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A shallow-water whale-fall experiment in the north Atlantic

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Abstract: The study of hydrothermal vent and seep fauna is associated with great costs due to the deep and distant locations. Whale-falls, which are thought to have habitat conditions which overlap seep ecosystems, may be used as a model system to explore questions such as the evolution of dispersal strategies and interactions between hosts and their symbiont microbes. Our discovery of whale-fall fauna at a whale carcass sunk at shelf depth in a Swedish fjord contrasts the apparent lack of specialized organisms from shallow water seep environments. Representatives of a whale-fall fauna found at the Swedish study site include bacterial mat feeding dorvilleid annelids and the whale-bone eating pogonophoran worm *Osedax mucofloris* Glover et al., 2005. We are maintaining whale-fall fauna alive in aquaria, and initial results from these studies suggest that *O. mucofloris* has a continuous reproduction life-history strategy.

Keywords: Annelida • Siboglinidae • Continental shelf • Seep • Vent • *Osedax mucofloris* • North Sea • Minke whale • Pilot whale

Introduction

One of the more surprising discoveries in recent marine biology is the diverse and specialized fauna found at sunken whale carcasses, now known as “whale-falls” (e.g. Smith et al., 1989). To date more than 400 species have been found associated with whale-falls (Baco & Smith, 2003; Smith & Baco, 2003). Among these, over 30 species are presumably endemic to whale-falls of which several are annelids (Rouse et al., 2004; Dahlgren et al., 2004; Glover et al., 2005a; Glover et al., 2005b). The whale-fall community undergoes successional stages characterized by different faunal assemblages, from a scavenger stage where soft tissue is primarily removed to expose the bones, through a period when opportunists and whale-bone or bacterial mat specialists inhabit the organically enriched bones and surrounding sediments (Smith & Baco, 2003). For most of these species, however, we have no data on autecology or life history traits and only a few have been formally described. Whale-falls at different depths are exposed to radically different environments caused by chemical, physical and biological factors (Smith, 2006). Taphonomic processes, such as the decomposition rate of bone, may be strongly influenced by depth (Allison et al., 1991). Different factors connected to depth are also thought to influence faunal composition and the occurrence of obligate species at hot vents and seeps (Sahling et al., 2003; Tarosov et al., 2005).

Data collection at most known whale-falls requires access to advanced submersibles, reducing the possibilities for a rigorous sample design. Recurrent samples are important due to the dramatically different faunal communities at different stages while a whale-fall community develops (Smith & Baco, 2003). Samples at different spatial scales, including sites in all major ocean basins, are important to address questions related to species distribution, dispersal strategies, phylogeography, population genetics and population dynamics. The whale-fall habitat may serve as a model for studies of other chemosynthetic ecosystems, such as hydrothermal vents.

Preliminary results from the Atlantic whale-fall site in shallow waters have opened up new research opportunities that can address a wide range of questions in ephemeral habitat biology (Glover et al., 2005a). The long term objectives for the Atlantic whale-fall study are 1) describe shallow-water whale-fall fauna in the north Atlantic, 2) determine an approximate viable carcass size to support whale-fall fauna, 3) examine rates of gene-flow between north Atlantic whale-fall populations, 4) study reproductive biology of whale-fall fauna maintained in aquaria, 5) investigate functional anatomy of whale-fall specialists, including potential bacterial endosymbioses and 6) determine phylogenetic relationships of whale-fall specialists and their closest relatives to evaluate evolutionary hypotheses.

Materials and methods

Two stranded dead whales were recovered from the shoreline and towed to the laboratory for ballast attachment and preparation. In October 2003, the intact remains of a 5.3 m female Minke whale (*Balaenoptera acutorostrata* Lacépède, 1804) were sunk at a depth of 125 m. Prior to sinking the whale, biopsies of blubber and muscle tissue were taken for assessment of organochlorine compounds and other toxicants by the Swedish Museum of Natural History. In January 2005 the decomposing carcass of a 4.5 m Pilot whale (*Globicephala melas* Traill, 1809) was sunk at a depth of 30 m. The whale was found high on the beach with the tail fin missing, the buccal cavity open and with some ribs and posterior vertebra exposed. Up to 100 kg of steel ballast each, *e.g.* scrap railroad track, was attached to

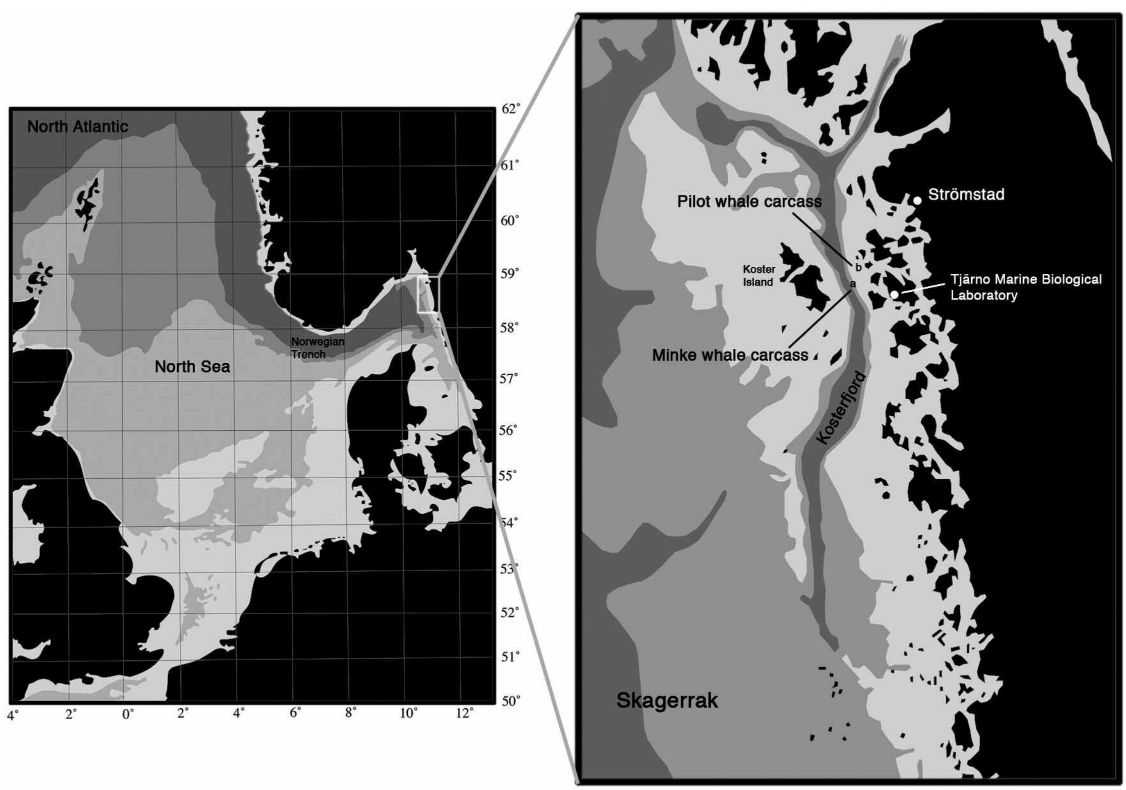

Figure 1. Map showing the North Sea, and the location of the experimental sites next to Tjärnö Marine Biological Laboratory.
Figure 1. Carte de la Mer du Nord, localisation des sites expérimentaux à proximité du laboratoire de biologie marine de Tjärnö.

the whale carcasses for secure implantation and long-term stability at the sea floor. In order to facilitate easy access and safety while using scuba divers for sampling, the pilot whale, implanted at a shallower depth, was marked with a surface buoy.

We chose the implantation site based on three major factors: 1) depth and connectivity to the deep Norwegian trench, 2) protection from demersal trawling activities, and 3) distance to a marine laboratory and a remotely operated vehicle (ROV) (Fig. 1). The Kosterfjord is not a fjord in its proper meaning, in that it is open to surrounding waters at both ends. The Kosterfjord is a 250 meter deep, 0.4-2 km wide and 48 km long horst running along the Swedish west coast, sheltered in the west by the Koster islands. The sill to the north-west is at 110 m and opens to the Norwegian Trench which has depths in access of 700 m and is connected to the deep North Atlantic (Fig. 1). Monthly mean values between 1967 and 1998 of temperature, salinity and oxygen levels at 125 m depth are given for a position 0.5 nautical miles southeast of the study site. In general, seasonal variations were small, with no changes in salinity, temperature varying from 5 to 7°C and dissolved oxygen from 4.6 to 6.3 ml.l^{-1} (Fig. 2). The Skagerrak may be one of the most investigated marine areas in the world, surrounded by 7 marine laboratories, one of which was founded in the 19th century. Frequent faunal surveys in shallow and deep waters have resulted in a relatively well known background fauna. The Koster area is used by many boats in the commercial shrimp (*Pandalus borealis* Kroyer, 1838) fishery which employ bottom otter trawls; we negotiated with local fishermen for a site aiming at minimum interference with fishing activities. The distance to shore was kept at a minimum to allow virtually undisturbed retrieval of bones with live fauna for laboratory experiments and observation. The choice of a site close to the lab also meant an efficient use of ship-time.

Remotely operated vehicles (ROVs, in this case Sperre Sub-Fighter, Phantom XTL and Phantom S4) were used to survey and sample the Minke whale experimental site at 125 m depth. The ROVs were fitted with custom designed, forward-mounted, plankton-net sampling scoops to recover small vertebrae and associated fauna. SCUBA was used to survey and sample the shallow Pilot whale site at 30 m depth. The pilot whale carcass was marked with a floating buoy and line, facilitating SCUBA operation.

Whale bones from both carcasses are being maintained at Tjärnö Marine Biological Laboratory in aquaria with chilled (7°C) flowing seawater passing through sand-filters. Live populations of *Osedax mucofloris* Glover et al., 2005 have been maintained for a minimum of 7 months on the Minke whale bones recovered from the experimental site. Outflow from the tanks is screened for embyros and larvae using a submerged 60 µm larval trap.

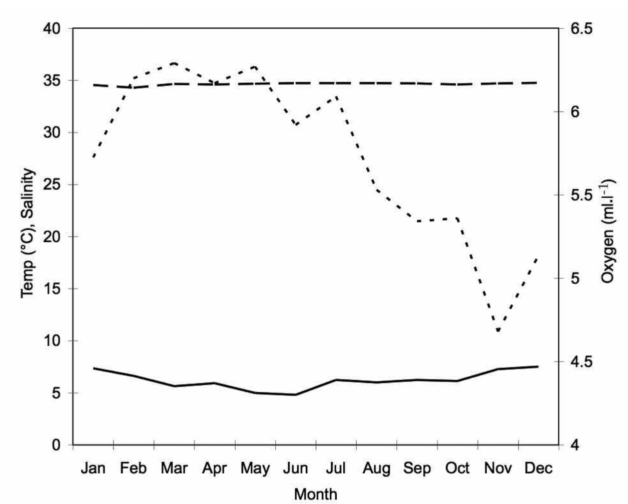

Figure 2. Monthly mean values of temperature, salinity and oxygen levels in Kosterfjorden, Sweden at 58°52,7'N; 11°05,3'E at 125 m depth. Data from Swedish Meteorological and Hydrological Institute. The solid line is temperature, the dashed line is salinity and the dotted line is oxygen.

Figure 2. Valeurs mensuelles moyennes de température (trait continu), salinité (tirets) et concentration en oxygène (pointillés) à Kosterfjorden, Suède (58°52,7'N; 11°05,3'E) à 125 m de profondeur. Données de l'Institut d'Hydrologie et de Météorologie Suédois.

Results

Based on video analyses we found that Atlantic hagfish (*Myxine glutinosa* Linnaeus, 1758), unknown species of sharks (evidence from bite-marks only) and other scavenging organisms consumed the flesh of the Minke whale (at 125 m), exposing bones within 5 weeks of implantation (Fig. 3). Dense populations of the lysianassid amphipod *Orchomene obtusa* (G.O. Sars, 1891), identified from collected specimens, were observed growing and reproducing on exposed bone surfaces from 5 weeks to 4 months. The Minke whale carcass was completely skeletonized after 6 months on the sea floor (Fig. 3). In August 2004, nine months after implantation, one vertebra was recovered from the Minke whale carcass, which was found to be riddled with *Osedax mucofloris*, the only known Atlantic species of the whale-fall obligate annelid group described earlier from the deep Pacific Ocean (Rouse et al., 2004).

The Pilot whale carcass (at 30 m depth) remained intact after 7 months, with no evidence of scavenging. Bones already exposed at implantation were, however, colonised by *Osedax mucofloris* after 7 months at the sea floor. The entire carcass was covered with a fluffy bacterial mat. In addition, four new species of annelids belonging to the

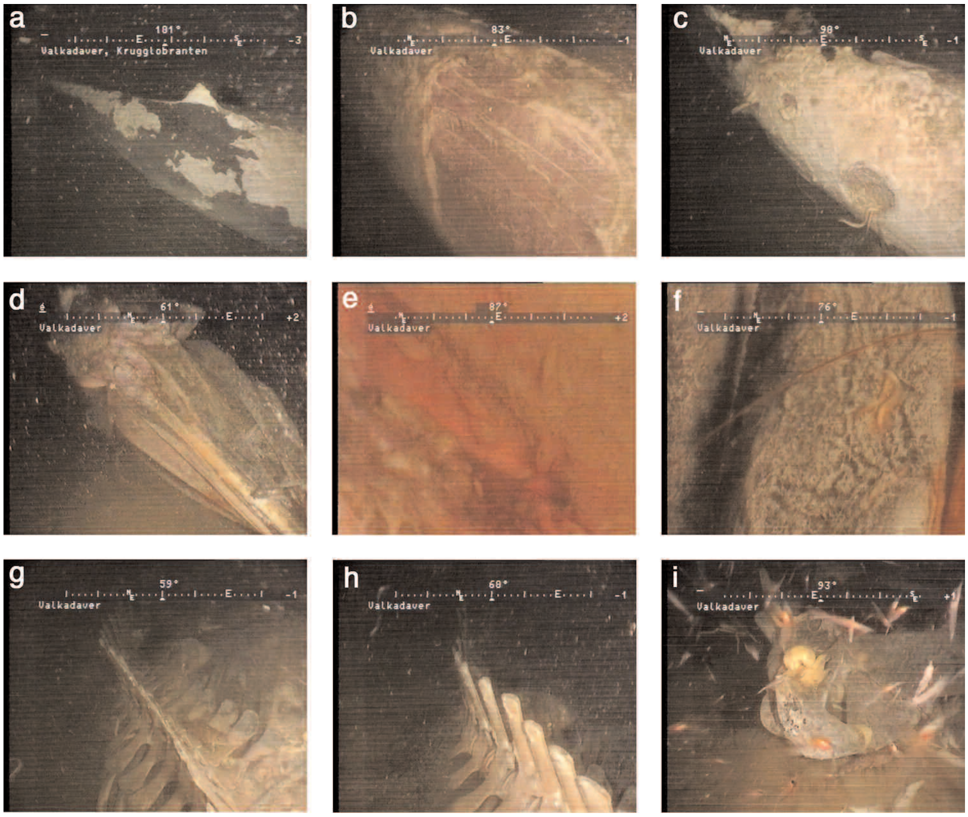

Figure 3. (a-i). Remotely operated vehicle video stills showing the decomposition of the Minke whale carcass over an 8 month time frame at 125 m depth. **(a-c).** 2 weeks since implantation, hagfish (*Myxine glutinosa* Linnaeus, 1758) and shark bite marks visible. **(d-e).** 5 weeks since implantation, abundant amphipods (*Orchomene obtusa* G.O. Sars, 1891) visible feeding in open wounds. **(f).** 4 months since implantation, unidentified polychaetes visible on surface of exposed bones. **(g-h).** 6 months since implantation, complete skeletonization, absence of hagfish, first records of *Osedax mucofloris* Glover et al., 2005. **(i).** 8 months since implantation, skeleton continues to support bone-specialist fauna.

Figure 3. (a-i). Extraits de la vidéo du véhicule sous-marin autonome montrant la décomposition de la carcasse de baleine de Minke sur une période de 8 mois à 125 m de profondeur. **(a-c).** 2 semaines après l'immersion, myxines (*Myxine glutinosa* Linnaeus, 1758) et traces de morsures de requins. **(d-e).** 5 semaines après l'immersion, nombreux amphipodes (*Orchomene obtusa* G.O. Sars, 1891) se nourrissant dans les blessures ouvertes. **(f).** 4 mois après l'immersion, polychètes non identifiés visibles sur les os exposés. **(g-h).** 6 mois après l'immersion, mise à nue complète du squelette, absence de myxines, premières observations de *Osedax mucofloris* Glover et al., 2005. **(i).** 8 mois après l'immersion, le squelette abrite toujours une faune inféodée aux ossements.

families Dorvilleidae and Chrysopetalidae have been found in association with both whale-falls and are currently being described (Wiklund et al., in prep.).

Embryo identification has been confirmed using a DNA barcoding approach (Hebert et al., 2003, Wiklund et al., unpublished data). Fecundity, embryo development and larval biology are being investigated by counting embryos produced by a known number of adult *Osedax*, suggesting a continuous reproductive strategy, with a rate of 5 eggs per female, per hour (Wiklund et al., unpublished data).

Discussion

In contrast to shallow water seeps (Sahling et al., 2003) and hydrothermal vents (Tarasov et al., 2005), our results suggest that whale-falls can maintain an obligate fauna even at shallow depths (Glover et al., 2005a; Haag, 2005). Whale carcasses that sink in the littoral zone are exposed to a range of scavenging organisms and wave action that affect the possibilities for fragile animals or a bacterial community to develop (Smith, in press). While sedimentation at most deep-sea sites probably can be ignored as a factor limiting the development of a whale-fall community, whale carcasses in near shore areas can be quickly buried by events such as submarine mudslides near river outlets or rapid deposition of storm layers (Brand et al., 2004). Another factor presumably important for the development of a whale-fall community is the size of the habitat, *i.e.* species, age and nutritional stage of the dead whale (Smith & Baco, 2003; Glover et al., 2005a; Smith, in press). Bone characteristics such as density and thickness are also potentially important (Smith & Baco, 2003). One study of small cetaceans (dolphins) sunk in the deep sea in the North Atlantic report that entire carcasses, including bones, were removed by scavengers in a few days (Jones et al., 1998).

Our investigations have revealed an abundant whale-fall fauna at shelf depths in the north Atlantic, comprised of both opportunistic species (e.g. dorvilleids) and apparent whale-fall endemics. The unusual whale-fall specialist *Osedax mucofloris* is present at both 125 m and in smaller numbers at 30 m on a relatively small cetacean. In contrast to the quick stripping of soft tissue from the Minke whale carcass at 125m, the Pilot whale, placed at 30 m depth 150 m east of the Minke whale, was virtually intact after 7 months at the seafloor. Based on this observation, we hypothesise that the time required from deposition at the sea floor to exposure of bone tissue in the Kosterfjord is largely determined by the presence of hagfish. The only species of hagfish known from the North East Atlantic ocean is *Myxine glutinosa* with a depth range of 40-1200 m (Fernholm, 1998).

Shallow-water whale falls may serve as an accessible model system for the study of some ecological and evolutionary processes at ephemeral reducing habitats, such as deep-sea hydrothermal vents and cold seeps. The evidence presented here suggests that small cetacean species (e.g. Pilot whales) with large population sizes (> 700,000) may be able to sustain whale-fall specialist species (such as *Osedax*) in the north Atlantic, greatly expanding the potential range of whale-fall habitats on a global scale. Future studies of gene-flow, reproductive biology and larval development in the laboratory will provide insight into deep-sea dispersal and biogeography of ephemeral chemosynthetic ecosystems.

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References

Allison P.A., Smith C.R., Kukert H., Deming J.W. & Bennett B.A. 1991. Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the bathyal Santa Catalina Basin. *Paleobiology,* **17**: 78-89.

Baco A.R. & Smith C.R. 2003. High species richness in deep-sea chemoautotrophic whale skeleton communities. *Marine Ecology Progress Series,* **260**: 109-114.

Brand L.R., Esperante R., Chadwick A.V., Porras O.P. & Alomia M. 2004. Fossil whale preservation implies high diatom accumulation rate in the Miocene-Pliocene Pisco Formation of Peru. *Geology,* **32**: 165-168.

Dahlgren T.G., Glover A.G., Baco A. & Smith C.R. 2004. Fauna of whale falls: systematics and ecology of a new polychaete (Annelida: Chrysopetalidae) from the deep Pacific Ocean. *Deep-Sea Research Part I,* **51**: 1873-1887.

Fernholm B. 1998. Hagfish systematics. In: *The biology of hagfishes* (J.M. Jørgensen, J.P. Lomholt, R.E. Weber, H. Malte eds). Chapman & Hall: London.

Glover A.G., Kallstrom B., Smith C.R. & Dahlgren T.G. 2005a. World-wide whale worms? A new species of *Osedax* from the shallow north Atlantic. *Proceedings of the Royal Society B,* **272**: 2587-2592.

Glover A.G., Goetze E., Dahlgren T.G. & Smith C.R. 2005b. Morphology, reproductive biology and genetic structure of the whale-fall and hydrothermal vent specialist, *Bathykurila guaymasensis* Pettibone, 1989 (Annelida: Polynoidae). *Marine Ecology,* **26**: 223-234.

Haag A. 2005. Marine biology: whale fall. *Nature,* **433**: 566-567.

Hebert P.D.N., Ratnasingham S. & de Waard J.R. 2003. Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society of London Series B,* **270**: 96-99.

Jones E. G., Collins M.A., Bagley P.M., Addison S. & Priede I.G. 1998. The fate of cetacean carcasses in the deep sea: observations on consumption rates and succession of scavenging species in the abyssal north-east Atlantic Ocean. *Philosophical Transactions of the Royal Society of London B,* **265**: 1119-1127.

Rouse G., Goffredi S.K., Vrijenhoek R.C. 2004. *Osedax*: bone-eating marine worms with dwarf males. *Science,* **305:** 668-671.

Sahling H., Galkin S.V., Salyuk A., Greinert J., Foerstel H., Piepenburg D. & Suess E., 2003. Depth-related structure and ecological significance of cold-seep communities - a case study from the Sea of Okhotsk. *Deep-Sea Research Part I,* **50**: 1391-1409.

Smith C.R., Kukert H., Wheatcroft R.A., Jumars P.A. & Deming J.W. 1989. Vent fauna on whale remains. *Nature,* **341:** 27-28.

Smith C.R. & Baco A.R. 2003. Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology: An Annual Review,* **41**: 311-354.

Smith C.R. 2006. Bigger is better: the role of whales as detritus in marine ecosystems. In: *Whales, Whaling and Ocean Ecosystems* (J. Estes Ed), University of California Press: Berkeley.

Tarasov V.G., Gebruk A.V., Mironov A.N. & Moskalev L. I. 2005. Deep-sea and shallow-water hydrothermal vent communities: two different phenomena? *Chemical Geology,* **224**: 5-39.