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Molluscs from a shallow-water whale-fall and their affinities with adjacent benthic communities on the Swedish west coast

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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 carcass were dominated by the bivalve Thyasira sarsi, which is known to contain endosymbiotic sulphur-oxidizing bacteria, while background sediments were dominated by another thyasirid, T. equalis, 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, 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 that 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.

Key words: Whale, Thyasiridae, organic-enriched sediments, chemosynthesis, North Atlantic

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). During the ‘mobile scavenger’ stage, which lasts months to years, sharks, hagfish and other scavenging organisms remove flesh and soft tissues. Polychaetes, crustaceans and other opportunistic small-sized animals thrive on organic remains during the subsequent ‘enrichment opportunist’ stage, which can last months to years. A complex community, lasting for decades, relies on the hydrogen sulphide and other chemical compounds produced by microbial consumption of the lipid-rich bones in the final ‘sulphophilic’ stage. During this stage, chemosynthetic bacteria – free-living or in symbiosis within vesicomyid clams, bathymodiolin mussels and vestimentiferan tube worms – are at the base of a food web where organic matter is primarily produced by the oxidation of inorganic compounds. Some of the animals found at whale-falls are restricted to vertebrate carcasses, such as the gutless (although heterotrophic) bone-eating worm Osedax Rouse, Goffredi & Vrijenhoek (Rouse et al. 2004; Rouse et al. 2011), while 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 over evolutionary time (the stepping stone hypothesis: Smith et al. 1989). Evidence consistent

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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). For instance, it has been hypothesized that the ancestors of bathymodiolin mussels were shallow-water species which might have acquired the ability to associate with sulphur-oxidizing bacteria, allowing them to first colonize organic habitats such as wood and whale-falls and then moving on to hydrothermal vents at ridges and cold seeps (Duperon 2010). However, natural whale-falls from shallow waters, commonly defined as less than 200 m deep (Dubilier et al. 2008; Dando 2010), are poorly documented both in the modern and fossil record and their faunal composition as well as the course of the ecological succession are poorly known (see 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 and rare bathymodiolin testifying for the sulphophilic stage, has provided some insights with regard to ecological succession at shelf depths (Dominici et al. 2009; Danise et al. 2010).

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 Oseadax mucofloris Glover, Kallstrom, Smith & Dahlgren, 2005 (Glover et al. 2005; Dahlgren et al. 2006; Schander et al. 2010a), whereas studies of temporal processes at very shallow (<40 m) whale-falls in the Gullmar Fjord, Sweden, show 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). Several species of dorvilleid and chrysopetalid polychaetes documented at shelf-depth 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, b). With regard to molluscs, isolated reports indicate the presence of the bathymodiolin mussel Idas simpsoni (Marshall, 1900) at <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 (Dall, Bartsch & Rehder, 1938). 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, northeastern Pacific (Braby et al. 2007).

Given this patchy record, many questions remain open with regard to the faunal composition of shallow-water whale-fall communities. One of the main questions is if they host obligate species, as their deep-sea counterparts, or if they are colonized by a subset of the local fauna tolerant of sulphide, similar to shallow-water seep and vent communities (Sibuet & Olu 1998; Tarasov et al. 2005; Dando 2010). Here we present a species-level study of molluscs associated with a 5-m long minke whale (Balaenoptera acutorostrata Lacepède, 1804) 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 Linnaeus, 1758), sharks and other scavenging organisms consumed the flesh and exposed the bones within 5 weeks of implantation, and that the carcass was completely skeletonized after 6 months on the sea floor (Dahlgren et al. 2006). Nine months after sinking the carcass, it was colonized by Oseadax mucofloris, the first species of Oseadax 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 deployment. Sediment samples were collected at the whale-fall site and at the surrounding soft-bottom sediments, in order to compare the whale-fall mollusc fauna with the organisms commonly living in the area. The Kosterfjord samples were then merged into a larger data set built from literature data on mollusc relative abundances at a regional scale, including samples from active methane seep, fjords, coastal and open marine environments.

Our main aim was to understand whether shallow-water whale-fall communities host obligate taxa or if they are colonized by species commonly living in the surrounding soft bottoms. To answer this question, we (i) analysed the community structure of the mollusc fauna associated with a shallow-water whale-fall and (ii) evaluated the differences in taxonomic composition and community structure between the whale-fall community, the surrounding background community and the macrofaunal community at various marine settings around the west coast of Sweden.

**Materials and Methods**

**Study area**

The Kosterfjord is directly connected with the North Atlantic, and because of the prevailing open-ocean
marine conditions (including high salinity) it is not a typical fjord (Palm et al. 2004). It is situated in the northeastern part of the Skagerrak, which is the major gateway between the north Atlantic and the Baltic Sea. It is a 250-m deep, 62-km 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 northwest to the Norwegian Trough which in turn is connected to the deep North Atlantic.

The Skagerrak bottom is characterized by muddy sediments and a high content of organic matter (about 2% of total organic carbon in the sediments), 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 an anticlockwise 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 (southwest) and the Baltic Current from the southeast. 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 (Saetre 2007). 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 variations during the year of 4.8–7.5°C, with salinity ranges of 34.3–34.7 psu.

The Gullmar Fjord is a 27-km long real 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. The organic carbon content of the sediments is on average higher than in the Kosterfjord, with values between 2.2% and 3.8% (Dando & Spiro 1993). Periodically the water in the bottom of the basin has low oxygen levels. During the 1979–1980 winter, the bottom of the basin became anoxic, due to oxygen deficiency (Josefson & Widbom 1988).

**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 Sperre ROV (Remotely Operated Vehicle) equipped with a forward-mounted sampling scoop 16 cm long with a diameter of 8.4 cm. Sediments (4,420 cm³) were collected with three ROV scoops close to the whale bones (W1), stored in a sample basket (size 34 × 26.5 × 25 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 and B3) was collected using a Van Veen grab with a sampling area of 0.1 m² which would have penetrated to an average depth of 7–10 cm, and up to a maximum of 20 cm. The total volume of collected sediments was about 15,000 cm³ for each background sample (Table I).

The sediment samples were wet sieved through a 0.5 mm screen and preserved in ethanol (∼80%) before identification. 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, bryozaans, decapods, ostracods, brachiopods, fishes and whale bone fragments. Molluscs were determined at the species level and used for quantitative comparisons. Both shells from 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 unmatchable valves (i.e. 50 left and 48 right valves: 50 + (48/2) = 74 individuals). Gastropods were equated to the number of apices.

Data analyses

The Kosterfjord data set, including 1,575 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). Alpha diversity was measured using the Simpson index of diversity (D), which is an appropriate measure of diversity for species abundance data when sample size is not homogeneous (Clarke & Warwick 2001). The Simpson index of diversity ranges from 1 (one taxon dominates the community completely) to 0 (all taxa are equally present), and can be considered a measure of dominance.

The four Kosterfjord samples (n = 1,575) 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

| Sample Type       | Name   | Volume (cm³) | Sampling methods | Depth (m) | Latitude | Longitude | Distance from the whale (m) | Sampling date | Simpson index |
|-------------------|--------|--------------|------------------|-----------|----------|-----------|----------------------------|---------------|---------------|
| Whale-fall        | W1     | 4,420        | ROV scoop        | 125       | 58.926   | 11.05.728 | 0                          | May 2008      | 0.3022        |
| Background sediments | B1     | 15,500       | 0.1 m² Van Veen grab | 125       | 58.926   | 11.05.728 | 18                         | Jan. 2008     | 0.3022        |
| Background sediments | B2     | 15,500       | 0.1 m² Van Veen grab | 125       | 58.926   | 11.05.728 | 18                         | Jan. 2009     | 0.2421        |
| Background sediments | B3     | 15,500       | 0.1 m² Van Veen grab | 125       | 58.926   | 11.05.728 | 55                         | Jan. 2009     | 0.1297        |
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 \((n, \text{ abundance})\) and number of species \((S, \text{ richness})\) for each category.

The larger data set, made by merging the Kosterfjord data with literature data (Supplementary Material Tables SI–SII), includes (i) 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), (ii) three samples collected in the Gullmar Fjord during periods of low oxygen conditions (Josefson 1986, 1987, 1988), and (iii) 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 into samples from fjords (25), coastal areas (35) and open sea settings (22). The total data set is comprised of 97 samples, for a total of 105 mollusc species (gastropods, bivalves, scaphopods) and 26,298 individuals.

After removing species occurring only in one sample (singletons), multivariate analysis was performed on a data set with 68 species and 26,174 individuals (99.5% of the original data set). 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 axis 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 & Gorley 2006).

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 on or right next to the bones during the survey (nor in more than 20 bones brought to the laboratory and analysed over the year the carcass has been studied). Algal debris was trapped within the bones (e.g. \textit{Fucus serratus} Linnaeus, 1753) and the decapod \textit{Hyas araneus} Linnaeus, 1758 was frequently observed close to the skeleton (Figure 2). Bones were highly bioeroded and specimens of the bone-eating worm \textit{Osedax mucofloris} were recorded living on collected bone samples, 5 years after carcass deployment.

![Figure 2](image-url)
The sieving residue included molluscs, regular and irregular echinoids (*Brissopsis lyrifera* (Forbes, 1841) and *Spatangus purpureus* Müller, 1776), brachiopods (*Novocrania* sp. and terebratulids), benthic foraminifers, ostracods, serpulids, bryozoans, decapods, fish fragments and teeth and myxínid dental plates. Sample W1 was dominated by the bivalve *Thyasira sarsi* (Philippi, 1845) (51% of the total), followed by *Abra nitida* (O.F. Müller, 1776) (16.2%), *Tellimya ferruginosa* (Montagu, 1808) (8%), *Mytilus edulis* Linnaeus, 1758 (4.9%) and the nuculanid *Ennucula tenuis* (Montagu, 1808) (4.7%) (Figure 3).

Among the gastropods the most abundant were *Pusillina sarsii* (Lovén, 1846) (3.7%), *Cylichna cylindracea* (Pennant, 1777) (2.5%) and *Alvania punctura* (Montagu, 1803) (2%). Specimens of *T. sarsi* and *A. nitida* were observed alive during sieving operations. *Thyasira equalis* (Verrill & Bush, 1898) was the most abundant species in B1, B2 and B3 samples, accounting, respectively, for 43.1%, 22.9% and 27.8% of the total. Besides *T. equalis*, the background samples contained many protobranchiate bivalves, such as *E. tenuis*, *Yoldiella philippiana* (Nyst, 1845), *Nucula sulcata* Bronn, 1831, *Nuculana minuta* (Müller, 1776) and *N. pernula* (Müller, 1779) (Figure 3). Also *A. nitida* and *Parvicardium minimum* (Philippi, 1836) were represented in significant quantities in the background sediments.

The background samples B2 and B3, which are located north of the whale-fall site, exhibit higher species richness and a more even distribution than W1 (Figure 4). B1, which is to the south of the minke whale, yielded fewer individuals than all the other samples. Although W1 derives from a smaller volume of sediments compared with the background samples (see Table I), 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 Simpson index of Dominance (*D*) helps to interpret the results from rarefaction curves (Table I). W1 has the highest value of *D*, being dominated by a few species. Also B1, which is downstream to the whale-fall site, has a higher value of *D* with respect to the samples located north of the carcass.

**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 them are mixotrophic and can derive
part of their nutrition heterotrophically by particulate feeding (Dufour & Felbeck 2006). In particular, studies on the nutritional dependence of the two bivalves on chemosynthetic symbiotic bacteria show that *T. equalis* has fewer symbiotic bacteria in its gills compared to *T. sarsi*, indicating that the nutritional importance of carbon fixed by the bacteria is less in *T. equalis* (Dando & Spiro 1993; Dufour 2005). *Thyasira sarsi* instead derives 50–100% of its tissue carbon from carbon fixed by bacteria (Spiro et al. 1986; Schmaljohann et al. 1990). The chemosymbiotic trophic group has the highest abundance in all the four samples, but the lowest species richness (Figure 5). Like chemosymbiotic deposit feeders, surface deposit feeders have a high overall abundance but low species richness, being represented only by the semelid *Abra nitida*, more abundant in W1 than in the background community. Subsurface deposit feeders (nuculids, nuculanids, yoldiids and dentaliids) have both high abundance and high diversity in B1, B2 and B3 (38%, 46% and 47.9%, respectively). The same subsurface deposit feeders are present in all samples, but their abundance in W1 is the lowest (8.4%). Suspension feeders have high species richness, both in whale-fall and background fauna. The mytilids *Mytilus edulis* and *Musculus discors* (Linnaeus, 1767) and the montacutid *Tellimya ferruginosa* (Montagu, 1808) are found in sample W1, whereas pectinids, anoimids and cardiids are typical of B1, B2 and B3. Herbivores are diverse but rare in all samples. Those associated with the whale-fall, such as the rissoids *Rissoa lilacinæ* Récluz, 1843 and *Pusillina sarsii*, are typical of shallower settings where they are associated to algae (*Laminaria* spp.) or seagrass (*Zostera marina* Linnaeus, 1753) (Wareén 1996). The rissoid species *Onoba cf. tumidula* Sars, 1878 was recently found also at relatively shallow water vents (557–713 m) in the North Atlantic (Schander et al. 2010b), suggesting a rather wide environmental range for the whole family. Carnivores are the least represented among the trophic categories; only the burrowing *Cylichna cylindracea* was present in the whale-fall sample.

**Extreme vs. normal benthic environments**

The samples collected at the Kosterfjord whale-fall and in the surrounding sediments were compared with samples from a shallow-water North Sea methane seep area, from soft sediment samples collected in the Gullmar Fjord at 115 m depth at times of hypoxic bottom water conditions and with samples collected in normal marine bottoms along

![Figure 5. Trophic analysis expressed through percent of number of individuals (abundance) and number of species (richness).](image-url)
the Swedish west coast. The CLUSTER agglomerative diagram shows that samples group in four main clusters at rather high value of similarity (around 0.4: Figure 6). Cluster 1 includes samples from ‘organic-rich sediments’, i.e. the whale-fall sample (W1) and the three samples from the Gullmar Fjord (GLF1, 2, 3), the latter with an organic carbon content between 2.2% and 3.8% (Dando & Spiro 1993). Cluster 2 groups samples 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 6; Supplementary Material Table SII). This result confirms that the distribution of species abundances in samples is relatively unaffected by the heterogeneity of the data set, which includes data collected with different sampling and processing methods (see Supplementary Material Table SII). Consistent with the CLUSTER analysis, in the DCA diagram, the four main sample clusters show practically no overlap (Figure 7). 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 CLUSTER analysis, fjords and onshore samples were grouped together, in the DCA they are well separated and form two distinct subclusters where fjord samples have low DC2 values and onshore samples have high DC2 values. The ordination of samples along DC1 follows a depth gradient (see Supplementary Material Figure S1). Onshore and fjord sample scores have 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 axis 2 of the ordination (DC2). Gullmar Fjord samples have the lowest
DC2 values, followed by W1, fjord samples and some of the samples from the methane seep area. Onshore and offshore samples have high DC2 scores instead.

SIMPER analysis allowed us to highlight which taxa are responsible for the similarity within samples forming the five main groups (Table II). 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 *Thyasira sarsi* and *Abra nitida*, with a cumulative contribution of 76.7%. Even though *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* (Montagu, 1803), *A. nitida*, nuculids like *Ennucula tenuis* and *Nucula nitidosa* and the gastropod *Hyala vitrea* (Montagu, 1803), which contribute with different percentages 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 5 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*. Our data, although limited to one sample at the whale-fall site, suggest that the high abundance of *T. sarsi* in the sediments close to the carcass is connected with the decay of the whale organic matter, which created an ephemeral habitat with high sulphate reduction rates. Previous studies show in fact that the density of *T. sarsi* is dependent upon the sulphate reduction rate in the sediment, i.e. a certain degree of reliance on chemosynthesis (Dando et al. 2004). Sulphide conditions could have been further locally favoured by the presence of dislocated macroalgae drifting along the seabed and trapped by the bones, which alone can 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, 1994;
Dando & Spiro 1993; Rosenberg et al. 2002, Kutti et al. 2008), with a depth range of 50–340 m (Dufour 2005). Conversely, the dominant species in the background sediments, \( T. \text{equalis} \), the most common thyasirid on the North European continental shelf, thrives in sediments with less-organics with respect to \( T. \text{sarsi} \), possibly avoiding hydrogen sulphide-rich sediments (Dando & Southward 1986).

The opportunist species \( A. \text{nitida} \), 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. 2008). The abundance of \( T. \text{equalis} \) at the whale-fall site, a small bivalve living symbiotically in the burrow of the echinoid \( E. \text{cordatum} \) (Pennant, 1777) (Gillan & De Ridder 1997), is indicative of the occurrence of the echinoid itself. \( E. \text{cordatum} \), a deep burrower, may not have been collected due to the shallow depth of our sampling. The species hosts ectosymbiotic sulphide-oxidizing bacteria, \( \text{Thiothrix}-\text{like} \), 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 \( E. \text{cordatum} \) 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 (Bromley et al. 1995). As for \( E. \text{cordatum} \), the presence of other deeper burrowers may have been overlooked in this study because of the shallow sampling depth within the sediment. Among these missing taxa may be the lucinid bivalves, which host sulphur-oxidizing bacteria in their gill tissue and live in burrows of up to 20 cm in depth (Dando et al. 1986).

**Taphonomic and sampling bias**

One potential bias in this study is that both dead and alive specimens were counted; hence some considerations need to be made on the implications for the faunal composition of the analysed samples. In fact, as a consequence of the adopted methodology, (i) dead shells may have increased species richness, and (ii) \( \text{in situ} \) and transported taxa may have been mixed, affecting the ecological interpretation of the encountered communities.

\( T. \text{equalis} \) shells were not found at the whale-fall, which was unexpected given that \( T. \text{equalis} \) was living at the whale-fall site prior to implantation, as

### Table II. Characteristic species of each group of samples calculated using the SIMPER similarity percentage analysis.

| Species            | Av. abund. | Av. similarity | Sim/SD | Contribution% | Cumulative% |
|--------------------|-------------|----------------|--------|---------------|-------------|
| **‘Organic-rich sediment’ samples** Average similarity = 64.89 |             |                |        |               |             |
| Thyasira sarsi      | 6.83        | 30.26          | 7.47   | 46.63         | 46.63       |
| Abra nitida         | 4.67        | 19.52          | 4.19   | 30.08         | 76.72       |
| **‘Onshore’ samples** Average similarity = 60.38 |             |                |        |               |             |
| Kurtiella bidentata | 7.31        | 30.04          | 3.18   | 49.76         | 49.76       |
| Hyala vitrea        | 4.43        | 15.09          | 1.61   | 25            | 74.75       |
| Varicorbula gibba   | 1.5         | 4.27           | 1.3    | 7.07          | 81.83       |
| Abra nitida         | 1.75        | 4              | 1.02   | 6.63          | 88.46       |
| **‘Fjord’ samples** Average similarity = 57.38 |             |                |        |               |             |
| Abra nitida         | 5.94        | 19.59          | 2.9    | 34.14         | 34.14       |
| Kurtiella bidentata | 3.96        | 8.99           | 1.11   | 15.67         | 49.81       |
| Nucula nitidosa     | 2.21        | 6.41           | 2.77   | 11.18         | 60.99       |
| Hyala vitrea        | 2.65        | 6.37           | 1.48   | 11.1          | 72.09       |
| Thyasira flexuosa   | 2.15        | 6.14           | 1.82   | 10.7          | 82.79       |
| Varicorbula gibba   | 1.26        | 3.01           | 1.3    | 5.24          | 88.03       |
| **‘Offshore’ samples** Average similarity = 48.91 |             |                |        |               |             |
| Abra nitida         | 4.45        | 12.49          | 2.26   | 25.53         | 25.53       |
| Ennucula tenuis     | 3.43        | 8.44           | 1.98   | 17.25         | 42.78       |
| Hyala vitrea        | 2.63        | 5.67           | 1.16   | 11.59         | 54.38       |
| Thyasira equalis    | 2.56        | 5.34           | 1.3    | 10.92         | 65.29       |
| Tellimya tenella    | 1.79        | 3.72           | 1.03   | 7.61          | 72.9        |
| Parvicardium minimum| 1.76       | 3.7            | 1.09   | 7.56          | 80.46       |
| **‘Methane seep area’ samples** Average similarity = 48.91 |             |                |        |               |             |
| Thyasira equalis    | 6.16        | 25.82          | 2.87   | 47.9          | 47.9        |
| Thyasira obsOLETA   | 4.44        | 15.06          | 1.52   | 27.94         | 75.84       |
in the background sediments. One possible explanation could be linked to a taphonomic bias. During the decay of the carcass, sulphide-rich sediments at the whale-fall site might have become acidic due to the oxidation of sulphide and completely dissolved dead shells. The microbial oxidation of organic matter and reduced species like \( \text{H}_2\text{S} \) can in fact decrease porewater pH immediately below the sediment–water interface and produce a strong carbonate undersaturation (Cai et al. 2006). In this scenario most of the background community shells could have been dissolved after the whale implantation, and our picture purely resembles the whale-fall community. A second explanation could instead be linked to a sampling bias. Because we collected only one sediment sample at the whale-fall site, it is not possible to exclude that \( T. \text{equalis} \) was present in the sediments close to the rest of the carcass.

The whale-fall community has a lower diversity with respect to the background community located north of it (samples B2 and B3). To the contrary, the background community located 18 m south (sample B1) is closer in species number and diversity to the whale-fall community. This suggests that currents might have transported whale organics (e.g. blubber) or decaying seaweeds from the carcass to this control site. The organic load related to the minke whale might have partially enriched the sediments there, probably not sufficiently to attract \( T. \text{sarsi} \) but enough to have a detrimental effect on other species.

Both the whale-fall and the background communities record the presence of coastal species, such as the mytilids \( \text{Mytilus edulis} \) and \( \text{Musculus cf. discors} \) and littorinid gastropods. They were probably transported down-slope by bottom currents and as a consequence were not alive when sampled. Most of the gastropods found at the whale-fall site, including the rissoids, are known to dwell on seaweeds, and were possibly moved together with drifting algae, as shown by algal debris around whale bones (Figure 2). Because alive and dead specimens were not distinguished, 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. 2010b).

Environmental gradients on the Swedish shelf

At the species level, multivariate comparison of the Kosterfjord samples with samples collected from soft-bottom sediments across the west Swedish coast allowed for 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 (Figure 7). This result is in accordance with the interpretation that in marine environments water depth is the single most important factor indirectly controlling the distribution of benthic organisms (see Gauch 1982), as it has been amply proven in other case studies (Scarponi & Kowaleski 2004; Dominici et al. 2008; Konar et al. 2008).

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 show low DC2 scores (Figure 7). Among them are samples from the Gullmar Fjord, where bottom waters are periodically affected by low oxygen conditions (Josefson 1987; Josefson & Widbom 1988; Dando & Spiro 1993). These three samples were collected between 1985 and 1987, at a time of re-colonization of the sediments by \( T. \text{sarsi} \) after a period of oxygen depletion resulting in the death of the bottom fauna in the winter 1979–1980 (Josefson & Widbom 1988). 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 \( T. \text{sarsi} \), 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 \( T. \text{sarsi} \) 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 (Figure 7), the DC2 score may be a direct measure of the degree of sulphide concentration and an indirect measure of oxygen level in the soft-bottom sediments.

Moreover, the whale-fall and the Gullmar Fjord samples might have a similar faunal composition because at the time of sampling they were in a similar successional stage of faunal recovery. W1 was in fact collected 5 years after the impact of the carcass on the sea floor and GLF1–3 were collected 5–7 years
after the hypoxic event that eliminated all the fauna from the Gullmar Fjord.

**Whale-falls in shallow waters**

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 living at similar water depth. In comparison with whale-falls sunk just below the 200 m depth threshold in the northwest Pacific (Fujiwara et al. 2007), the Kosterfjord whale-fall lacks molluscs typical of deep-water reducing environments, such as mytilid mussels (*Adipicola pacifica*) and cocculinid limpets. Among the bathymodiolin mussels, *Idas simpsoni* has been described from trawled bones on the North Sea shelf (Marshall 1900; Wären 1991; Tebble 1996) and in oil-polluted areas (Hartley & Watson 1993; Southward 2008). However, during multiple ROV surveys and the careful examination of multiple recovered bones and sediment samples, *I. simpsoni* was never found at the Kosterfjord whale-fall. One of the few other examples of the monitoring of a whale-fall in relatively shallow waters (385 m depth, northeast Pacific) does not bear evidence of the development of a complex megafaunal community (Braby et al. 2007). Concerning benthic molluscs, during 6 surveys across a 13-month period, only rare buccinid gastropods were found in the sediments surrounding the carcass. The causes might be related to high scavenging rates and frequent disturbance from sediment flows at the whale-fall site (Braby et al. 2007).

These available case studies, which show different possible scenarios, suggest how the community structure and dynamics of whale-falls in shallow water merit substantial further study.

**Conclusions**

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 chemosautrophs. This result is similar to that recorded from a fossil analogue 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 seven new species of polychaetes have been recorded from the Kosterfjord whale-fall, of which just three are present at other organic-rich settings such as fish farms (Glover et al. 2005; Wiklund et al. 2009a, b). 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 the Kosterfjord whale-fall site is in contrast with the pattern for Mollusca. From an ecological perspective, our data suggest that shelf-depth whale-falls are a natural analogue 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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**References**

Agrenius S. 2001. Övervakning av mjukbottenfaunan längs Sveriges västkust. Rapport från verksamheten året 2001. Avtal nr 2120103. 30 pages. (in Swedish)

Agrenius S. 2002. Övervakning av mjukbottenfaunan längs Sveriges västkust. Rapport från verksamheten året 2002. Avtal nr 2120203. 39 pages. (in Swedish)

Agrenius S. 2003. Övervakning av mjukbottenfaunan längs Sveriges västkust. Rapport från verksamheten året 2003. Avtal nr 2120303. 47 pages. (in Swedish)

Agrenius S. 2005. Övervakning av mjukbottenfaunan längs Sveriges västkust. Rapport från verksamheten året 2005. Avtal nr 2120503. 58 pages. (in Swedish)

Braby CE, Rouse GW, Johnson SB, Jones WJ, Vrijenhoek RC. 2007. Bathymetric and temporal variation among *Osedax* boneworms and associated megafauna on whale-falls in Monterey Bay, California. Deep-Sea Research I 54:1773–91.

Brigmon RL, De Ridder C. 1998. Symbiotic relationship of *Thiothrix* spp. with an echinoderm. Applied and Environmental Microbiology 64:3491–95.

Bromley RG, Jensen M, Aagaard U. 1995. Spartangoid echinoids: Deep-tier trace fossils and chemosymbiosis. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 195:25–35.

Cai W-J, Chen F, Powell EN, Walker SE, Parsons-Hubbard KM, Staff GM, et al. 2006. Preferential dissolution of carbonate
Palm A, Cousins I, Gustafsson O, Axelman J, Grunder K, Broman D, et al. 2004. Evaluation of sequentially-coupled POP fluxes estimated from simultaneous measurements in multiple compartments of an air-water-sediment system. Environmental Pollution 128:85–97.

Pavlyuk ON, Trebukhova YA, Tarasov VG. 2009. The impact of implanted whale carcass on nematode communities in shallow water area of Peter the Great Bay (East Sea). Ocean Science Journal 44:181–88.

Rosenberg R, Agrenius S, Hellman B, Nilsson HC, Norling K. 2002. Recovery of marine benthic habitats and fauna in a Swedish fjord following improved oxygen conditions. Marine Ecology Progress Series 234:43–53.

Rouse GW, Goffredi SK, Vrijenhoek RC. 2004. Oseadox: Bone-eating marine worms with dwarf males. Science 305:668–71.

Rouse GW, Goffredi SK, Johnson SB, Vrijenhoek RC. 2011. Not whale-fall specialists, Oseadox worms also consume fish bones. Biology Letters 7:736–39.

Saetre R. 2007. The Norwegian Coastal Current: Oceanography and Climate. Trondheim: Tapir Academic Press. 160 pages.

Scarponi D, Kowalewski M. 2004. Stratigraphic paleoecology: Bathymetric signatures and sequence overprint of mollusk associations from upper Quaternary sequences of the Po Plain, Italy. Geology 32:989–92.

Schander C, Rapp HT, Dahlgren TG. 2010a. Oseadox mucosalis (Polychaeta, Siboglinidae), a bone-eating marine worm new to Norway. Fauna Norvegica 30:5–8.

Schander C, Rapp HT, Kongsrud JA, Bakken T, Berge J, Cochrane S, et al. 2010b. The fauna of hydrothermal vents on the Mohn Ridge (North Atlantic). Marine Biology Research 6:155–71.

Schmaljohann R, Faber E, Whiticar MJ, Dando PR. 1990. Co-existence of methane- and sulphur-based endosymbiosis between bacteria and invertebrates at a site in the Skagerrak. Marine Ecology Progress Series 61:119–24.

Sibuet M, Olu K. 1998. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. Deep Sea Research 45:517–67.

Smith CR. 2006. Bigger is better: The role of whales as detritus in marine ecosystems. Chapter 22 in: Estes J, editor. Whales, Whaling and Ocean Ecosystems. Berkeley, CA: University of California Press, p 284–99.

Smith CR, Kukert H, Wheatcroft RA, Jumars PA, Deming JW. 1989. Vent fauna on whale remains. Nature 341:27–28.

Smith CR, Baco AR. 2003. Ecology of whale falls at the deep-sea floor. Oceanography and Marine Biology: An Annual Review 41:311–54.

Southward EC. 1986. Gill symbionts in thyasirids and other bivalve molluscs. Journal of the Marine Biological Association of the United Kingdom 66:889–914.

Southward EC. 2008. The morphology of bacterial symbiosis in the gills of mussels of the genera Adipica and Idas (Bivalvia: Mytilidae). Journal of Shellfish Research 27:139–46.

Spiro B, Greenwood PB, Southward AJ, Dando PR. 1986. $^{13}$C/$^{12}$C ratios in marine invertebrates from reducing sediments: Confirmation of nutritional importance of chemooautorophic endosymbiotic bacteria. Marine Ecology Progress Series 28:233–40.

Tarasov VG, Gebruk AV, Mirononov AN, Moskalev LL. 2005. Deep-sea and shallow-water hydrothermal vent communities: Two different phenomena? Chemical Geology 224:5–39.

Tebble N. 1966. British Bivalve Seashells: A Handbook for Identification. London: The British Museum (Natural History). 212 pages.

Temara A, De Ridder C, Kuenen JC, Robertson LA. 1993. Sulfide oxidizing bacteria in the burrowing echinoid, Echinocardium cordatum (Echinodermata). Marine Biology 115:179–85.

Todd JA. 2000. Introduction to molluscan life habits databases, updated 27 March 2001. http://eusmilia.geology.uiowa.edu/database/mollusc/mollusclifestyles.htm (accessed 20 December 2012)

Tomašových A, Kidwell SM. 2009. Preservation of spatial and environmental gradients by death assemblages. Paleobiology 35:122–48.

Wären A. 1991. New and little known Mollusca from Iceland and Scandinavia. Sarsia 76:53–124.

Wären A. 1996. Ecology and systematics of the northern European species of Rissoa and Pusillina (Prosobranchia: Rissoidae). Journal of the Marine Biological Association of the United Kingdom 76:1013–59.

Weering TCE van, Berger GV, Kalf J. 1987. Recent sediment accumulation in the Skagerrak, northeastern North Sea. Netherlands Journal of Sea Research 21:177–89.

Wilkund H, Glover AG, Johannessen P, Dahlgren TG. 2009a. Cryptic speciation at organic-rich marine habitats: a new bacteriovore annelid from whale-fall and fish farms in the North-East Atlantic. Zoological Journal of the Linnean Society 155:774–85.

Wilkund H, Glover AG, Dahlgren TG. 2009b. Three new species of Ophryotrocha (Annelida: Dorvilleidae) from a whale-fall in the North-East Atlantic. Zootaxa 2228:43–56.

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