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

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

between the Kosterfjord whale-fall community and the community developed in one of the Swedish fjords (Gullmar Fjord) during hypoxic conditions. This study indicates that at shallow-water whale falls, the sulphophilic stage of the ecological succession is characterized by generalist chemosynthetic bivalves commonly living in organic-rich, sulphidic environments.

INTRODUCTION

In the deep sea, the arrival of a whale carcass generates an organic-rich “island” in an otherwise food-poor deep-sea, supporting a highly specialized and diverse assemblage of animals that exhibit a series of successional stages (Smith & Baco 2003). Sharks, hagfish and other scavenging organisms remove flesh and soft tissues (the mobile scavenger stage), polychaetes, crustaceans and other opportunistic small-sized animals thrive on organic remains (the enrichment opportunist stage), whilst a long-lasting and complex community relies on the hydrogen sulphide and other chemical compounds produced by microbial consumption of the lipid-rich bones (the sulphophilic stage: Smith & Baco 2003). During the sulphophilic stage chemosynthetic bacteria - free living or in symbiosis within vesicomyid clams, bathymodiolin mussels and siboglinid tube worms – are at the base of a food web where organic matter is primarily produced by the oxidation of inorganic compounds. Some of these animals are restricted to vertebrate carcasses, such as the gutless (although heterotrophic) bone-eating worm *Osedax* (Rouse et al. 2004, 2011), whilst chemosynthetic taxa are often found at other deep-sea reducing habitats, including hydrothermal vents and hydrocarbon seeps (Smith & Baco 2003, Dubilier et al. 2008).

As they are not restricted to a specific geological setting, whale falls may have played a key-role in the dispersal of chemosynthetic fauna among these habitats (the stepping stone hypothesis: Smith et al. 1989). Evidence consistent with this hypothesis includes molecular studies suggesting that some obligate taxa, specialist at deep-water extreme habitats, originated from shallow-water ancestors living on organic falls (Distel et al. 2000, Jones et al. 2006, Duperron 2010). However, natural whale falls from shallow waters, commonly defined as less than 200 m deep (see Dubilier et al. 2008, Dando 2010), are poorly documented in modern settings (see Smith 2006), and their faunal composition as well as the course of the ecological succession poorly known. The shelf-depth sea floor has much higher organic carbon content and hence the organic input from a whale carcass may represent a less significant contribution to nutrient budgets in comparison with the deep sea (Smith 2006).

The only report of a fully developed natural (i.e not artificially sunk) whale-fall community in shallow waters comes from the fossil record, where the discovery of a late Pliocene (about 3 Ma old) baleen-whale with large lucinid clams testifying for the sulphophilic stage, gave some insights with regard ecological succession at shelf depths (Dominici et al. 2009, Danise et al. 2010).

As natural whale falls are rarely encountered on the sea floor, the artificial sinking of whale carcasses and the subsequent monitoring of ecological succession is an extremely useful tool to analyse how community structure changes over time and to understand the relationships with other shallow and deep-water reducing environments. Time-series studies carried out so far on modern shallow-water whale falls in the North Sea show the presence on the shelf of some obligate taxa, such as the siboglinid *Osedax mucofloris* (Glover et al. 2005, Dahlgren et al. 2006). Several species of dorvilleid and chrysopetalid polychaetes documented at shallow whale falls are also present at other shallow sites characterized by high levels of organic carbon flux, such as fish farms (Dahlgren et al. 2004, Wiklund et al. 2009a, 2009b).

Studies of temporal processes at very shallow (<40 m) whale falls in the Gullmar Fjord, Sweden, show that decomposition of small cetacean carcasses at shelf-depth settings is initially considerably slower than at deep-sea sites, and that the carcasses are consumed by generalist mobile scavengers already known from the same area (Glover et al. 2010). The monitoring of a minke whale sunken at 30 m depth in the Sea of Japan reports the exclusive presence of non-selective deposit feeders associated with the carcass (Pavlyuk et al. 2009). With regard to molluscs, time-series studies have not yet been conducted in shallow waters, although isolated reports indicate the presence of the bathymodiolin mussel *Idas simpsoni* at 0-300 m depth in the North Sea living attached to whale bones (Marshall 1900, Tebble 1966, Warén 1991). Artificial whale falls sunk just below the 200 m depth threshold in the northwest Pacific (219–254 m: Fujiwara et al. 2007) show a general composition of the fauna similar to that of deep-water reducing habitats, with a chemosynthesis-based fauna mainly represented by the bathymodiolin mussel *Adipicola pacifica*. In contrast to this finding no evidence for a sulphophilic stage was found at a whale carcass artificially sunk at 385 m depth in the Monterey Submarine Canyon, north-eastern Pacific (Braby et al. 2007).

Here we present a species-level study of molluscs associated with a 5 m long minke whale (*Balaenoptera acutorostrata*) experimentally implanted in October 2003 at a depth of 125 m in the Kosterfjord (Skagerrak, Sweden). Time-series studies previously carried out on the

same site have shown that the Atlantic hagfish (*Myxine glutinosa*), sharks and other scavenging organisms consumed the flesh and exposed the bones within 5 weeks of implantation, and that the carcass was completely skeletonised after 6 months on the sea floor (Dahlgren et al. 2006). Nine months after sinking the carcass was colonized by *Osedax mucofloris*, the first species of *Osedax* known from a shelf-depth whale-fall, and the first from the Atlantic Ocean (Glover et al. 2005, Dahlgren et al. 2006). Our sampling was performed 5 years after the sinking of the carcass. Sediment samples were collected at the whale fall sites and at the surrounding soft bottom sediments in order to compare the whale fall mollusc fauna with the organisms commonly living in the area. Our primary objective was to analyse the community structure of the benthic mollusc fauna associated with a shallow-water whale-fall. Our second aim was to evaluate the differences in taxonomic composition and community structure between the whale fall community, the surrounding background community and the macrofaunal community related to other ephemeral, sulphide-rich habitat of the same area. For this reason the Kosterfjord samples were merged into a larger dataset built from literature data on mollusc relative abundances at a regional scale. The set includes data from one large pockmark in the North Sea (150–168 m: Dando et al. 1991), from soft sediment samples collected in the Gullmar Fjord at 115 m depth at times of hypoxic bottom water conditions (Josefson 1986, 1987, 1988), and from soft sediment samples of the west coast of Sweden (21–106 m: Agrenius 2001, 2002, 2003, 2005).

STUDY AREA

The Kosterfjord is situated in the north eastern part of the Skagerrak, the major gateway between the north Atlantic and the Baltic Sea. It is a 250m deep, 62km long submarine trench parallel to the coastline of Sweden to the east and sheltered by the Koster islands to the west (Figure 1). The trench is a fault fissure connected in the north-west to the Norwegian Trough which in turn is connected to the deep North Atlantic. As a consequence of its connection with the North Atlantic and the prevailing open-ocean marine conditions (including high salinity) the Kosterfjord is not a typical fjord (Palm et al. 2004).

The Skagerrak bottom is characterized by muddy sediments and a high content of organic material (about 2% of organic carbon), with sedimentation rates of 0.20 cm/year in the Northern sector (Josefson 1985, Van Weering et al. 1987). The overall oceanographic regime is driven by a counter clockwise circulation pattern, where dense, saline (30–35 psu) and oxygenated oceanic water underflows the more brackish (8–30 psu) surface water outflow of

the Baltic Sea. The main surface currents entering the area are the Jutland Current from the North Sea (south-west) and the Baltic Current from south-east. The mixing between these two currents forms the Norwegian Coastal Current, with a predominating northern heading, which flows out of the Skagerrak on the Norwegian side. This surface circulation is compensated by a deep counter current that brings the saline Atlantic water through the 700 m deep Norwegian Trench into the Skagerrak (Wisshak et al. 2005). However, the temperature and salinity of the surface waters are subject to strong seasonal fluctuations; in deeper waters the fluctuation is present with lower amplitude. Measurements of bottom water temperature at 125 m depth in the Kosterfjord indicate only small variations during the year of 4.8–7.5 °C, with salinity 34.3–34.7 psu (Dahlgren pers. obs.).

The Gullmar Fjord is a 27 km long fjord on the west coast of Sweden, about 70 km south of the Kosterfjord. It has a sill at 42 m water depth which restricts water flow to the deep basin of 115 m water depth. Periodically the water in the bottom of the basin has low oxygen levels. During the 1979–1980 winter the bottom of the basin became azoic, due to oxygen deficiency (Josefson & Widbom 1988).

MATERIALS AND METHODS

Sampling. For the present study four sediment samples were collected and analysed for their mollusc composition. Sample W1 was collected in May 2008 from the minke whale skeleton at 125 m depth, samples B1, B2 and B3 (background samples) were collected in January 2009 at a distance from whale bones, respectively 18 m south, 13 and 55 m north from the whale, at 125–126 m depth. The sampling at the whale fall was conducted with a small Speere ROV (Remotely Operated Vehicle) equipped with a forward-mounted sampling scoop 16 cm long with a diameter of 8.4 cm. 4420 cm³ of sediments were collected with three ROV scoops close to the whale bones (W1), stored in a sample basket (size 34x26.5x25 cm) and retrieved. Due to its size and shape the scoop was able to collect only surface sediments (max sampled depth ~5 cm). Each of the three background sediment samples (B1, B2, B3) was collected using a Van Veen grab with a sampling area of 0.1 m² and that would have penetrated to on average of 7–10 cm, and up to a maximum of 20 cm. The total volume of collected sediments was about 15000 cm³ for each background sample (Table 1).

The sediment samples were wet sieved through a 0.5 mm screen and preserved in ethanol (~80%) before identification. No attempt was made to separate live from dead individuals. The residue was washed with hydrogen peroxide and sorted under a binocular microscope for

all recognizable hard shelled biogenic components. The latter include molluscs, serpulids, echinoids, bryozoans, decapods, ostracods, brachiopods, fishes and whale bone fragments. Molluscs were determined at the species level and used for quantitative comparisons. Both live and dead specimens were counted. The total number of bivalve individuals was counted as the highest number of right or left valves and half of the remaining, the latter roughly corresponding to the number of unmatched valves (i.e., 50 left and 48 right valves: $50 + (48/2) = 74$ individuals). Gastropods were equated to the number of apices. Nomenclature used follows Hansson (1998).

Data analyses. The Kosterfjord dataset, including 1575 specimens belonging to 45 mollusc species, formed the basis for the analyses of sample diversity and trophic structure. Rarefaction curves (Hurlbert 1971) were calculated to compare mollusc sample species richness of the whale fall sample (W1) with species richness of the background samples (B1, B2, B3). The height of a rarefaction curve is a function of community species richness, and its curve steepness is a function of species evenness, allowing a comparison of diversity in samples of different sizes (Hayek & Buzas 1997, Gray 2000). Diversity indices were also calculated for each sample, each influenced to some degree by community structure. The Simpson index is affected by the 2-3 most abundant species and represents the probability that 2 individuals chosen at random from a sample belong to the same species (Hayek & Buzas 1997). Shannon's index (H) provides a measure of uncertainty in the identity of an individual pulled randomly from a sample (Hayek & Buzas 1997), with low H indicating a fairly high certainty of outcome (i.e. low diversity). H is thus insensitive to rare (especially singleton) species. Fisher's α is a number close to that of species expected to be represented by only a single (i.e. rare) individual (Hayek & Buzas 1997). The four Kosterfjord samples (n=1575) were also used for trophic analysis. Seven trophic categories were distinguished consistently following the Molluscan Life Habits Databases (Todd 2000). Abbreviations appropriate for the present study were used: chemosymbiotic deposit feeders (DC), suspension feeders (SU), subsurface deposit feeders (DU), surface deposit feeder (DS), herbivores, including herbivores on fine-grained substrates, herbivores on rock, rubble or coral substrates and herbivores on plant or algal substrates (HE) and predatory carnivores, including scavengers (CP). Comparisons were expressed through percent of number of specimens (n, abundance) and number of species (S, richness) for each category.

The larger dataset, made by merging the Kosterfjord data with literature data (Appendix 1), includes five samples from a North Sea pockmark with active methane seeps and three from

the surrounding sediments at 150-166 m depth (Dando et al. 1991), three samples collected in the Gullmar Fjord during periods of low oxygen conditions (Josefson 1986, 1987, 1988), and 82 samples from the west coast of Sweden ranging from 26 to 106 m depth (Agrenius 2001, 2002, 2003, 2005). The latter were collected in the Kattegat and the Skagerrak and are subdivided in samples from fjords (25), coastal areas (35) and open sea settings (22). The samples from the North Sea pockmark were collected with a Smith-McIntyre grab sampling 0.1 m², a gravity corer or a multiple corer (S1 to S6), and with a box corer sampling 0.085 m² (R1, R5, R8) (Dando et al. 1991) (Appendix 2). The samples from the Gullmar Fjords were taken with a modified Smith-McIntyre grab, covering a bottom area of 0.1 m² and taking a sediment volume of 15.5 l (Appendix 2). Each sample (GF1, GF2, GF3) is the mean of 5 replicate grabs (Josefson 1986, 1987, 1988). Each of the Kattegat and the Skagerrak samples derives from the sum of four replicate sub-samples collected with a 0.1m² Smith-McIntyre grab (Agrenius 2001, 2002, 2003, 2005) (Appendix 2). Macrofauna was collected by washing the sediment through a 0.5mm mesh sieve for the North Sea pockmark samples, and through a or 1mm mesh sieve for all the others. The total dataset is made of 97 samples, for a total of 105 mollusc species (gastropods, bivalves, scaphopods) and 26.298 individuals. None of the previous studies specify if live specimens or both live and dead shells were counted, so that it is assumed that the whole dataset is inclusive of both dead and live specimens. If only live specimens were included, the merging of live and live/dead assemblages in the same dataset (e.g. the Kosterfjord dataset and the data derived from the literature) would not alter significantly the results of our analysis. It is shown by a previous analysis of 85 habitat-level live dead molluscan data sets that a strong correlation exists between live and death assemblages, with species dominant in a single live census also dominating the local death assemblage, and species rare or unsampled alive being also rare dead (Kidwell, 2002). Furthermore death assemblages are known to capture environmental gradients as much as living assemblages (Tomašových & Kidwell 2009, Albano & Sabelli 2011, Weber & Zuschin submitted) and comparisons of evenness based on many collections provide reasonably accurate estimates of differences in average large-scale community structure (Olszewski & Kidwell 2007), so that a study based on both live and death assemblages is considered as informative as one based solely on live specimens. In addition, variation in life span is known to yield little bias of proportional abundances when passing from the live to the death assemblage (Kidwell & Rothfus 2010).

After removing species occurring only in one sample (singletons), multivariate analysis was performed on a dataset with 68 species and 26.174 individuals (99.5% of the original dataset). To overcome problems connected with comparing samples of different size, abundances were transformed into percentages. Percentages were then square-root transformed to de-emphasize the influence of the most abundant taxa and increase the effect of rare species (Clarke & Warwick 2001), allowing for a stronger correspondence with known environmental gradients (see Tomašových & Kidwell 2009). Hierarchical agglomerative cluster analysis was performed using the paired group method and the Bray–Curtis algorithm (Q mode cluster). Data were elaborated through detrended correspondence analysis (DCA), a multivariate statistical technique widely used with ecological data to ordinate taxa along underlying ecological gradients (Hill & Gauch 1980). In a DCA plot, axis 1 reflects the primary source of ecological variation in the composition of fauna and axes 2 the additional sources of variation beyond the principal gradient. A similarity percentage analysis (SIMPER, see Clarke & Warwick 2001) was performed to determine which species were responsible for similarity within groups of samples. Those species for which the ratio of mean similarity to standard deviation of similarity is >1 typify the sample group, and were listed in the comparisons. Diversity indices, cluster analysis and DCA analysis were performed with the software PAST (Hammer et al. 2001). SIMPER analysis was performed with the software PRIMER (Clarke & Warwick 2001). To avoid ambiguities in the final interpretation, the results of the multivariate analyses were evaluated considering possible effects of sampling methods on one side, and of taphonomic processes on species abundances in time-averaged death assemblages on another (Tomašových & Kidwell 2011).

RESULTS

Whale fall and background community structure. During sampling at the whale fall site the skull, one mandible and some ribs were still visible on the sea floor. Exposed bones were covered in a mixture of bacterial mats (associated with blackened bone regions, indicative of sulphide release) and muddy sediments. No molluscs were seen lying directly over or around the bones during the survey (nor in more than 20 bones brought to the laboratory and analysed over the years). Algal debris was trapped within the bones (e.g. *Fucus serratus*) and the decapod *Hyas araneus* was frequently observed close to the skeleton (Figure 2). Bones

were highly bioeroded and specimens of the bone eating worm *Osedax mucofloris* were recorded living on collected bone samples, five years after carcass deployment.

The sieving residue included molluscs, regular and irregular echinoids (*Brissopsis lyrifera* and *Spatangus purpureus*), brachiopods (*Crania* sp. and terebratulids), benthic foraminifers, ostracods, serpulids, bryozoans, decapods, fish fragments and teeth and myxinid dental plates. Sample W1 was dominated by the bivalve *Thyasira sarsi* (51% of the total), followed by *Abra nitida* (16.2%), *Tellimya ferruginosa* (8%), *Mytilus edulis* (4.9%) and the nuculanid *Ennucula tenuis* (4.7%) (Figure 3). Among the gastropods the most abundant were *Pusillina sarsii* (3.7%), *Cylichna cylindracea* (2.5%) and *Alvania punctura* (2%). Specimens of *Thyasira sarsi* (Figure 4A) and *Abra nitida* (Figure 4B) were observed alive during sieving operations. *Thyasira equalis* was the most abundant species in B1, B2 and B3 samples, accounting respectively for the 43.1%, 22.9% and 27.8% of the total. Besides *T. equalis*, the background samples contained many protobranchiate bivalves, such as *Ennucula tenuis*, *Yoldiella philippiana*, *Nucula sulcata*, *Nuculana minuta* and *N. pernula* (Figure 3). Also the semelid *Abra nitida* and the cardiid *Parvicardium minimum* were represented in significant quantities in the background sediments.

The background samples B2 and B3 exhibit higher species richness and a more even distribution than W1, that is, W1 is dominated by fewer species (Figure 5). Although W1 derives from a smaller volume of sediments compared with the background samples (see Table 1), it contains a larger number of individuals, and its rarefaction curve reaches an asymptotic shape. This indicates that if a larger volume of similar sediments had been collected from the whale fall, no further taxa would have been added. The diversity indices help to interpret results from rarefaction curves (Table 2). W1 has the highest value of D, the Simpson index of Dominance, being dominated by a few species, and the lowest value of H, the Shannon's index. The Shannon's index is more affected by species in the middle of the species rank sequence which are rare at the whale fall but are abundant in the background samples. The background sediments are in fact characterized by a higher number of rare species than W1, as also highlighted by their high values of the Fisher's α index. B1, the sample with the lower number of individuals, has intermediate values.

Trophism. The two predominant thyasirids, *Thyasira sarsi* (dominant at W1) and *Thyasira equalis* (dominant at B1, B2, and B3), are infaunal chemosymbiotic deposit feeders 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

with active methane seepage, whether they were collected from the side of the pockmark (R5, R8, S1, R1, S2) or from the surrounding bottom sediments not directly related to methane seepage (S4, S5, S6). Cluster 3 contains samples from the Swedish west coast with average depth < 50 m, comprising those from fjords and those from onshore settings. Cluster 4 groups all offshore soft bottom samples, i.e., with an average depth > 50 m. The Kosterfjord background samples (B1, B2, B3) became included in the latter group, in particular with samples collected in the same area at 91-102 m depth (SK13 and SK14: Figure 7, Appendix 2). This result confirms that the distribution of species abundances in samples is relatively unaffected by sampling and processing methods. Consistently with the cluster analysis, in the DCA diagram the four main sample clusters show practically no overlap (Figure 8). The first two axes of the ordination, DC1 and DC2, are representative of the full distribution of data, explaining 90.7 % of the variance (DC1 = 65.7%, DC2 = 25%). A small overlap occurs between onshore and offshore samples, consistently with a gradual depth-related transition between samples. If in the dendrogram fjords and onshore samples were grouped together, in the DCA they are well separated, forming two distinct sub-clusters, fjord samples at low DC2 values and onshore samples at high DC2 values. The ordination of samples along DC1 follows a depth gradient (see Appendix 3). Onshore and fjord samples score the lowest DC1, onshore samples ranging 28-59 m depth, fjord samples 21-47 m. Offshore samples have intermediate DC1 values, their depth gradually shifting from 50 to 125 m with increasing DC1 scores. Consistently, W1 and samples from the Gullmar Fjord, collected at a depth of 115 m, have intermediate DC1 values. Samples from the methane seep area, collected between 150 and -166 m, rest on the right part of the diagram. Samples are also widely scattered along DC2. Gullmar Fjord samples have the lowest DC2 values, followed by W1, fjord samples and some of the samples from the methane seep area, merging with onshore and offshore samples at high DC2 scores. Concerning the possible occurrence of both dead and live assemblages in our dataset, when samples are pooled, we can expect that variation in species composition among samples will be higher when living or death assemblages are ordinated separately. The centroid of such pooled assemblages should be located between the centroids of living and death assemblages (Tomašových & Kidwell 2011). Given the distribution of environmentally separable groups of sample in the multidimensional space, at clearly separable DC2 values (Figure 8), an eventual separation of live and dead assemblages within each cluster would not alter the significance of the difference between clusters.

SIMPER analysis allowed us to highlight which taxa are responsible for the similarity within samples forming the five main groups (Table 3). The whale fall and the Gullmar Fjord samples have the highest similarity among the five groups. In particular, their similarity is given by the occurrence in all of them of the bivalves *T. sarsi* and *A. nitida*, with a cumulative contribution of the 76.7%. Even if *T. sarsi* occurs in two of the samples collected inside of the North Sea pockmark (R8 and S1), the largest contribution to the similarity between samples from the methane seep area is given by the thyasirids *T. equalis* and *T. obsoleta*. Onshore, offshore and fjord samples are dominated by the bivalves *Kurtiella bidentata*, *Abra nitida*, nuculanids like *Ennucula tenuis* and *Nucula nitidosa* and the gastropods *Hyla vitrea*, which contribute with different percentage within each group.

DISCUSSION

The Kosterfjord whale fall. The quantitative analysis of the Kosterfjord samples shows that the presence of a minke whale carcass on the sea floor at shelf depths still influences the composition and structure of the benthic community five years after its implantation. Although some species are shared between the whale fall and the background community, the whale-fall community clearly shows a lower diversity in its species composition, a different ranking of species, and dominance of the chemosymbiotic bivalve *Thyasira sarsi*. The Kosterfjord whale fall is similar to sites with high organic input in shallow water environments (see Pearson & Rosenberg 1978). Rarefaction curves and diversity indices show a markedly lower diversity in the area close to the source of organic matter with respect to the background sediments. The high abundance of *T. sarsi* in the sediments closely associated with the skeleton suggests that the decay of the whale organic matter created an ephemeral habitat with high sulphate reduction rates, i.e. a certain degree of reliance on chemosynthesis. The density of *T. sarsi* is in fact dependent upon the sulphate reduction rate in the sediment (Dando et al. 2004). Sulphide conditions could have been further favored by the presence of macroalgae trapped within the bones, which can alone introduce reduced compounds in the sediments (Dando et al. 1993). The species *T. sarsi* is widely distributed in the NE Atlantic and is generally found in association with organic-rich sediments with high total sulphide concentrations (Dando & Southward 1986). In the North Sea and in the Skagerrak *T. sarsi* is associated with sewage-polluted fjords, anoxic fjords, fish farms and active methane seeps (Dando et al. 1991, Dando & Spiro 1993, Dando et al. 1994, Rosenberg et al. 2002, Kutti et al. 2007), with a depth range of 50-340 m (Dufour 2005). Conversely, the dominant species in the background sediments and absent in the whale fall

collection, *T. equalis*, is the most common thyasirid on the North European continental shelf, preferring sediments with less-organics with respect to *T. sarsi*, possibly avoiding hydrogen sulphide rich sediments (Dando & Southward 1986).

The opportunist species *Abra nitida*, common along the northern part of the Swedish west coast, is a density-dependent species unaffected by turbid conditions (Josefson 1982). Its high abundance at the whale-fall site could be linked to the presence of high organic content, as observed in fish farm areas with increased food supply (Kutti et al. 2007). The abundance of *Telloyia feruginosa* in the whale-fall sample, a small bivalve living symbiotically in the burrow of the echinoid *Echinocardium cordatum* (Gillan & De Ridder 1997), is indicative of the occurrence of the echinoid itself. *Echinocardium cordatum*, a deep burrower, may not have been directly collected due to the shallow depth of our sampling. The species hosts ectosymbiotic sulphide-oxidizing bacteria, *Thyothrix* like, in its intestinal caecum and is known to burrow below or at the level of the oxidized-reduced interface, ingesting both surface and deep reduced sediments. This symbiosis opens an access for *E. cordatum* to sulphide-rich habitats (Temara et al. 1993, Brigmon & De Ridder 1998) and adds further evidence for the presence of a chemosynthetic ecological niche at this shallow-water whale fall site (Bromely et al. 1995). As with *E. cordatum*, the presence of other deeper burrowers may have been overlooked because of the shallow sampling depth within the sediment. Among these missing taxa may be the lucinid bivalves, chemosymbiotically hosting sulphur-oxidizing bacteria in their gill tissue and living in burrows of up to 20 cm depth (Dando et al. 1986).

Both the whale fall and the surrounding sediment communities record the presence of coastal species, such as the mytilids *Mytilus edulis* and *Musculus cf. discors* and littorinid gastropods, which were probably transported down-slope by bottom currents. Most of the gastropods found at the whale fall site, including the rissoids, are known to dwell on sea weeds, and were possibly transported by drifting algae, as shown by algal debris around whale bones (Figure 2). Because alive and dead specimens were not distinguished during our sampling procedures, it is not possible here to support the hypothesis that some rissoid species could be adapted to live also in reducing environments, as recently found in some North Atlantic vents (Schander et al. 2010).

Environmental gradients on the Swedish shelf. The species level, multivariate comparison of the Kosterfjord samples with samples collected from soft-bottom sediments across the

west Swedish coast allowed a better interpretation of environmental parameters controlling the faunal composition at the Kosterfjord whale fall. In this study, the ordination of samples along the principal axis of the DCA is controlled by water depth. The faunal composition changes continuously along a depth gradient, with shallower samples on the left side of the diagram and deeper on the right side. This result is in accordance with the interpretation that in marine environments water depth is the single most important factor controlling the distribution of benthic organisms (see Gauch 1982), and as amply proven in other case studies (Scarponi & Kowaleski 2004, Dominici et al. 2008, Danise 2010).

The significance of the DC2 ordination is generally more difficult to interpret, because variations in water depth sum up continuously changing values of other parameters that directly affect the distribution of benthic species, such as food availability, water energy, substrate texture, seasonality, oxygen content and salinity. Samples from reducing soft bottoms are mainly distributed at low DC2 scores, particularly those from the Gullmar Fjord, where bottom waters are periodically affected by low oxygen conditions (Josefson 1987, Josefson & Wibdon 1988, Dando & Spiro 1993). The three samples included in this study were collected between 1985 and 1987, at a time of re-colonization of the sediments by *T. sarsi* after a period of oxygen depletion resulting in the death of the bottom fauna. Dando & Spiro (1993) report high concentrations of total reduced sulphur in the Gullmar Fjord sediments in 1986, together with negative $\delta^{13}\text{C}$ values in the gills of collected specimens of *T. sarsi*, indicating a significant carbon input from autotrophic endosymbiotic bacteria. In addition, samples from the large North Sea pockmark are characterized by the presence of high total sulphide concentrations in the surface layers, as compared to surrounding areas (Dando et al. 1991). In particular, both samples R8 and S1 which have low DC2 values, host the bivalve *T. sarsi* with negative $\delta^{13}\text{C}$ values (Dando et al. 1991). Since macrobenthic communities associated with fjords, organic enriched sediments and high sulphide methane seeps all occur in the lower part of the diagram and communities from open marine, oxygenated, environments in the upper part, the DC2 score may be a direct measure of the degree of sulphide concentration and an indirect measure of oxygen level of soft bottom sediments.

The general picture that can be drawn from our study of north European shelf molluscs shows that the benthic community structure at the Kosterfjord whale fall is similar to that of communities developed in other organic-rich, sulphide environments. In particular, among the secondary colonisers of the enriched sediments at the whale fall are the symbiont-

containing thyasirids, suggesting an ecological succession similar to that of other organic rich-sediments (Pearson & Rosenberg 1978, Dando et al. 2004). A global comparison of whale-fall communities is hampered by the lack of relevant studies at comparable environmental conditions. In comparison with 219-254 m whale-fall communities in the northwest Pacific (Fujiwara et al. 2007), the Kosterfjord whale fall lacks molluscs typical of deep water, such as the mytilid mussels (*Adipicola pacifica*) and the cocculinid limpets. Among the bathymodiolin mussels, *Idas simpsoni* has been described from trawled bones on the North Sea shelf (Marshall 1900, Warén 1991, Tebble 1996) and in oil-polluted areas (Hartley & Watson 1993, Southward 2008), but was not found at the Kosterfjord whale fall during the ROV survey, careful examination of multiple recovered bones or in sediment samples. In a time-series study of oil-polluted sediments around North Sea wells and platforms, the benthic community responded to high levels of oil contamination with the appearance of the bathymodiolin *I. simpsoni*, followed by *T. sarsi* when oil concentrations gradually lowered (Hartley & Watson 1993).

Conclusion

Our evidence suggests that the Kosterfjord whale-fall mollusc community is structured around species that exploit a variety of food sources on the continental shelf, including heterotrophs and chemoautotrophs. This result is similar to that recorded from a fossil analog from the Pliocene of Italy (Dominici et al. 2009, Danise et al. 2010). However, it is in contrast with the data on the polychaete fauna. To date a total of 7 new species of polychaete have been recorded from the Kosterfjord whale fall, of which just 3 are present at other organic-rich settings such as fish-farms (Glover et al. 2005, Wiklund et al. 2009a, 2009b, Wiklund pers. comm.). This may well be partly because the polychaete fauna of organic-rich habitats is less well studied than the mollusc fauna, but the presence of specialists such as *Osedax mucofloris* at Kosterfjord is in contrast with the pattern for Mollusca. From an ecological perspective, our data suggest that shelf-depth whale-falls are a natural analog to areas of organic pollution, such as oil spillages and fish farms, and as such may well offer interesting insights into natural bioremediation at these habitats. From an evolutionary perspective, small carcasses at shelf-depths may provide an avenue for speciation in 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) of 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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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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724 **FIGURES**

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Figure 1

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Figure 8

TABLES

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

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

Table 2

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

Table 3