Evolution of annelid diversity at whale-falls and other marine ephemeral habitats

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2009

UNIVERSITY OF GOTHENBURG

ISBN 978-91-628-7863-4
Printed by Geson Hylte Tryck, Göteborg, Sweden 2009
Cover photo: Craig R Smith

SP
Certifierad
ISO 14001

MILJÖMÄRKT
341 701
Trycksak

Dissertation abstract

Helena Wiklund (2009). Evolution of annelid diversity at whale-falls and other marine ephemeral habitats.
University of Gothenburg, Department of Zoology, PO Box 463, SE-405 30 Göteborg, Sweden

When whales die and sink to the sea-floor, they provide a sudden, enormous food supply to organisms in the vicinity. At first, larger mobile scavengers remove the flesh, but also when only the bones remain, the whale-fall can still sustain macrofauna communities for several years. Some organisms have adapted so well to this kind of food source that they would have problems living elsewhere, e.g. species within the polychaete genus *Osedax* which have developed a root system which can bore into the bones to reach nutrients. Other organisms are not so specialized on the bones, but rather on the sulphur-oxidizing filamentous bacterial mats covering the bones. Polychaetes from several families have been observed grazing the bacterial mats, and some of the species reported from whale-falls have also been found in other ephemeral, chemosynthetic habitats like e.g. hydrothermal vents, cold seeps and beneath fish farms, where filamentous mat-forming bacteria also occur. In this thesis, nine new species from two polychaete families are described from whale-falls and fish farms in Scandinavian waters, and from whale-falls and sunken wood off the Californian coast. Their phylogeny is investigated using molecular data. The genetic data are further used to separate morphologically cryptic species from ephemeral habitats in different ocean basins.

Keywords: Dorvilleidae, Chrysopetalidae, Siboglinidae, whale-fall, cryptic species

ISBN 978-91-628-7863-4

List of papers

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals (I-IV).

I. Dahlgren TG, Wiklund H, Källström B, Lundälv T, Smith CR, Glover AG. 2006. A shallow-water whale-fall experiment in the north Atlantic. Les Cahiers de Biologie Marine 47(4): 385-389.
II. Wiklund H, Glover AG, Johannessen PJ, Dahlgren TG. 2009. 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: 774-785.
III. Wiklund H, Glover AG, Dahlgren TG. In press. Three new species of *Ophryotrocha* (Annelida: Dorvilleidae) from a whale-fall in the North East Atlantic. Zootaxa.
IV. Wiklund H, Altamira I, Glover AG, Smith CR, Baco-Taylor A, Dahlgren TG. Manuscript. Five new species of *Ophryotrocha* (Annelida: Dorvilleidae) from whale-fall and sunken wood habitats off California.

All new taxon names mentioned in this thesis are disclaimed for nomenclatural purposes (ICZN Article 8.2).

Introduction

This thesis is mainly about annelids that live on dead whales or other organic-rich remains at the seafloor. Annelids are segmented worms, and well-known representatives from this group include the earthworms and leeches (Clitellata). Some of their less known relatives, the polychaetes, are mainly marine worms and although the total number of species is unknown, one estimation is around 9000 described polychaete species (Rouse and Pleijel, 2001). Polychaetes occur on almost every extension of the sea floor, from shallow intertidal to several thousand meters down in the deep sea. They may be free living, hunting prey on the sea floor or grazing algae, or attached to a substrate and either capture food that is floating by, or filter the water for food particles. Some species are commensals or parasites of other organisms. Among the polychaetes that have been the focus for this study, *Osedax mucofloris* Glover et al., 2005 is attached to the substrate (Paper I), and the others are free living worms that are more or less specialized as grazers on bacterial mats (Papers II-IV).

Whale-fall fauna

When large whales die and sink to the sea floor, the carcasses constitute a massive food supply to the organisms in the vicinity. Although this food supply is limited both in space and time, some organisms seem to have adapted to the energy source provided and become more or less specialized on whale-falls or similar habitats on the sea floor. Krogh (1934) first speculated that whale-falls may be important food sources at the sea floor. Although he suggested that the whale carcasses would be a huge addition of food to the otherwise probably starving inhabitants of the deep-sea, he did not discuss the possibility that organisms could be specialized and endemic to the habitat. When for the first time a whale-fall was studied *in situ* using a submersible, the scientists reported an abundance of bivalves and gastropods as well as large assemblages of bacterial mats, but did not mention any polychaete findings (Smith et al., 1989).

In the last two decades, several whale carcasses or parts of whale skeletons have been discovered or experimentally sunk at different sites and depths globally, e.g. off the Californian and Hawaiian coasts in the USA, off the Swedish coast, off the coasts of Japan, Scotland, Antarctica, New Zealand, Denmark, Greenland, Faroe Islands, and on the Mid-Atlantic Ridge. Many of these experiments were implanted very recently (within the last 2 years) and rather few observations have been made on them until now. However, not many of the species found at the older whale-fall sites have been described yet either, and of the many polychaetes discovered and collected, few have been formally described from these special habitats (Table 1).

In the initial studies, scientists noted that a decomposing whale-fall went through several successional stages (Smith and Baco, 2003). The initial stage is the 'mobile scavenger stage', where most of the flesh is consumed by scavenging organisms such as sleeper sharks, hagfish and crustaceans. The second stage is the 'enrichment opportunist stage', characterised by high densities of macrofauna (including polychaetes) in the sediment surrounding the whale carcass, and on the surface of the bones (Smith and Baco, 2003). In the third stage, the 'sulphophilic stage', the bones become covered by bacterial mats, which in turn are consumed by a mat-grazing macrofaunal community.

However, a whale carcass is a complex environment and the succession is not rigid in time, as different parts of a carcass might simultaneously go through different succession stages. While scavengers are consuming the flesh, a bone poking out through the tissue might already be covered with filamentous bacteria, and the bone-eating polychaete *Osedax* Rouse et al., 2004 can be present, as has been recorded both in deep-sea (Goffredi et al., 2004), and in a shallow water whale-fall (Paper I). There are also large differences between whale-falls at different depths and different sites. In Bennett et al. (1994) their quantitative work on taxonomic composition on a whale-fall below 1000 m depth off California reported a dominance of molluscs (80% of total abundance), while on the Swedish shallow whale-falls (<200m depth) very few molluscs have been found. It is most likely that these shifts in community composition are driven by both abiotic (depth, sedimentation rate, temperature, oxygen) and biotic (larval availability, recruitment, predation, competition, succession) factors (Paper I; Smith & Baco, 2003; Braby et al., 2007; Glover et al., 2008).

Other ephemeral habitats that have similarities to whale-falls include hydrothermal vents and cold seeps, where the primary producers (phytoplankton and algae) are replaced by

Table 1. Polychaete species described from whale-falls, including new species from manuscripts in this thesis

Locality	Position	Depth	Polychaete species	Reference
Santa Catalina Basin, USA	33°14'N, 118°30'W	1240 m	*Harmothoe craigsmithi*	Pettibone, 1993
Santa Catalina Basin, USA	33°14'N, 118°30'W	1240 m	*Peinaleopolynoe santacatalina*	Pettibone, 1993
Monterey Bay, USA	36°36'N, 122°26'W	2891 m	*Osedax frankpressi*	Rouse et al., 2004
Monterey Bay, USA	36°36'N, 122°26'W	2891 m	*Osedax rubiplumus*	Rouse et al., 2004
Santa Cruz Basin, USA	33°29'N, 119°22'W	1674 m	*Vigtorniella flokati*	Dahlgren et al., 2004
Tjärnö area, Sweden	58°53'N, 11°06'E	125 m	*Osedax mucofloris*	Glover et al., 2005
Kagoshima Bay, Japan	31°20'N, 129°59'E	200 m	*Osedax japonicus*	Fujikura et al., 2006
Monterey Bay, USA	36°46'N, 122°05'W	1018 m	*Osedax roseus*	Rouse et al., 2008
Monterey Bay, USA	36°36'N, 122°26'W	2891 m	*Vrijenhoekia balaenophila*	Pleijel et al., 2008
Tjärnö area, Sweden	58°53'N, 11°06'E	125 m	*Vigtorniella ardabilia*	Wiklund et al., 2009
Tjärnö area, Sweden	58°53'N, 11°06'E	125 m	*Ophryotrocha craigsmithi*	Wiklund et al., in press
Tjärnö area, Sweden	58°53'N, 11°06'E	125 m	*Ophryotrocha eutrophila*	Wiklund et al., in press
Tjärnö area, Sweden	58°53'N, 11°06'E	125 m	*Ophryotrocha scutellus*	Wiklund et al., in press
Santa Cruz Basin, USA	33°29'N, 119°22'W	1674 m	*Ophryotrocha batillus*	Wiklund et al., manuscript
Santa Cruz Basin, USA	33°29'N, 119°22'W	1674 m	*Ophryotrocha flabella*	Wiklund et al., manuscript
Santa Cruz Basin, USA	33°29'N, 119°22'W	1674 m	*Ophryotrocha langstrumpi*	Wiklund et al., manuscript
Santa Cruz Basin, USA	33°29'N, 119°22'W	1674 m	*Ophryotrocha magnadentata*	Wiklund et al., manuscript
Santa Cruz Basin, USA	33°29'N, 119°22'W	1674 m	*Ophryotrocha nauarchus*	Wiklund et al., manuscript

chemoautotrophic microorganisms dependent on the flux of reduced compounds (sulfide or methane), that the geological settings provide. A key similarity between vents, seeps and whale-falls is the presence of bacterial mats. This is relevant to several of the organisms studied in this thesis, which utilise the mats as nutrition. Other organic material at the sea-floor can also sustain a specialised fauna, and in e.g. sunken wood several species have been found that also occur at whale-falls and in vent and seep habitats (Smith & Baco, 2003). Anthropogenic influences can also create bacterial mat habitats. The sediments forming beneath fish farms are examples of such human-disturbed habitats with an ephemeral nature that are similar in some characteristics to large whale-falls or sunken wood (small, localised, temporary sources of enrichment) (Diaz & Rosenberg, 2008). Bacterial mats occur beneath fish farms owing to an overload of nutrients to the sediment, and we have shown that organisms apparently specialist on 'natural' bacterial mats may also live at these anthropogenically created habitats (Paper II and III).

Studies comparing the different habitats (vent, seep, whale) with regard to the number of taxa present have indicated that diversity in the form of macrofauna species is highest in whale-fall communities, with species numbers as high as 185 species on a single whale-fall compared to 229 species globally on cold seeps and 121 species on the most diverse vent field (Baco and Smith, 2003). This high species richness on whale-falls might be due to the high trophic diversity, with sulphophiles, whale-bone eaters, generalized organic-enrichment opportunists and background fauna (Baco and Smith, 2003). However, since most of the taxa found on whale-falls are still undescribed, and the number of species are only a rough estimate, it is quite difficult to make such a comparison. Until now, there have not been many records of species overlaps between the habitats, although this could be a result of the low number of reports of formally described or identified species. This is a good example of when a large taxonomy backlog is leading to problems comparing data collected at different sites. In particular it is impossible to estimate the number of whale-fall endemic species (an indicator of 'hotspot' biodiversity) without formal taxonomic studies.

However, there are clearly some macrofaunal species that overlap between the different habitats, e.g. the polynoid *Bathykurila* *guaymasensis* Pettibone, 1989 occurs at both hydrothermal vents and whale-falls (Glover et al., 2005a), and the siboglinid *Escarpia spicata* Jones, 1985 has been recorded from vents, seeps, and a whale-fall (Feldman et al., 1998). In the studies done within this thesis, there is evidence for species overlap between whale-fall and fish-farm (Paper II, III), between whale-fall and hydrothermal vent (Paper IV), and between whale-fall and sunken wood (Paper IV). Whales live and die worldwide and whale-falls can thus occur on the sea-floor anywhere in the world, while hydrothermal vents and cold seeps are restricted to certain areas by the geological formations on the sea-floor. Thus, sunken whale carcasses may provide refugia for some of the bacterial mat depending organisms, and also facilitate distribution over vast reaches of the open-ocean floor (the 'stepping-stone' hypothesis, Smith et al., 1989). Fish farms and other anthropogenically produced hypoxic areas might also function as refugias for the bacterial grazers, and may facilitate the spreading of the organisms in areas where 'natural' bacterial mats are scarce. However, the efficiency of fish farms in terms of effective use of the fish food, is constantly being improved, and as a result, the organic enrichment at the sea floor is too. This might be critical to the bacterial mat depending animals, although an undisturbed sediment probably harbours a higher species diversity.

Sampling and experimental approach

The animals studied in the accompanying papers were collected from natural whale-falls located through surveys, experimentally-implanted wood and whale-falls and from whale bones recovered and maintained in aquaria. Samples were collected by SCUBA (for sites less than 30m), remotely operated vehicle (ROV) and deep-sea submersible (for the California localities). The experimental approach has allowed us to make further insights into the feeding behaviour, ecology and successional processes on these ephemeral habitats.

In Sweden, two whale carcasses were implanted close to the Sven Loven Centre for Marine Sciences Tjärnö (SLC-Tjärnö) which has allowed regular and easy access using small inshore vessels, SCUBA and ROV dives to less than 200 m depth. A 9 m female minke whale carcass was implanted at 125 m depth in October 2003, and subsequently sampled using ROV on regular occasions (approximately every 6 months) up to present day. The early dives in 2003, 2004 and 2005 used Phantom XL ROVs which lacked manipulators necessary to collect bones. A net was improvised on the front of the ROV and the pilot was able to collect bones by driving the ROV into the whale fall. Later dives (2006 onwards) with the Speere Sub-Fighter ROV (with manipulator) allowed us to carefully collect bones and transfer them to an enclosed 'bone box' for transport to the surface where the associated fauna was studied further (Paper I, II and III). A small (3 m) pilot whale carcass was experimentally implanted at 30 m depth in January 2005, and sampling was done by SCUBA and ROV dives (Paper I).

When searching bones for errant fauna, it might be necessary to keep the bone in a relaxation chemical for a while, for polychaetes magnesium chloride was used. After some minutes the animals fell out of the bone matrix allowing them to be collected. This was particularly important for the studies of polychaetes in these papers as some of them are small and able to crawl deep inside holes in the bone made by *Osedax* and naturally occuring crevices.

Studies were made of the animals in aquarium tanks, with retreived whale bones kept in chilled (+6°C), sand-filtered seawater drawn from 40m depth. This is an as good as possible alternative to studying them *in situ*, and such settings provided valuable information about the animals food preferences and reproduction patterns. However, it is still experimental and it is important to keep in mind that the circumstances are different from the animals normal environment and this can of course influence the behaviour in many ways. For example, in Bennett et al. (1994), the scientists noted that there was no macro-fauna on the bacterial mats found on whale-falls *in situ*, but that there were high abundances of molluscs on the clear, blackened parts of the bones. In our aquarium studies of polychaetes on minke whale bones, there is no sign of them avoiding the bacterial mats, on the contrary we have observed both chrysopetalids and dorvilleids on the mats, grazing and crawling up and down through the mat-like matrix formed by the filamentous bacteria (Papers I, II and III).

Polychaetes from different families, but with the same taste for food

The polychaetes that have been reported from whale-falls to date, come from different clades in the polychaete family-level phylogenetic tree (Fig. 1). Hence, the adaptations for this special habitat are apparently not limited to one specific clade. In the family Siboglinidae Caullery, 1914, many species are adapted to a life in anoxic or chemosynthetic environments, e.g. species of *Siboglinum* Caullery, 1914 that occur in cold seeps and in anoxic sediments. They rely on symbiotic bacteria for feeding, and these symbiotic bacteria utilize methane (*Siboglinum poseidoni* Flugel and Langhof, 1983) or sulphur (all the other *Siboglinum* species described so far). Siboglinidae also include the giant vestimentiferans *Riftia pachyptila* Jones, 1981, that have been recorded from hydrothermal vents, and the whale-bone specialist, *Osedax* spp. that has been recorded from most whale-falls studied so far. *Osedax* is unique in having a root system that bores down into the bone, an adaptation that probably makes it unlikely for the worm to inhabit other substrates. Apart from egg sacs inside the root, *Osedax* harbours symbiotic bacteria that apparently provide energy to the animal, hence the boring is required to reach new supplies of nutrition for the bacteria (Goffredi et al., 2005).

Some of the polychaetes on whale-falls live a more errant life, and they seem to be dependent on the bacterial mat covering the whale-bones rather than the whale-bones themselves. Those bacterial mat dependent species arise from different clades in the polychaete tree, e.g. from Polynoidae Kinberg, 1856, Hesionidae Grube, 1850, Chrysopetalidae Ehlers, 1864 and Dorvilleidae Chamberlin, 1919 (Fig. 1).

Several taxa of Polynoidae have been recorded from whale-falls (e.g. Pettibone, 1993; Bennett et al., 1994; Smith and Baco, 2003; Goffredi et al., 2004), although not many of them have been identified to species level. Because of this it is not clear if all of them are specialized on the whale-fall habitat, or if they also occur in the background fauna and use the whale-fall as an additional food source. However, three of the species that have been identified from whale-falls are *Harmothoe craigsmithi* Pettibone, 1993, *Peinaleopolynoe santacatalina* Pettibone, 1993 and *Bathykurila guaymasensis* Pettibone, 1989. The first two species have so far only been found at whale-falls, but the third, *B. guaymasensis*, has been recorded from both whale-falls and from hydrothermal vents (Pettibone, 1989, 1993; Glover et al., 2005a).

One species of Hesionidae has been described from a whale-fall in Monterey Bay, California (Pleijel et al., 2008). This species, *Vrijenhoekia balaenophila* Pleijel et al., 2008, was present at the whale-fall during several years of sampling, from 2002 to 2006 (Pleijel et al., 2008). It was first observed in the early decomposition stage when the whale carcass was quite intact and still had flesh and intestines, but even at this early stage, filamentous bacterial mats had started to develop at the whale-fall (Goffredi et al., 2004). Since the species also was present at later samplings, in 2004 and 2006, when all of the carcass soft tissue was gone and the bones were covered with bacterial mats, it seems likely that one of the food sources for it is bacteria. However, there are no direct observations of feeding in this species. Another hesionid species, *Sirsoe methanicola* (Desbruyères and Toulmond, 1998), inhabiting cold seep habitats, is reported to have filamentous bacteria in the gut, and stable isotope values from the worms also correspond to a diet consisting of sulphur-oxidizing bacteria (Fisher et al., 2000).

The group Chrysopetalidae consists of approximately 40-45 species in 11 genera (Rouse and Pleijel, 2001). Based on morphology and one study using molecular data (Dahlgren et al., 2000), the group is divided into two clades depending on the form of the dorsal paleae, which are broad and flattened in the group containing e. g. the genera *Chrysopetalum* Ehlers, 1864, *Paleanotus* Schmarda, 1861 and *Bhawania* Schmarda, 1861, and thin and cylindrical in *Vigtorniella* Kisseleva, 1996 and *Dysponetus* Levinsen, 1879. Several of the species in this group have been recorded from sunken wood, and one species has been found on both hydrothermal vent and cold seep habitats (Watson, 2001), but so far only species from *Vigtorniella* have been recorded from whale-falls (Paper II). The first *Vigtorniella* species to be described from a whale-fall, *Vigtorniella flokati* Dahlgren et al., 2004, was abundant both on the whale bones and in the sediment surrounding the carcass (Smith and Baco, 2003), but the data on feeding behaviour is inconclusive (Dahlgren et al., 2004). When *Vigtorniella ardabilia* Wiklund et al., 2009 was found on whale bones in shallow water, bacterial pellets were observed in the guts of many of the specimens (Paper II). There was no information on gut content in the description of the chrysopetalid *Thrausmatos dieteri* Watson, 2001, which has been reported from hydrothermal vent and cold seep habitats (Watson, 2001).

Dorvilleidae, a group of worms in the clade Eunicida (Fig. 1), are abundant in the lists of polychaetes from chemosynthetic habitats, and species from the genus *Ophryotrocha* Claparède and Mecznikow, 1869 in this group have been reported from all of the habitats - hydrothermal vents (e.g. Blake, 1985; Blake and Hilbig, 1990; Paxton and Morineaux, 2009), cold seeps (e.g. Levin et al., 2003; Levin and Mendoza, 2007), fish farms (Paper III; Paxton, 2009) and whale-falls (e.g. Smith and Baco, 2003; Paper III; Paper IV). Several of the *Ophryotrocha* specimens sampled at whale bones have had filamentous bacteria in their guts, and even if they belong to a group of opportunistic worms, probably capable of living off a range of food sources, it is obvious that on these kind of habitats, bacteria is an important food item for them. This has been shown in stable isotope analyses of other polychaetes in similar habitats. Van Dover and Fry (1994) made a carbon isotope study of some invertebrates associated with bacterial mats at hydrothermal vents, to investigate the role of microbes as food. Among the invertebrate consumers in their study were representatives from the polychaete genus *Paralvinella* Desbruyères and Laubier, 1982, which were commonly found with filamentous bacteria in their guts, and the isotope analyses were consistent with a bacterial mat diet for these worms (Van Dover and Fry, 1994). Filamentous bacterial mats usually consist of several species or strains of bacteria from genera such as *Beggiatoa* and *Thiothrix* (Levin, 2005). This could lead to niche partitioning by closely related species grazing on the bacteria. In stable isotope analyses of three dorvilleid species co-occurring in a seep, the isotopic signatures were markedly different, suggesting different diet preferences (Levin, 2005).

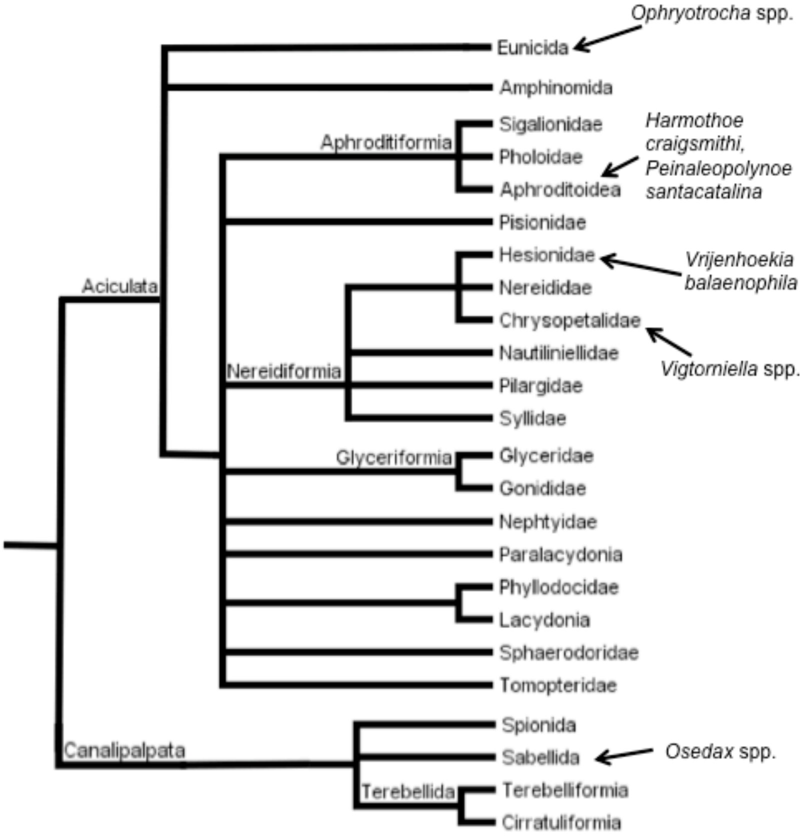

Figure 1. Tree of Polychaeta (modified from Rouse and Pleijel, 2001) with whale-fall species from different families.

Cryptic species

Cryptic species, or sibling species as they have been called by e.g. Knowlton (1993), are morphologically identical species that diverge in characters such as habitat preferences or life history, and they can be discovered by means of genetic data. In marine environments, it was thought that boundaries to gene flow was weak and that larvae could spread easily across ocean basins, and thus many invertebrate species were thought to be cosmopolitan. However, with increased knowledge about currents and other oceanographic features, as well as larval development and dispersal, this view has been challenged (e.g.

Palumbi, 1994). Knowlton (1993) presented a list of 91 genera of marine invertebrates, where sibling species had been discovered, and among them were 19 polychaete genera (Knowlton, 1993). Most of these analyses did not include genetic data, and in a later paper, nine more polychaete genera were added to the list (Knowlton, 2000). Since then, numerous new findings have been reported, among them polychaetes of the genera *Paranaitis* Southern, 1914 (Nygren et al., 2009), *Scoloplos* Blainville, 1828 (Bleidorn et al., 2006), and *Oasisia* Jones, 1985 living on hydrothermal vents in the East Pacific Ocean (Hurtado et al., 2002).

In Paper II, we describe a new chrysopetalid species found on a whale-fall in Sweden and in sediment sampled beneath a fish farm in Norway. The new species, *Vigtorniella ardabilia*, is morphologically identical to a previously described species from a whale-fall off the Californian coast, *V. flokati*. The first described *Vigtorniella* species, *Vigtorniella zaikai* Kisseleva, 1996, was reported to have long-lived larvae, and rearing experiments in the laboratory indicated that they could survive up to nine months in the water column before settling at the sea-floor and developing into adults (Sergeeva et al., 1999). Despite the possibility, at least in time scale, of dispersal between the Pacific Ocean and the Atlantic Ocean, we decided to describe the Atlantic species as a different one, based on the genetic divergence of e.g. 11% in COI between the two whale-fall *Vigtorniella* species (Paper II).

Also among *Ophryotrocha* species at whale-falls from different oceans, we find cryptic species. *Ophryotrocha scutellus*, from a whale-fall in Sweden and sediment sampled beneath a fish farm in Norway (Paper III), and *Ophryotrocha batillus* from a whale-fall off the Californian coast (Paper IV), are identical in external morphology. An obvious difference between this sibling pair and the *Vigtorniella* pair is the reduced likelihood for larval dispersal, which is rather low in *Ophryotrocha* since they have direct development, with larvae developing into small, benthic juveniles looking like small adults, usually within days after hatching (Paxton and Åkesson, 2007; personal observations). Thus, it is unlikely that long-distance larval dispersal is significant unless the larvae are transported in, for example, ballast water on transatlantic vessels. The two *Ophryotrocha* siblings from the different oceans are clearly closely related, as shown in the phylogenetic analyses, but the genetic difference between them is too large to lump them together into the same species (Paper IV). *Ophryotrocha scutellus* have been observed live for several weeks, but we have no comparable data for *O. batillus*, and therefore we can only use preserved morphology and molecular data in trying to identify the species. An important question that arises is on what basis should holotypes be designated for cryptic species? If all visible morphological characters, so far as they can be studied, are identical, is it really of any use to keep formalin-fixed material as holotypes in museums, or should an ethanol-preserved specimen be preferred? In the cases here with *Vigtorniella* or *Ophryotrocha*, it is not yet any problem since the cryptic species occur in different ocean basins, but if morphologically identical and genetically different species co-occur in a habitat, it could be a problem to use formalin-fixed holotypes unless a piece of tissue is taken from the specimen prior to formalin-fixation, and this tissue can be kept in ethanol or frozen at -80C for future genetic studies. Museums around the world need to co-ordinate in providing both formalin-fixed, ethanol and frozen tissue collections facilities that are future-proof.

Phylogeography and evolution - more questions than answers

In Chrysopetalidae, only two species from one genus, *Vigtorniella*, have been reported from whale-fall habitats so far. There has not been any phylogenetic study based on genetic data collected from all the chrysopetalid genera. However, judging from morphology, the chrysopetalid species found at both hydrothermal vent and cold seep habitats, *Thrausmatos dieteri*, seems to fall within the clade with broad, flattened palae, and is thus not closely related to *Vigtorniella*. This could indicate that adaptations to chemosynthetic habitats have occurred at least twice in the chrysopetalid clade. In Polynoidae, the three whale-fall species described until now are from three different genera, and at least *Harmothoe* Kinberg, 1856 is a speciose genus, with some of its members reported to be predators. It seems clear that polynoids from very different clades have adapted to whale-fall habitats, and they are able to utilize bacterial mats as a food source while their close relatives feed in other ways. Within Dorvilleidae, *Ophryotrocha* is one of the larger genera with approximately 50 described species, and as new areas in the sea are being investigated, even more species are being added to the list. However, here, as with the polynoids, it is not species from a single clade that have adapted to the bacterial mat habitats, rather the mat-dwelling species are widely spread within the *Ophryotrocha* tree (Fig. 2).

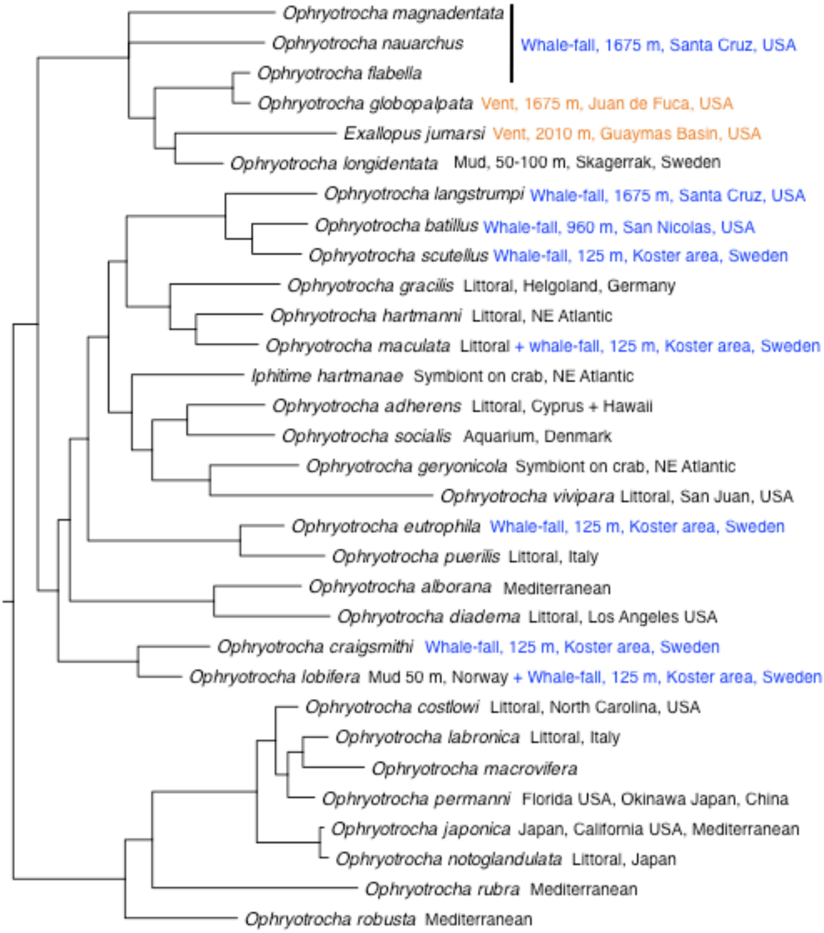

Figure 2. Phylogenetic tree of some *Ophryotrocha* species, with their collection localities.

It is not easy to speculate in how a whale-fall species from California (*Ophryotrocha batillus*) is more closely related to a Swedish whale-fall species (*O. scutellus*) than it is to another whale-fall species from

California (*O. langstrumpi*) (Paper IV). However, there are many dorvilleid species from chemosynthetic environments awaiting description, and probably also more awaiting discovery at the sea-floor. Until we have more information it is difficult to draw any conclusions about their distribution patterns. Kojima et al. (2002) used molecular phylogenetic analyses to reveal two undescribed vestimentiferan species of the genus *Escarpia* Jones, 1985 from cold seep and vent areas around Japan. One of their new species was in their phylogenetic tree more closely related to two *Escarpia* species in the East Pacific, *E. laminata* Jones, 1985 and *E. spicata* than it was to the other Japanese *Escarpia*, and they hypothezise that depth could be a key isolating factor (Kojima et al., 2002). With whale-fall *Ophryotrocha*, depth does not seem to be a factor influencing the phylogeny of the species, since *O. scutellus* is from shallow water, but its two closely related species *O. batillus* and *O. langstrumpi* are found at whale-falls and wood parcels below 900 m depth.

On some phylogenetic methods

When trying to understand relationships between organisms and hence, their evolution, phylogenetic trees are a crucial aid in sorting the data and presenting the information in an easy-to-understand way. However, when building these trees from the data collected, there is an immense array of programs to choose between, and choosing the right method is not an easy task for beginners in the field. Before it was easy and cheap to get access to molecular data, most phylogenetic studies used only morphological characters to study relationships between the organisms in question, and one of the methods commonly used to analyse morphological data is Maximum Parsimony (MP) (used in Paper II and III). This method chooses the tree or trees that require the fewest possible evolutionary changes based on the data at hand, since parsimony assumes that the easiest solution to a problem is the most likely solution. This could cause a problem when analysing molecular data because in some genes, the mutation rate is high, and there could be multiple substitutions in some sites. That is, if an ancestor sequence has an A in a site and a descendant has a T, parsimony would assume that there has been one mutation, from A to T, in that site. That might not be the case, it could have gone from e.g. A to C and then to T. Missing these hidden substitutions could lead to an incorrect phylogenetic tree. Still, MP is a fast method, and it could be useful for slowly mutating genes where multiple substitutions at sites are less likely than in genes with higher mutation rates.

Likelihood methods take mutation rates into account, and commonly used programs are Maximum Likelihood using PAUP* (Swofford, 2002) and MrBayes (Ronquist and Huelsenbeck, 2003) used in Paper II, III and IV). Likelihood gives the probability that the tree has given rise to the data we collected. When estimating Maximum Likelihood, a certain model of sequence evolution is used together with the observed dataset and a tree. The tree consists of both the topology and the branch lengths, and the tree with the greatest likelihood given the observed dataset and the evolutionary model is the optimal tree. In Bayesian analyses, the tree with the maximum posterior probability is considered to be an estimate of the 'true tree', as posterior probability is the probability that a tree is true given the data.

Some genes evolve faster than others, and this difference can be used to investigate events at different time scales. Slow evolving genes, such as 18S, can resolve clades and nodes that appeared a long time ago, while fast evolving genes, e.g. mitochondrial cytochrome c oxidase I (COI) are often better at showing evolution in a more recent time. These genes also have a different heredity pattern, where 18S is a nuclear gene, following the Mendelian inheritance pattern, while mitochondrial genes are mostly transferred only maternally. The different genes are often combined into one large dataset in phylogenetic analyses, to provide as much information as possible. However, before doing so, it can be interesting to analyse the genes separately, to see if there is incongruence between the evolutionary pattern. The genes have different mutation rate, and it is possible when combining the dataset to apply different evolutionary models to different genes in the program MrBayes (Papers II, III and IV).

How do we know if the tree we see is a correct tree? In ecology, experiments are made with replicates, and if the same result is seen in many replicates, it is a stronger evidence than if the result is only seen once. For phylogenetic analyses, searching for the true tree is time consuming, and some methods have been developed to measure some kind of reliability on the result. Bootstrapping is a commonly used method in Maximum Parsimony and Maximum Likelihood analyses.

It resamples the sample (with replacement) a chosen number of replicates, and the resulting value shows, in our case, in how many of the replicates a given clade is recovered. That is, if a clade has a bootstrap value of 100%, it occurs in all the sampling replicates. When using MrBayes, we get posterior probability values on the clades. Posterior probability is the probability that the clade is correct given the data.

Conclusions and future prospects

The study of organisms living in chemosynthetic environments is still new, and rather few systematic comparisons have been done between the different types of habitats (e.g. Tunnicliffe et al., 1998, Smith et al., 2002, Smith & Baco, 2003). One factor affecting the lack of records of species overlap between similar ephemeral chemosynthetic habitats is the huge amount of material that has been collected, but so far not sorted or identified. Species lists from the collections need to be published, and for that, taxonomists need to not only identify the animals, but most likely also describe many of them as new species, a time consuming process. As shown in this thesis and in other studies from similar habitats, cryptic species appear to be common among at least some of the invertebrate groups (Paper II and IV, Hurtado et al., 2002). Without the use of DNA data, cryptic species pairs would probably be reported as one single cosmopolitan species, and we would not only underestimate the true biodiversity, but also miss the opportunity to gain an important understanding of evolution and speciation in these organisms. It is therefore essential that future taxonomic studies describing these new species include molecular information in the descriptions. A group of polychaetes that is particularly common in all chemosynthetic habitats is Dorvilleidae, and further study of the phylogeny and taxonomy of this group will improve our understanding of the biogeography and evolution of taxa at chemosynthetic and ephemeral sites.

Summary of included papers

Paper I. Dahlgren TG, Wiklund H, Källström B, Lundälv T, Smith CR, Glover AG. 2006. A shallow-water whale-fall experiment in the north Atlantic. Les Cahiers de Biologie Marine 47(4): 385-389.

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.

Paper II. Wiklund H, Glover AG, Johannessen PJ, Dahlgren TG. 2009. 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: 774-785.

Vigtorniella ardabilia sp. nov., a new chrysopetalid annelid, is described from a whale-fall in Sweden and from sediment samples collected beneath fish farms in Norway. The new *Vigtorniella* species is morphologically almost identical to *Vigtorniella flokati* from whale-falls in the Pacific Ocean, although molecular evidence from four genes shows that they are different species. Population genetic structure and phylogenetic relationships of *V. ardabilia* sp. nov. were assessed using molecular data from the nuclear genes 18S and 28S, and the mitochondrial 16S and cytochrome c oxidase subunit I (COI). High levels of gene flow are reported between contrasting organic-rich environments in the North Atlantic (fish farms and whale-fall). Observations of feeding biology and habitat suggest that *V. ardabilia* specializes on bacterial mats, rather than on whale-falls, although the two species of *Vigtorniella* for which data were available show very different feeding behaviours. Our results further showed an unexpectedly low divergence rate in *Vigtorniella* for the mitochondrial markers, suggesting stabilizing selection. Analyses carried out with parsimony, maximum likelihood, and MrBayes all placed the genus

Vigtorniella as sister group to *Dysponetus*, suggesting a close evolutionary link to sediment-dwelling fauna.

Paper III. Wiklund H, Glover AG, Dahlgren TG. In press. Three new species of *Ophryotrocha* (Annelida: Dorvilleidae) from a whale-fall in the North East Atlantic. Zootaxa.

Three new *Ophryotrocha* species are described from sites with high levels of organic carbon flux including a whale-fall at 125 m depth off the Swedish coast and sediment sampled at 104 m depth beneath a fish farm in a Norwegian fjord. Phylogenetic analyses based on the nuclear gene H3 and the mitochondrial genes COI and 16S using MrBayes and Maximum Likelihood analyses show that *Ophryotrocha eutrophila* sp. nov. is a close relative to *Ophryotrocha puerilis*, while *Ophryotrocha craigsmithi* sp. nov. falls together with *Palpiphitime lobifera*, and *Ophryotrocha scutellus* sp. nov. occur within the 'hartmanni' clade. The genus *Ophryotrocha* is in our study monophyletic only if the genera *Iphitime* and *Palpiphitime* are included. Two representatives of *Ophryotrocha* previously described from anthropogenically-enriched sediments are here reported for the first time in very high abundance from a naturally occurring habitat. We suggest that whale falls are important habitats for the evolution of ecosystem services such the degradation of complex organic compounds.

Paper IV. Wiklund H, Altamira I, Smith CR, Glover AG, Dahlgren TG. Manuscript. Five new species of *Ophryotrocha* (Annelida: Dorvilleidae) from whale-fall and sunken wood habitats off California.

Five new *Ophryotrocha* species are described from five whale-falls and two wood-falls off the Californian coast. Phylogenetic analyses based on the nuclear gene H3 and the mitochondrial genes COI and 16S using MrBayes and Maximum Likelihood analyses were performed on 38 dorvilleid taxa and one outgroup. *Ophryotrocha batillus* sp. n. is morphologically identical to *O. scutellus* described from a shallow water whale-fall in the North Atlantic, although the two cryptic species differ genetically. *Ophryotrocha langstrumpi* sp.

n. is in the phylogenetic analyses closely related to the two sibling species. *Ophryotrocha flabella* sp. n. is similar to *O. globopalpata*, and although there are a few morphological differences, the genetic divergence is low between the two species. *Ophryotrocha nauarchus* sp. n. show a sexual dimorphism, with males having appendages on the first chaetiger. This species and *Ophryotrocha magnadentata* sp. n. falls within a clade with *O. flabella* sp. n. and *O. globopalpata*, and that clade also includes *O. longidentata* and *Exallopus jumarsi*.

Acknowledgements

Here I am, having produced a PhD thesis, and when I started reading biology I was so sure I would never even do a Bachelor or (even less) a Master degree! This means that I've got a lot of encouragement and help along the road, or I wouldn't have gotten this far. One of the most important persons in this process is my supervisor, Thomas Dahlgren. Thank you very, very much for being an enthusiastic, encouraging, and knowledgeable supervisor. My second supervisor, Adrian Glover, is also always enthusiastic and helpful. That I actually took my first degree in biology was thanks to Arne Nygren and Fredrik Pleijel, who introduced me to polychaete systematics and molecular phylogeny. A lot of the work for this thesis was done in the molecular lab, and I couldn't have done it without Anna Ansebo and Inger Holmqvist to tell me where to find what and how to mix it. My fellow PhD-students have been very important during this period, thank you Judith Fuchs, Pierre de Wit, Lisa Matamoros, Emma Vodoti, Daniel Gustafsson, Jenny Eklöf, Erika Norlinder, and all PhD-students in systematics at the Botany Department for interesting discussions, and co-working at courses, and nice after-works! All the others in our part of the zoology house - thanks to Urban Olsson for advice in the lab when desperation was near, to Per Sundberg, Christer Erséus, Malin Strand and Matthias Obst for always being encouraging and supporting. Bertil Åkesson provided me with plenty of *Ophryotrocha* worms and shared his knowledge about them. We have had a lot of collaborators, and for some of the work done in this thesis I would like to thank Iris Altamira and Craig R. Smith for letting me come to Hawaii to look at their worms, which we now are trying to describe. Thanks to Kirsty Kemp, Caroline Verna and Nick Higgs for making smelly and disgusting fieldwork enjoyable. I also want to thank the staff at the

Zoology Department, especially Bernth Carlsson, Erika Hoff, Lena Sjöblom and Ann-Sofie Olsson, and the staff at Sven Lovén Centre for Marine Sciences - Tjärnö.

Family and friends keeping me anchored in the world outside biology: My mother Ulla and my father Jan have been happy for me having the best job in the world for five years, my sister Maria and her family - Vlatko, Daniel, Simon and Jonatan, all came to admire the beauty of polychaetes (at least they said they do...), my brother Stefan - thanks especially for the financial support in the beginning of my studies! My friends Lena Samuelsson and Åsa Rosén for keeping on inviting me to Stockholm even though I must have bored them enormously with my constant worm-talk.

Financial support was obtained from GU resestipendium, Wilhelm och Martina Lundgrens vetenskapsfond, Synthesys, Helge Ax:son Johnsons stiftelse, Knut & Alice Wallenbergs stiftelse, Stiftelsen Lars Hiertas Minne, Rådman och fru Ernst Collianders stiftelse, Kungliga vetenskaps- och vitterhetssamhället (KVVS), Kungliga Vetenskapsakademin (KVA), Vetenskapsrådet.

Sadly, a large number of worms died in the making of this thesis, may they rest in peace.

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Svensk sammanfattning

Ibland spolas en död val upp på en strand och liknar då en strandad ubåt, massiv, blänkande och ganska malplacerad. De flesta valar sjunker dock till havets botten när de dör och för djuren i dess närhet bildar den en välkommen näringskälla, i djuphavet motsvarande upp till 2000 års normalt nedfall från den solbelysta havsytan. Nedbrytningen av ett valkadaver sker i flera steg. Först kommer djur som äter upp kött och späck, till exempel hajar och pirålar, men även skelettdelarna kan livnära specialiserade organismer en lång tid. Några av de djur som lever på valbenen har specialiserat sig så mycket på sin födokälla att de skulle få det svårt att leva någon annanstans. Detta gäller för havsborstmasken *Osedax* som har ett rotsystem som borrar sig in i valbenen på jakt efter näring, likt ett träds rötter. Andra djur som lever på valskelett är inte lika specialiserade på benen som *Osedax* utan har istället specialiserat sig på att äta av de tjocka bakteriemattor som lever av valkadavren. I denna avhandling beskrivs nio nya arter av havsborstmaskar som betar av bakteriemattorna. Fyra av de nya arterna har hittats på valkadaver på 125 m djup i den nya nationalparken Kosterhavet utanför Strömstad på Sveriges västkust. De andra fem av de nybeskrivna arterna lever på valskelett och sjunket trä i djuphavet utanför Kaliforniens kust i USA. Med hjälp av molekylära data har deras släktskap undersökts och DNA-analyser har även använts för att upptäcka sk kryptiska arter, arter som till det yttre är identiskt lika men som skiljer sig genetiskt i lika stor utsträckning som andra, utseendemässigt olika arter. Släktskapanalyserna har visat att anpassningen till ett liv på valkadaver och andra liknande näringsrika miljöer har skett vid flera tillfällen och av arter från olika utvecklingslinjer. Avhandlingen visar också att det som tidigare antogs vara kosmopoliska arter eftersom de hittas i hav jorden runt kan vara kryptiska arter. Detta har betydelse både för vår uppfattning om djurens förmåga att sprida sig och uppskattningar om hur många arter som finns på vår jord.