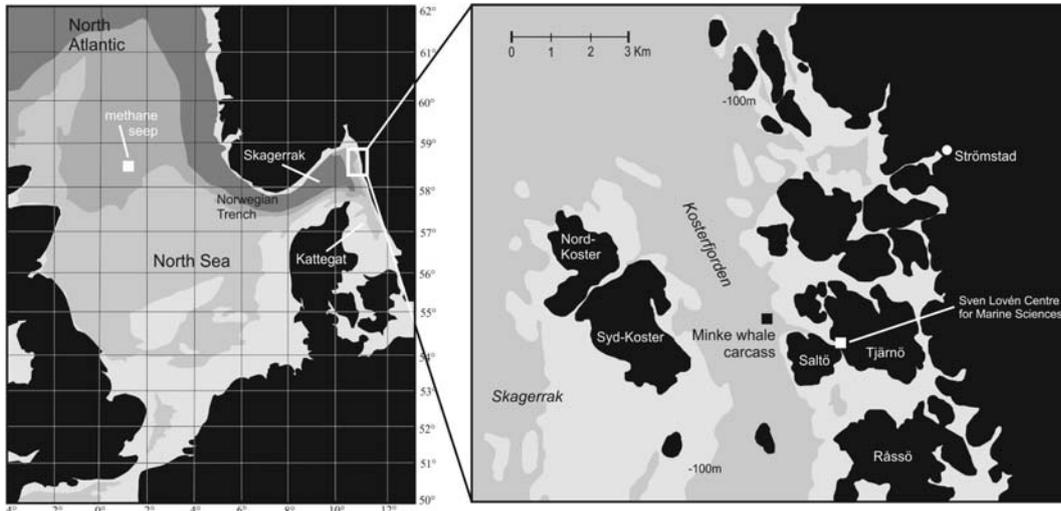
718 **Table 3.** Characteristic species of each group of samples calculated for standardized data set
719 and square-root transformed abundances using similarity percentage analysis (SIMPER,
720 Clarke & Warwick 2001).

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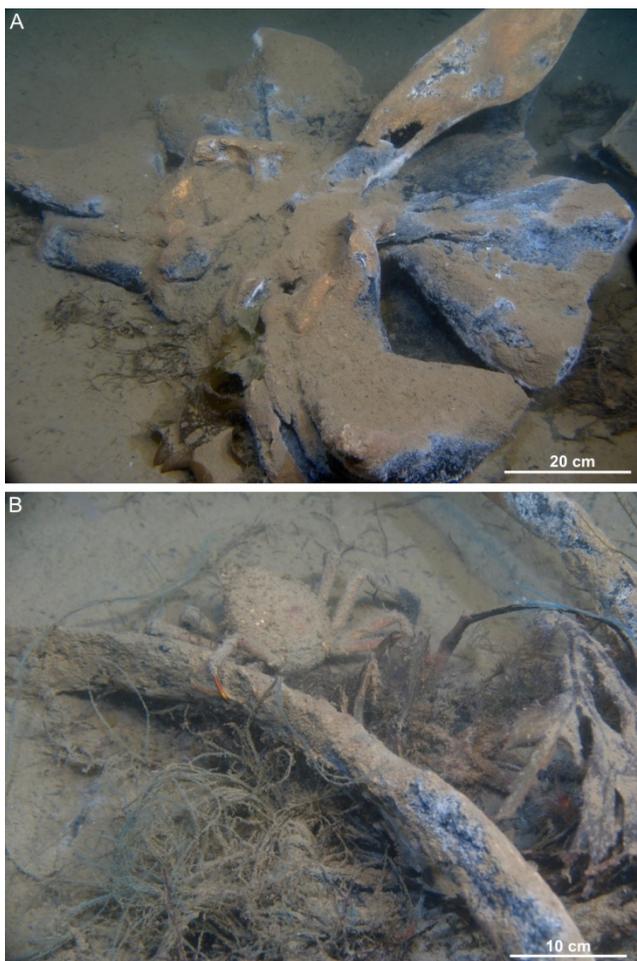
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724 **FIGURES**



725

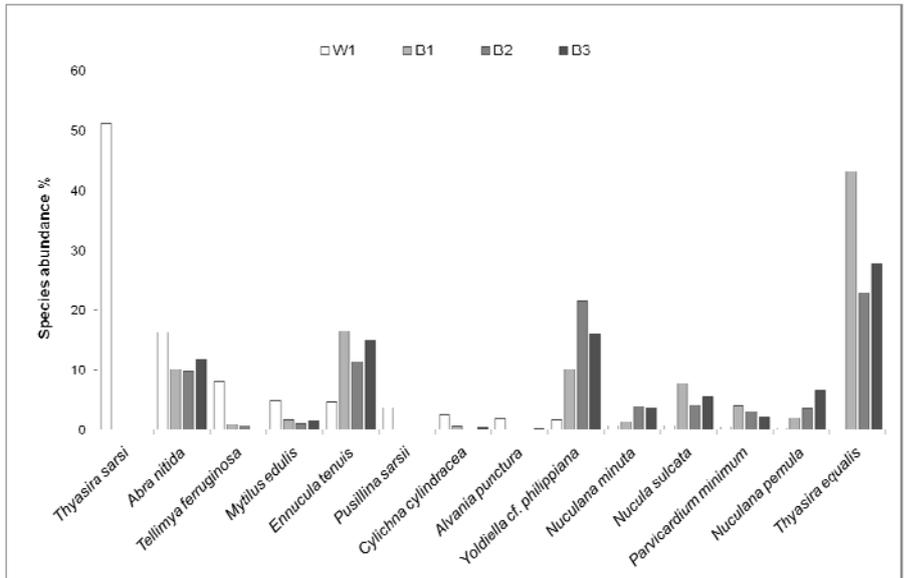
Figure 1



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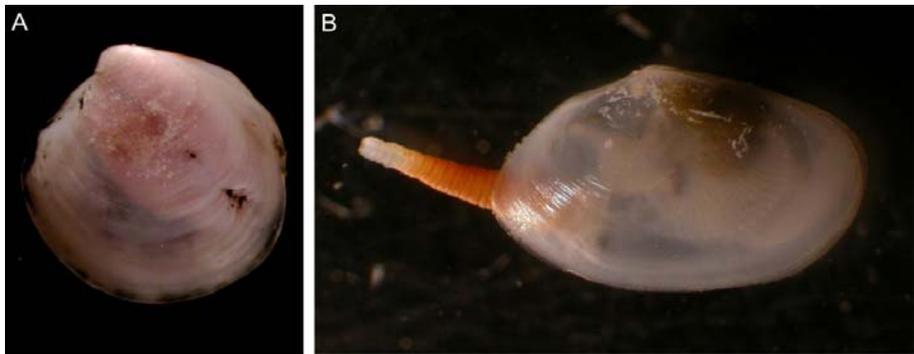
Figure 2

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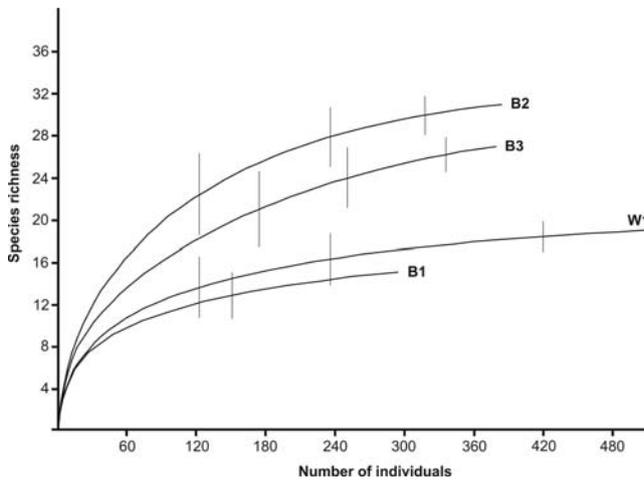
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Figure 3



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Figure 4



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Figure 5

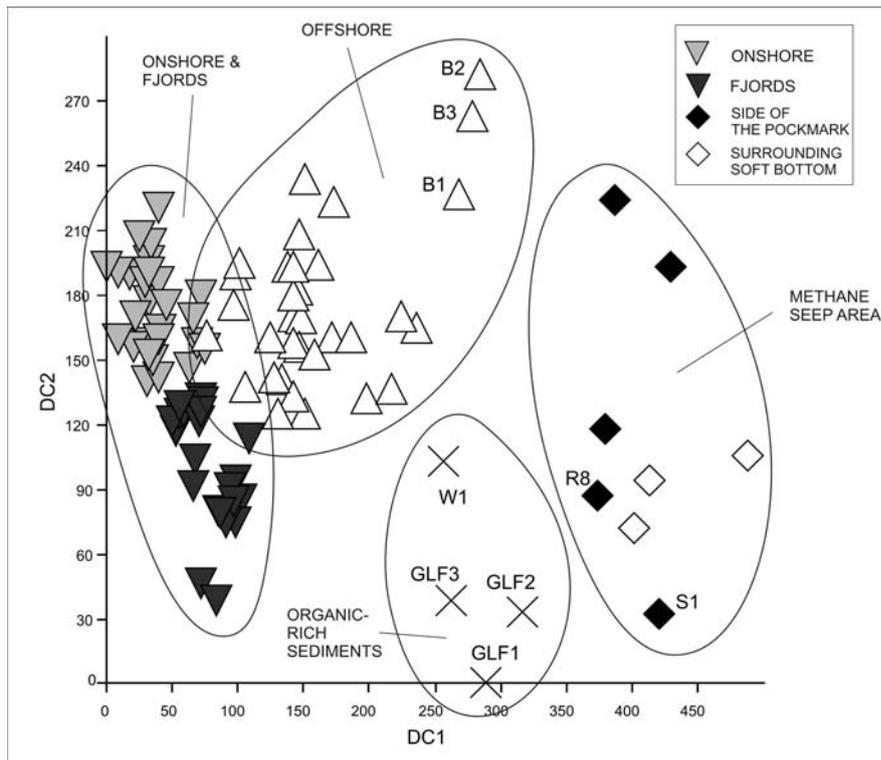


Figure 8

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737 **TABLES**

Sample	Name	Volume (cm ³)	Sampling methods	Depth (m)	Latitude (N)	Longitude (E)	Distance from the whale (m)	Sampling date
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

738

739 **Table 1**

Sample	N° of species	N° of individuals	Simpson index of Dominance (D)	Shannon index (H)	Fisher's α index (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

Table 2

740

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