Whale-Fall Ecosystems: Recent Insights into Ecology, Paleoecology, and Evolution

Craig R. Smith,[1] Adrian G. Glover,[2] Tina Treude,[3] Nicholas D. Higgs,[4] and Diva J. Amon[1]

[1]Department of Oceanography, University of Hawaii, Honolulu, Hawaii 96822; email: craig.smith@hawaii.edu, divaamon@hawaii.edu

[2]Department of Life Sciences, Natural History Museum, SW7 5BD London, United Kingdom; email: a.glover@nhm.ac.uk

[3]GEOMAR Helmholtz Centre for Ocean Research Kiel, 24148 Kiel, Germany; email: ttreude@geomar.de

[4]Marine Institute, Plymouth University, PL4 8AA Plymouth, United Kingdom; email: nicholas.higgs@plymouth.ac.uk

Keywords

ecological succession, chemosynthesis, speciation, vent/seep faunas, *Osedax*, sulfate reduction

Abstract

Whale falls produce remarkable organic- and sulfide-rich habitat islands at the seafloor. The past decade has seen a dramatic increase in studies of modern and fossil whale remains, yielding exciting new insights into whale-fall ecosystems. Giant body sizes and especially high bone-lipid content allow great-whale carcasses to support a sequence of heterotrophic and chemosynthetic microbial assemblages in the energy-poor deep sea. Deep-sea metazoan communities at whale falls pass through a series of overlapping successional stages that vary with carcass size, water depth, and environmental conditions. These metazoan communities contain many new species and evolutionary novelties, including bone-eating worms and snails and a diversity of grazers on sulfur bacteria. Molecular and paleoecological studies suggest that whale falls have served as hot spots of adaptive radiation for a specialized fauna; they have also provided evolutionary stepping stones for vent and seep mussels and could have facilitated speciation in other vent/seep taxa.

INTRODUCTION

Chemolithoautotrophic: characterized by a form of microbial metabolism in which energy is obtained from the oxidation of inorganic compounds and carbon from the fixation of CO_2; also commonly call chemoautotrophy

The fate of sunken whale carcasses has been the subject of scientific speculation for at least 80 years (Krogh 1934), and hints that whale falls harbor an unusual fauna first appeared in the taxonomic literature more than 150 years ago (Woodward 1854, Smith & Baco 2003). Nonetheless, whale-fall ecosystems were not recognized until the discovery in 1987 of a chemolithoautotrophic assemblage on a balaenopterid skeleton in the deep sea off California (Smith et al. 1989), which unexpectedly resembled the recently discovered communities at hydrothermal vents and cold seeps (Corliss et al. 1979, Hecker 1985). As with vents and seeps, the initial whale-fall find led to a quick succession of discoveries of unusual, often chemolithoautotrophic, communities on modern whale falls in the deep North and South Pacific (Fujioka et al. 1993, Dell 1995, Smith & Baco 2003) and on fossil whale skeletons from the deep northeast Pacific dating back to the Oligocene (Squires 1991, Hachiya 1992, Goedert et al. 1995) (**Figure 1**). These discoveries spawned the first whale-carcass implantation experiments, conducted off southern California, to study whale-fall community ecology and phylogenetics (Smith 1992, Smith et al. 2002).

The initial whale-fall work was reviewed by Smith & Baco (2003) and included several major findings. First, whale falls are abundant over regional scales in the deep sea and support a widespread, characteristic fauna, with extraordinary local species richness. Second, faunal communities on carcasses of large adult whales can pass through at least three successional stages, potentially lasting for decades (see **Figure 2** and sidebar, Whale-Fall Community Succession).
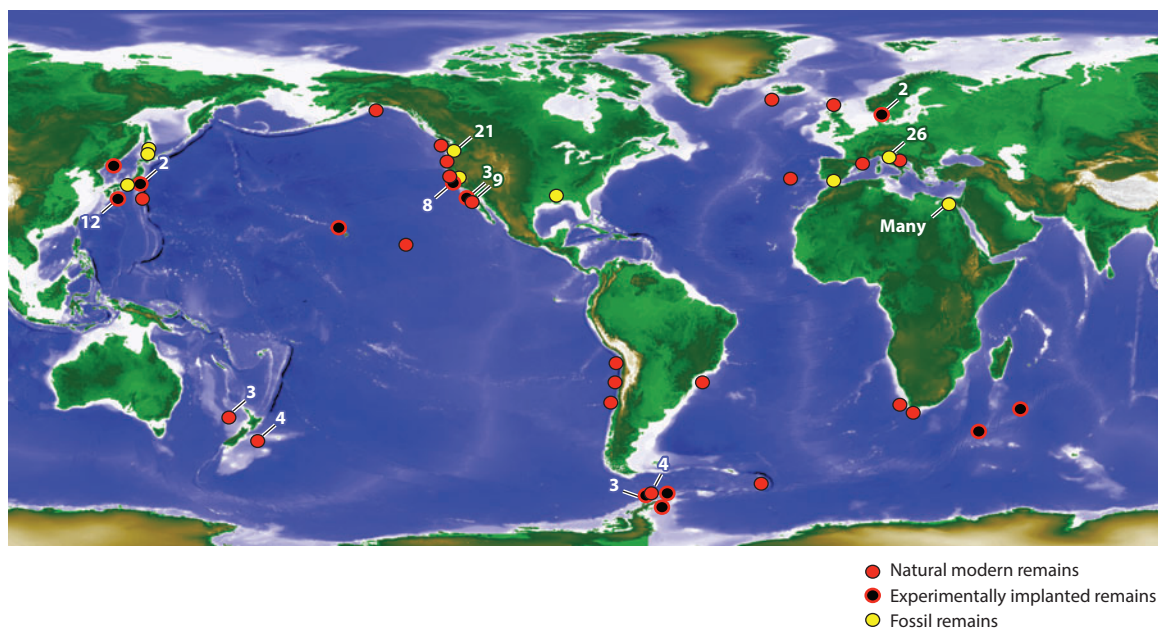

Figure 1

Known locations of modern and fossil whale remains at the seafloor. Red circles outlined in black indicate natural modern whale remains, black circles outlined in red indicate experimentally implanted whale remains (including whole carcasses and bones), and yellow circles indicate fossil whale remains. The references for the modern whale falls are as follows: Dell 1987, 1995; McLean 1992; Wada et al. 1994; Waren 1996; Smith & Baco 2003; Bolotin et al. 2005; Milessi et al. 2005; Dahlgren et al. 2006; Fujiwara et al. 2007; Pavlyuk et al. 2009; Pelorce & Poutiers 2009; Lundsten et al. 2010a,b; Amon et al. 2013; Glover et al. 2013; K.E. Smith et al. 2014; personal observations by D.J. Amon and C.R. Smith; and personal communications from K. Halanych, D. Honig, V.O. Melnik, and P.Y.-G. Sumida. For fossil references, see **Supplemental Table 1**. Base map provided by E. Wiebe, University of Victoria.
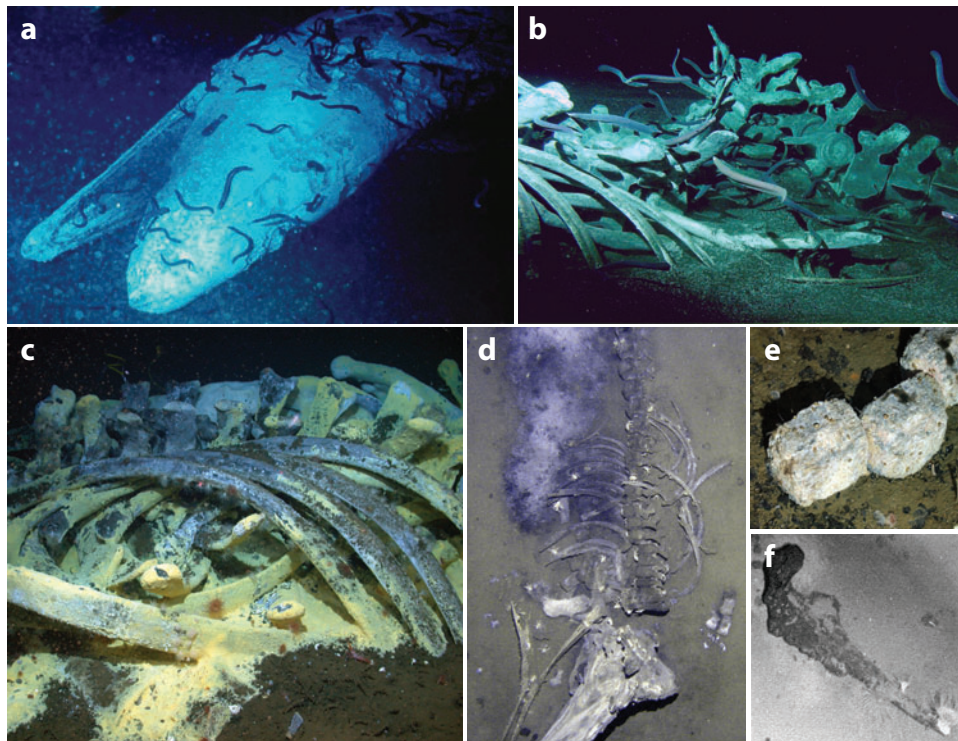
Supplemental Material

Figure 2

Stages of ecological succession observed at modern whale falls. (*a*) The mobile-scavenger stage at an implanted ∼30-ton gray-whale carcass in the Santa Cruz Basin on the California margin at 1,675 m, 1.5 months after emplacement. Numerous hagfish (*Eptatretus deani*) are feeding on the carcass. Large bite marks from sleeper sharks (*Somniosis pacificus*) are also evident. (*b*) The enrichment-opportunist stage at the same gray-whale carcass after 1.5 years at the seafloor. Only a few hagfish are present, and virtually all of the soft tissue has been removed from the skeleton. The white spots on the sediment are juvenile bivalves, gastropods, dorvilleid polychaetes, and cumacean crustaceans responding to conditions of organic enrichment near the whale fall. (*c*) The sulfophilic stage at the same gray-whale carcass after 6.8 years at the seafloor. Thick white and yellow mats of sulfur-oxidizing bacteria, along with anemones, are visible on the bones. Vesicomyid clams, a shrimp, and ampharetid polychaete tubes can be seen in the surrounding sediments. (*d*) The sulfophilic stage at a natural mysticete whale fall in the Clarion-Clipperton Zone in the central Pacific at 4,850 m. The blackened areas of sediment indicate the presence of sulfides resulting from the anaerobic decay of whale biomass. White bacterial mats are visible on blackened sediments and on some of the bones. Galatheid crabs are also visible on the carcass. (*e*) The sulfophilic stage at a natural whale fall in the South Sandwich Arc in the Southern Ocean at 1,444 m. White and pink bacterial mats are visible on the vertebrae, along with *Osedax* worms and *Pyropelta* limpets. (*f*) The reef stage on a manganese-encrusted whale bone in the Clarion-Clipperton Zone at ∼4,800 m. Three anemones are living on the bone. Based on the presence of the manganese crust, this bone likely arrived at the seafloor more than 10,000 years ago. Photographs are from C.R. Smith (panels *a–c*), V.O. Melnik (panels *d* and *f*), and the Natural Environmental Research Council, UK (panel *e*).

Finally, deep-sea whale remains appear to harbor a suite of whale-fall specialists, but they can also serve as dispersal stepping stones for some generalized, sulfide-dependent animals found at deep-sea vents and seeps.

Since 2003, studies of natural whale falls and experimentally implanted whale remains have increased dramatically, with more than 70 modern deep and shallow sites investigated in four

WHALE-FALL COMMUNITY SUCCESSION

Deep-sea whale-fall communities have been hypothesized and observed to pass through up to four stages of eco-logical succession:

1. The mobile-scavenger stage: Soft tissue is removed from the carcass by dense aggregations of large, active necrophages.

2. The enrichment-opportunist stage: Dense assemblages of heterotrophic macrofauna (especially polychaetes and crustaceans) colonize the bones and organically enriched sediments surrounding the carcass.

3. The sulfophilic (or "sulfur-loving") stage: An assemblage that includes chemolithoautotrophs colonizes the bones and sediments as sulfide is emitted from the anaerobic bacterial decomposition of bone lipids and other tissue. Methane can also be released during anaerobic tissue decay, fostering free-living or endosymbiotic bacterial methanotrophs.

4. The reef stage: After the depletion of organic material, the mineral remains of the skeleton are colonized primarily by suspension feeders exploiting flow enhancement and hard substrates.

As with all ecological successions, community changes are continuous, and the stages overlap. The duration and overlap of stages can vary substantially with carcass size and seafloor habitat.

Supplemental Material

ocean basins (**Figure 1**). In addition, paleo-whale-fall communities have been discovered at more than 50 sites on four continents (**Figure 1**, **Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). The initial whale-fall review by Smith & Baco (2003) has been cited ∼300 times in the scientific literature (Google Scholar), and the ecological term whale fall, coined by Allison et al. (1991), has appeared in more than 800 scientific publications (Google Scholar), including research papers, encyclopedias, popular science books, and university and high-school textbooks. Here, we review results from the study of whale-fall ecosystems over the past decade, focusing on new insights and tests of the initial ecological and evolutionary hypotheses.

NEW INSIGHTS

Whale Falls as Habitats: Remarkable Qualities

Whale falls have several remarkable qualities that yield unusual, energy-rich ecosystems at the ocean floor. Great whales include the largest animals that have ever lived, with adult body masses ranging from 8 to 160 metric tons (Lockyer 1976). This size provides a refuge from most predators, with the consequence that great-whale biomass typically enters marine detrital food webs as essentially intact carcasses (Smith 2006, Pershing et al. 2010).

The bodies of most great-whale species, except for right and sperm whales, have a density slightly greater than seawater's (Reisdorf et al. 2012), and most natural whale mortality results from nutritional or disease stress during migrations, yielding reduced buoyancy and carcass sinking (Smith 2006). In addition, sinking whale carcasses reach the seafloor relatively intact because they descend rapidly following lung deflation and because there are no significant scavengers of sinking whales in the ocean water column (Britton & Morton 1994, Smith 2006).

There is substantial evidence that whale falls remain and decompose at the seafloor even at relatively shallow depths. Allison et al. (1991) estimated that increasing hydrostatic pressure would prevent decomposing whale carcasses from floating to surface waters from depths greater than

1,000 m. Recent observations suggest that 1,000 m is a substantial overestimate of the permanent sinking depth, especially in cold waters. For example, a complete humpback whale carcass was observed at the seafloor in the advanced stages of scavenging at 150 m in Alaskan waters (Smith 2006), and experimentally implanted intact minke, sperm, gray, fin, and pilot whale carcasses ($n = 18$) have shown no evidence of refloating over periods of 0.5–3 years at depths of 30–382 m (Dahlgren et al. 2006, Fujiwara et al. 2007, Pavlyuk et al. 2009, Lundsten et al. 2010b). Finally, based on a variety of evidence, Reisdorf et al. (2012) concluded that cetacean carcasses "may rise from water depths up to 50 m, but never from below 100 m" (p. 72).

Whale carcasses also are remarkable in consisting largely of energy-rich material, in particular lipids and proteins. Approximately 87% of great-whale biomass is in lipid-rich soft tissues, and the skeletons of whales can also contain large reservoirs of oil (Smith 2006). A recent synthesis of whaling data suggests that the skeletons of great whales have substantially higher average lipid content (~20%) than those of small cetaceans such as dolphins (~9%) (Higgs et al. 2011b). The bone-lipid content in great whales also varies substantially with whale maturity (juveniles have much lower bone-lipid content than adults) and along the skeleton (Higgs et al. 2011b). In particular, the jaws, skull, and caudal vertebrae tend to have high lipid content (20–84%); the ribs, scapula, sternum, and lumbar vertebrae tend to have intermediate lipid content (15–30%); and the thoracic and cervical vertebrae tend to have relatively low lipid content (5–20%).

Because of the enormous body sizes and allometric scaling, the mass of lipids in great-whale skeletons and whole carcasses can be very large. The total lipid content of the skeletons of both mysticetes and odontocetes scales with body length to a power of >4, and the skeletons of adult great whales therefore contain 2–14 metric tons of lipid (Higgs et al. 2011b). This is 2–4 orders of magnitude greater than the lipid content of the skeletons of dolphins and killer whales (Higgs et al. 2011b). In addition, the surface/volume ratios of the bones of great whales are much lower than those of small cetaceans (Higgs et al. 2011b). The high lipid content and low surface/volume ratios of large whale bones, as well as the robust nature of the bone mineral matrix in adults, appear to be major drivers of the size, structure, and duration of whale-fall communities, leading to emergent properties in the creation of persistent seafloor ecosystems (see below).

A final notable characteristic of whale falls is a heterogeneous distribution in the ocean in space and time (**Figure 1**). Many mysticetes migrate thousands of kilometers annually between feeding and calving grounds (Roman et al. 2014), yielding stress and enhanced mortality (Gulland et al. 2005). Thus, the falls of mysticetes are likely to be concentrated along whale migration routes (e.g., along the margins of most ocean basins) and especially in the regions of low-latitude calving (Gulland et al. 2005, Smith 2006, Roman et al. 2014). Sperm whales have a more oceanic distribution and may provide the main source of cetacean detritus in abyssal basins (Roman et al. 2014); nonetheless, they are also concentrated in feeding grounds (e.g., the equatorial Pacific), where falls are more likely. Finally, the occurrence of whale falls has varied over very recent time, with substantial reductions in frequency in many regions driven by intense whaling in the nineteenth and twentieth centuries (Smith 2006). This heterogeneity in space and time is likely to have influenced the biogeography and diversity of whale-fall communities and may have led to the first anthropogenic species extinctions in the deep sea, in the form of whale-fall specialists (Butman et al. 1995, Smith 2006, Roman et al. 2014).

Community Ecology and Ecosystem Function at Modern Whale Falls

The past decade has yielded important new insights into the structure, function, and biodiversity of both microbial and metazoan assemblages at whale falls. Here, we review some of the most exciting new findings.

Rare biosphere: a diversity of microbial populations occurring at low abundance in the deep sea; it may represent a nearly inexhaustible source of genomic innovation (Sogin et al. 2006)

Sulfate-reducing bacteria: bacteria that degrade organic compounds with sulfate as the terminal electron acceptor; during this process, sulfate is reduced to sulfide

Methanogens: archaea that generate methane from different substrates; methanogenesis is thought to be the terminal step of organic matter degradation in sediments

Microbial community structure and function. Deep-sea whale falls stimulate a suite of microbial processes related to the degradation of whale biomass, including the utilization of reduced chemical end-members. Although the importance of microbes was recognized early on (Allison et al. 1991, Smith 1992, Deming et al. 1997), recent technical advances have facilitated detailed studies of microbial activity and diversity at whale falls (**Supplemental Table 2**).

Microbial degradation of whale biomass in sediments and bones. Whale falls rapidly attract large mobile scavengers (**Figure 2**), whose sloppy feeding and high levels of activity spread whale biomass over and into surrounding sediments (Smith & Baco 2003, Smith 2006), eliciting in turn a rapid microbial response. The dispersion of whale biomass leads to a bull's-eye of elevated microbial enrichment and degradation activity in the sediment, which declines to background conditions beyond ∼10 m (Goffredi et al. 2008, Treude et al. 2009, Goffredi & Orphan 2010). Goffredi & Orphan (2010) found that the relative proteolytic activity (indicating the potential for organic carbon breakdown) in sediments underlying a seven-month whale carcass was up to six times higher than that of the surrounding environment. Sediment enrichment with whale biomass leads to a successive temporal and spatial decline in microbial diversity around the carcass and a concurrent increase in microbial biomass (Goffredi et al. 2008, Treude et al. 2009, Goffredi & Orphan 2010). The low diversity and high abundance of microorganisms are most likely a result of both specialization to nutrient enrichment and high growth rates.

The origin of the microbes involved in this degradation could be local sediments, the water column, mobile scavengers, or the whale carcass itself. The potential recruitment of microorganisms from a rare biosphere (Sogin et al. 2006, Pedrós-Alió 2012) in the sediments is still under debate (Goffredi & Orphan 2010). Likewise, whale gut flora could initiate degradation processes inside the whale prior to the dispersal of biomass by scavengers; gas production from microbial degradation processes inside the body is commonly observed in dead whales (Allison et al. 1991, Reisdorf et al. 2012). A diversity analysis from two different whale falls separated by 30 km in distance and 1,000 m in depth suggested "that the deposition of whale-fall biomass on the seafloor is more influential on the bacterial community than specific location" (Goffredi & Orphan 2010, p. 344).

Both sulfate reduction and methanogenesis are important processes for biomass degradation in sediments surrounding whale carcasses (Goffredi et al. 2008, Treude et al. 2009, Goffredi & Orphan 2010). Near the carcass, high concentrations of sulfide (up to 11 mM) and methane (up to 4.2 mM) are correlated with high activities of sulfate reduction and methanogenesis, respectively (Naganuma et al. 1996, Goffredi et al. 2008, Treude et al. 2009, C.R. Smith et al. 2014). Sulfate-reducing bacteria (Desulfobacteraceae and Desulfobulbaceae) and methanogenic archaea (Methanomicrobiales and Methanosarcinales) dominate the whale-fall sediment microbial community (Goffredi et al. 2008, Goffredi & Orphan 2010). At 1 atm of pressure, whale-fall sediments responded quickly to the addition of whale biomass, showing simultaneous sulfide and methane production (Treude et al. 2009). Apparently, the excess of potential electron donors, such as hydrogen and methylamines, provided by the whale biomass eliminated competition between sulfate reducers and methanogens.

The importance of other degradation processes in sediments around deep-sea whale falls is less well studied. Iron is an alternative, thermodynamically attractive electron acceptor, and Goffredi & Orphan (2010) found that total iron concentrations around whale falls were high (∼20,000 ppm). Sediments impacted by whale biomass feature dark discolorations indicative of black iron sulfides or pyrite (Treude et al. 2009, C.R. Smith et al. 2014) (**Figure 2**). The absence or unexpectedly low concentration (<60 μM) of free sulfide in black sediments despite high rates of sulfate reduction further suggests that the sediments have a high capacity to chemically consume sulfide with iron (Goffredi et al. 2008, Treude et al. 2009).

Once stripped by scavengers, the lipid-rich whale bones provide an additional energy source and habitat for microorganisms. Bone lipids are energy rich but difficult to exploit because they are embedded in a bone matrix made of apatite and collagen. It is therefore not surprising that large adult bones provide the most persistent energy sources at whale falls. Even 7 years after deployment, bacterial sulfate reduction activity penetrated only a few millimeters into the matrix of an adult gray-whale vertebra (diameter 23 cm) (Treude et al. 2009). The center of a 16-cm vertebra of a large balaenopterid whale fall was still intact (i.e., free of microbial cells and rich in lipids) after 50 years at the seafloor, whereas peripheral zones revealed high microbial cell density in areas of advanced lipid depletion (Deming et al. 1997, Schuller et al. 2004). Similarly, fossil whale bones revealed a decline of pyrite, a potential chemical end-member of bacterial sulfate reduction activity, from the bone periphery to the center (Shapiro & Spangler 2009).

These examples illustrate that the microbial colonization and degradation of adult whale bones can occur gradually from the outside to the center and are probably limited by the delivery of electron acceptors from seawater through the hydrophobic bone matrix, as well as by the erosion of bones through bone-consuming microbes and metazoans, including the bone-eating worm *Osedax* (see below and **Supplemental Figure 1**). Specific bacterial lipid biomarkers found in the center of fossil whale bones suggest that sulfate reducers and other heterotrophic microorganisms, such as collagen-degrading actinomycetes, may eventually colonize the entire bone to exploit the organic matter (Thiel et al. 2014). Microbial penetration of bones may be significantly enhanced in the presence of bone-boring metazoans such as *Osedax* (Higgs et al. 2010, Kiel et al. 2010). The peripheries of bones inhabited by *Osedax* worms become successively more porous, and black staining by pyrite around *Osedax* burrows suggests that sulfate-reducing bacteria penetrate the bone together with the worm (Higgs et al. 2011a).

As in whale-fall sediments, microbial communities in whale bones appear to have reduced species and phyletic diversity compared with other microbial environments (Tringe et al. 2005), most likely as a result of specialization on rich bone nutrient resources. Bones are typically exposed to the sediment below and the water column above and therefore offer contact surfaces for the entry of both benthic and pelagic microorganisms. Differences in microbial cell abundance between the sediment- and water-facing sides of a bone cross section suggested that microbial colonization is more efficient from the sediments (Deming et al. 1997).

Secondary microbial consumers. The microbial degradation of whale biomass in sediments and bones produces sulfide and methane, which are favorable energy sources for chemolithoautotrophic microorganisms. Whale-fall habitats therefore likely undergo a temporal microbial succession from primarily heterotrophic to more heterotrophic/chemosynthetic metabolisms until the whale biomass is completely exploited. Mats of filamentous chemolithoautotrophic sulfide-oxidizing bacteria such as *Beggiatoa* species are observed on deep-sea whale bones and adjacent sediments for years after carcass arrival (Smith & Baco 2003, Lundsten et al. 2010b) (**Figure 2**). Because sulfur oxidation with oxygen or nitrate generates ample energy for fast microbial growth, sulfide-oxidizing bacteria are expected to respond quickly to available free sulfide. In whale-fall sediments, however, the accumulation of free sulfide can be retarded through reactions with iron (see above) (Treude et al. 2009). It is thus not surprising that whale falls feature specific deltaproteobacteria (e.g., *Desulfocapsa sulfexigens*) (Goffredi & Orphan 2010) that disproportionate sulfur, which is energetically more favorable as long as metals maintain sulfide concentrations below 1 mM (Thamdrup et al. 1993, Bottcher & Thamdrup 2001). Only after the oxidizing power of sediment metals is exhausted can a considerable sulfide gradient develop and support voluminous mats of sulfide-oxidizing bacteria. Sulfide oxidation on bone surfaces could also contribute to bone erosion because this process releases protons (Jørgensen & Nelson 2004). The detection of microborings

Heterotrophic: requiring organic compounds as the principal source of nutrition; heterotrophs depend on organic compounds produced from either photo- or chemoautotrophy

Chemosynthetic: characterized by the fixation of CO_2 fueled by the oxidation of reduced inorganic compounds to produce biomass; this type of biomass production differs from photosynthesis, which is fueled by energy from light

▶ Supplemental Material

restricted to the surfaces of whale bones suggests the involvement of exterior microorganisms in bone erosion (Shapiro & Spangler 2009, Higgs et al. 2011b). Such microorganisms that chemically dissolve whale bone might play a significant role in the release of phosphate to microbial populations in this carbon-rich but potentially phosphate-poor habitat.

Archaeal methanogenesis has been detected in whale-fall sediments (Goffredi et al. 2008, Treude et al. 2009) but has not been studied in the bones. Methane is an attractive microbial energy source and is oxidized by microorganisms using several different electron acceptors (Hanson & Hanson 1996, Boetius et al. 2000, Beal et al. 2009, Ettwig et al. 2010). Evidence of the aerobic oxidation of methane at whale falls is limited to bacterial fatty-acid methyl esters found in whale-fall sediments (Naganuma et al. 1996). Anaerobic methanotrophic archaea oxidizing methane with sulfate were detected in whale-fall sediments 45 months after deployment, marking a shift from methanogenic to methanotrophic processes (Goffredi et al. 2008). The extremely slow growth rate of these archaea, with doubling times of up to 4–7 months (Girguis et al. 2005, Nauhaus et al. 2007), probably prevents a faster establishment of this type of methanotroph.

Microbial symbioses at whale falls. Documented chemosymbiotic relationships at whale falls exploit only sulfide, although methane-oxidizing symbiotic relationships are conceivable given the high methane production rates in whale-fall sediments (Goffredi et al. 2008, Treude et al. 2009). Sulfide-oxidizing bacteria have been found in endosymbioses with clams (Baco et al. 1999), mussels (e.g., Deming et al. 1997, Lorion et al. 2009, Fujiwara et al. 2010), and vestimentiferan tube worms (Feldman et al. 1998). In most cases, the animals have degenerated digestive systems and depend on the symbionts for nutrition. In return for, e.g., sugars and amino acids, the animal host delivers the electron donor (H_2S), electron acceptor (O_2), and inorganic carbon source (CO_2) from the exterior environment to the internal bacteria. The description of the bone-eating polychaete *Osedax* (Rouse et al. 2004) at whale falls revealed a new type of metazoan-bacteria symbiosis to exploit a different energy source: organic material sequestered within the bones (see the discussion of *Osedax* below).

Metazoan biodiversity, ecology, and ecosystem function at deep-sea whale falls. The dramatic increase in the study of whale remains over the past decade (**Figure 1**) has greatly expanded our view of metazoan species richness, ecological succession, and evolution at deep-sea whale falls.

New species and evolutionary novelty. Deep-sea whale-fall studies are yielding new species at an accelerating rate and producing exciting discoveries of evolutionary and functional novelties. In the first 14 years of whale-fall studies, 21 new animal species (13 formally described and 8 putative new species) were recovered from deep-sea whale falls; these new species suggested the existence of a specialized fauna requiring whale falls to persist, analogous to the specialized faunas at hydrothermal vents and cold seeps (Smith & Baco 2003). Now, ~10 years later, we estimate that a total of 129 newly described and putative new species from seven phyla have been collected on whale remains, of which 37 have been formally described and 102 are potentially whale-fall specialists (**Supplemental Table 3**). More than 50% of this total species richness is in the phylum Annelida, including 31 species of dorvilleid polychaetes and another 31 within the bone-eating siboglinid genus *Osedax*.

▶ Supplemental Material

Clearly, we are still in the early stages of discovery of the deep-sea whale-fall fauna, because more than half of the species restricted to whale falls were collected from the California margin, where whale-fall studies are the most numerous and long-standing (**Figure 1**). Some other ocean regions, in particular the Southern Ocean and the southwest Indian Ocean, have already yielded a substantial diversity of whale-fall species (22 and 14 new species, respectively) even though

only limited and very recent studies of whale remains have been performed there (**Figure 1**, **Supplemental Table 3**). Given the accelerating rate of whale-fall species discovery and the limited whale-fall data from most oceanic regions, we predict that many hundreds of species of whale-fall specialists remain to be discovered in the deep sea, although the studies are still too haphazard to make a quantitative projection of the global richness of these species. In addition, there is clearly a substantial taxonomic backlog in the descriptions of new species, which will be essential to understanding the ecology, biogeography, and evolution of the whale-fall fauna.

It is noteworthy that, of the 129 putative new species from whale falls, only 12 have been found on whale remains at depths of less than 260 m (**Supplemental Table 3**), even though multiple whale-carcass and bone implantation experiments ($n \geq 18$) have been conducted in shallow North Pacific, North Atlantic, and Antarctica waters (**Figure 1**, **Supplemental Table 3**). The general paucity of novel taxa on shallow-water whale falls suggests that species-rich, specialized whale-fall communities develop only in the food-poor deep sea (Dominici et al. 2009, Pavlyuk et al. 2009, Danise & Dominici 2014), although it must be noted that five new species have been described from a single high-latitude shelf-depth whale fall (Glover et al. 2005b; Dahlgren et al. 2006; Wiklund et al. 2009a,b). In more energy-rich shallow-water ecosystems, whale falls are exploited primarily by generalized heterotrophic species, as has been observed for shallow hydrothermal vents and cold seeps (Tarasov et al. 2005, Dubilier et al. 2008). The extreme food limitations of deep-sea ecosystems far removed from the euphotic zone (Smith et al. 2008) appear to lead to strong selection for organisms that can exploit food-rich habitat islands at the ocean floor.

The new species on deep-sea whale falls include unique examples of functional novelty and adaptive radiation, with the bone-eating siboglinid polychaete genus *Osedax* providing perhaps the most striking example (**Supplemental Figure 1**). Worms now recognized as *Osedax* were first collected in abundance at multiple whale skeletons at bathyal depths off California and Oregon beginning in 1994, but they were morphologically so bizarre that they defied identification by polychaete specialists and were simply called "snot worms" (Baco-Taylor 2002; E. Southward, personal communication). The discovery of two large *Osedax* species abounding on a whale skeleton at 2,893 m in Monterey Canyon combined with molecular genetic studies finally yielded the description of this new genus in the annelid family Siboglinidae, the closest relatives of which are the giant vestimentiferan tube worms found at hydrothermal vents (Rouse et al. 2004).

Osedax worms are extraordinary in several ways. Although these organisms were first described only ~10 years ago, whale-bone studies have recovered at least 31 putative *Osedax* species in the Pacific, Atlantic, Indian, and Southern Oceans, suggesting a worldwide distribution and large depth range (21–4,000 m) (**Supplemental Table 3**). The worms are characterized by a bizarre palm-tree-like morphology, with a crown of reddish palps/gills, a mucus-clad trunk, and bulbous green or yellow root-like structures (large ovisacs) that penetrate cavities in bones (**Supplemental Figure 1**) (Rouse et al. 2004, Glover et al. 2005b). The life history of *Osedax* includes larval dispersal, dwarf males, environmental sex selection (apparently, only individuals settling on females become male), and high fecundity (Rouse et al. 2004, 2009; Miyamoto et al. 2013). These are all adaptations that maintain population connectivity across a network of widely dispersed, food-rich habitat islands. In fact, *CO1* DNA bar-coding indicates that one species, *Osedax rubiplumus*, occurs on whale bones on the California, Japan, and Antarctic margins, suggesting a large species range (**Supplemental Table 3**).

Like other siboglinids, *Osedax* worms lack a digestive tract and depend for nutrition on large colonies of symbiotic bacteria housed in a trophosome. Unlike other siboglinids, however, the *Osedax* trophosome occurs in the vascularized root system that penetrates the bone rather than in the elongated trunk (Katz et al. 2011) (**Supplemental Figure 1**). The root tissue contains bacteria in the order *Oceanospirillales* that produce enzymes to hydrolyze collagen and cholesterol

from bones, yielding nutrition to both symbionts and the *Osedax* hosts (Goffredi et al. 2005, 2007; Katz et al. 2010). The endosymbionts are newly acquired by the *Osedax* worms from the environment in each generation as the juvenile root system grows into bone (Goffredi et al. 2007, Verna et al. 2010). *Osedax* worms' use of marine mammal bones, their exploitation of collagen and cholesterol, and the morphology of the symbiont-bearing ovisac and root system make this form of bacterial endosymbiosis unique (Rouse et al. 2004).

Osedax species may also act as important ecosystem engineers by eroding whale bones through acid secretion, allowing the worms to absorb bone-trapped nutrients (Tresguerres et al. 2013). Where *Osedax* worms are abundant, bone erosion by this polychaete may facilitate the rapid destruction of juvenile whale skeletons (Lundsten et al. 2010b, Higgs et al. 2011a). Different *Osedax* species create burrows of varying sizes, shapes, and depths (Higgs et al. 2014b), and some species show preferences for particular types of bones within a carcass, suggesting habitat specialization and niche partitioning (Goffredi et al. 2007).

The distribution of *Osedax* is clearly very broad, with populations occurring in every ocean basin studied (**Supplemental Table 3**). Large natural *Osedax* populations have been found only on whale bones, although a few individuals of smaller species and small borings attributed to *Osedax* worms have been found on artificially implanted cow bones and on the bones of pinnipeds, birds, and teleosts (Glover et al. 2008, Jones et al. 2008, Vrijenhoek et al. 2008, Schander et al. 2010, Kiel et al. 2011, Rouse et al. 2011). Thus, at the generic level, *Osedax* worms appear to be capable of exploiting a variety of bone substrates. However, the large interspecific range in body sizes, burrowing morphologies, and bone preferences and the high species richness of *Osedax* (Vrijenhoek et al. 2009, Amon et al. 2014) are reminiscent of the siboglinid clade Vestimentifera, which includes large hydrothermal-vent specialists and smaller generalized species that colonize a broad range of sulfide-rich habitats (Dando et al. 1992, Van Dover 2000, Smith & Baco 2003). We hypothesize that the larger *Osedax* species (e.g., the 10-cm-long *Osedax rubiplumus*, which has root systems penetrating several centimeters) (**Supplemental Figure 1**) are likely to specialize on the bones of whales and perhaps other large marine mammals, whereas the complex of smaller, ~1-cm-long *Osedax* species are likely to include generalists capable of maintaining populations on much smaller bones derived from a variety of sources, including teleosts and birds.

The extraordinary diversity of dorvilleid polychaetes, including 29 newly described and putatively new species in the genus *Ophryotrocha* (**Supplemental Table 3**), also suggests an adaptive radiation at deep-sea whale falls. Wiklund et al. (2009a) hypothesized that many of these dorvilleid species evolved as specialists on bacterial mats at whale falls or other natural large organic falls and have recently exploited the organic-rich anthropogenic habitats associated with fish farms and sewage outfalls, consuming mats of sulfur-oxidizing bacteria. These authors suggested that whale falls are important habitats for the evolution of ecosystem services such as the degradation of complex organic compounds at sites of intense organic loading; a similar ecosystem function role has also been postulated for chrysopetalid worms in the genus *Vigtorniella* that have been found beneath fish farms and whale falls (Dahlgren et al. 2004, Wiklund et al. 2009b).

A variety of additional species also exhibit unusual adaptations to deep-sea whale-fall habitats. The sipunculid *Phascolosoma saprophagicum* feeds on lipids in whale-bone cavities (Gibbs 1987), and provannid gastropods in the new genus *Rubyspira* derive nutrition from decomposing whale skeletons by ingesting bone particles and associated bacteria, and possibly from thiotrophic symbionts that use sulfides derived from anaerobic bone-lipid decomposition (Johnson et al. 2010).

Colonization and succession. Smith & Baco (2003) presented a model of whale-fall community succession in the deep sea (see **Figure 2** and sidebar, Whale-Fall Community Succession) based

Supplemental Material

on studies of adult and juvenile mysticete carcasses (both natural and implanted) off southern California at depths of 960–1,960 m, with bottom-water oxygen concentrations of ∼0.5 to >2 mL/L (Smith & Demopoulos 2003, Treude et al. 2009). In this model, carcasses of adult whales pass through at least three overlapping successional stages: (*a*) a mobile-scavenger stage, lasting for months; (*b*) an enrichment-opportunist stage, lasting for months to years; and (*c*) a sulfophilic stage, lasting for years to decades. Smith & Baco (2003) also postulated a final reef stage on adult whale skeletons, dominated by suspension feeders living on lipid-depleted bones. For juvenile whale carcasses (e.g., gray whales up to 10 m long), they described much more rapid carcass decomposition and truncated, highly overlapping successional stages, with little evidence of chemoautotrophy after 2 years. This rapid carcass decomposition and limited sulfophilic stage were ascribed to the much smaller sizes, weaker calcification, and smaller lipid reservoirs of juvenile whale bones (Smith & Baco 2003). How has this successional model held up following the increasing number of studies of whale remains at the seafloor?

Successional patterns can be addressed using two approaches: observations of natural whale falls, especially those that have been dated (Schuller et al. 2004), and time-series studies of experimentally implanted intact whale carcasses. The experimental approach is particularly effective for establishing the timescales and drivers of successional processes.

Studies of natural whale falls indicate that all four successional stages can occur beyond the southern California margin. The mobile-scavenger stage has been observed on adult and juvenile whale carcasses at shelf depths off Alaska and Siberia (Smith 2006, Pavlyuk et al. 2009) and at bathyal depths off Antarctica (K.E. Smith et al. 2014), and this stage must be widespread owing to the ubiquity of scavengers in the oxygenated deep sea (Britton & Morton 1994, King et al. 2007, Higgs et al. 2014a). The enrichment-opportunist stage has been found on a juvenile gray-whale carcass at 2,893 m in Monterey Canyon (Goffredi et al. 2004, Braby et al. 2007), and the sulfophilic stage has been found on large whale carcasses at bathyal depths in the northeast Pacific (Lundsten et al. 2010a), the Southern Ocean (Amon et al. 2013), and the abyssal northwest and equatorial Pacific (Naganuma et al. 1996) (**Figure 2**). The reef stage has been observed at abyssal depths in the form of manganese-encrusted whale bones apparently more than 10,000 years old (Heezen & Hollister 1971) (**Figure 2**).

Time-series studies of whale carcasses also show patterns consistent with the Smith & Baco (2003) successional model, with some differences. Fujiwara et al. (2007) studied 12 sperm-whale carcasses emplaced on sandy sediments for 2 years off Japan, near the continental shelf break (depths of 219–254 m). The mobile-scavenger, enrichment-opportunist, and sulfophilic stages were all observed, but succession was more rapid than had been documented at adult whale carcasses in the deep sea off southern California (Smith & Baco 2003). The more rapid degradation and disappearance of whale skeletons at these relatively shallow depths appeared to result from a combination of higher water temperatures (∼13°C versus ∼4°C) accelerating microbial processes, the abundance of bone-eating *Osedax* worms, and more energetic currents eroding and burying the skeletons (Fujiwara et al. 2007).

Time-series studies of five juvenile gray whales and one headless adult blue whale have been conducted at depths of 382–2,983 m in Monterey Canyon for up to ∼7 years (Goffredi et al. 2004, Braby et al. 2007, Lundsten et al. 2010b). These depths included a range of oxygen concentrations (0.5–2.4 mL/L) and areas of enhanced currents and sediment mobility within Monterey Canyon (Puig et al. 2014). Studies on the juvenile carcasses indicated substantial overlap between the mobile-scavenger and enrichment-opportunist stages as well as a truncated sulfophilic stage (Lundsten et al. 2010b), as described by Smith & Baco (2003). Exposed whale bones at most carcasses were rapidly colonized by multiple species of bone-eating *Osedax* worms, which generally were becoming rare on juvenile skeletons after 2 to 3 years. By 4.5 to ∼8 years after carcass arrival,

juvenile skeletons were largely decomposed or buried, with the skull and jaw bones proving most persistent (Lundsten et al. 2010b). These juvenile carcasses showed no evidence of the reef stage of succession, in agreement with speculation by Smith & Baco (2003).

The adult blue-whale carcass in Monterey Canyon was not intact when emplaced (Lundsten et al. 2010b), so successional patterns were probably accelerated and unusually overlapping, yet they still resembled the Smith & Baco (2003) model. After 4.5 years, the vertebrae were still prominent and supported bacterial mats, mollusks, and polychaetes characteristic of the sulfophilic stage. It is difficult to say how long this adult carcass, if intact, would have lasted naturally because the persistent skull region had been removed.

These time-series studies of intact whale carcasses indicate some differences in deep-sea whale-fall successional rates and community composition depending on the water depth, temperature, and hydrodynamic regime (e.g., physicochemical erosion and sediment burial of bones); in particular, higher temperatures, active currents, and sediment transport yield more rapid carcass disappearance (Fujiwara et al. 2007, Lundsten et al. 2010b). Depth, temperature, and flow-regime-related changes in community structure and ecosystem function are typical of deep-sea habitats generally (Carney 2005, Rowe et al. 2008), and whale-fall succession appears to sustain similar environmental forcing. There are also strong body-size-related differences in deep-sea whale-fall succession, with the intact carcasses of adult great whales exhibiting succession for many years to decades, whereas juvenile whale carcasses show truncated succession and typical persistence times of a few years. We postulate that the much shorter persistence of juvenile whale skeletons results from a combination of the smaller sizes and higher surface/volume ratios of the bones, much lower levels of bone calcification, and lower bone-lipid content compared with the skeletons of adult great whales (Smith 2006, Higgs et al. 2011b). The rapid disappearance of lipid-poor juvenile bones and the persistence of skull bones and caudal vertebrae are consistent with the "bone oil prevents bone spoil" hypothesis of Higgs et al. (2011a) and resemble the observations of Amon et al. (2013), who found that high lipid content deters microbial and *Osedax*-mediated bone decomposition.

Osedax *as foundation species.* Following the discovery of *Osedax* worms on whale skeletons in Monterey Canyon, Braby et al. (2007) hypothesized that "*Osedax* may be a foundation species in Monterey whale-fall communities, regulating the longevity of whale bones and thereby affecting the succession of associated megafauna" (p. 1773). For juvenile whale carcasses—especially in Monterey Canyon, where *Osedax* species appear to be particularly abundant—bone erosion by these worms does contribute substantially to rapid skeleton decomposition, although other processes, including sediment burial, may also be important (Lundsten et al. 2010b). For large skeletons of adult great whales, there is little evidence that *Osedax* worms cause rapid skeleton destruction, especially for lipid-rich bones in the skull, jaws, and caudal regions. *Osedax* worms or their borings are evident on several adult whale skeletons that have persisted at the deep-sea floor for decades (Smith & Baco 2003, Schuller et al. 2004, Amon et al. 2013, Higgs et al. 2014b) or that showed very slow rates of bone degradation over a period of 7 years (Treude et al. 2009, C.R. Smith et al. 2014). All of these skeletons occurred in bottom waters with measured oxygen concentrations of $\geq$0.5 mL/L, i.e., at concentrations not limiting to *Osedax* species (Lundsten et al. 2010b). We postulate that on the large, well-calcified, oil-rich bones of adult great whales, *Osedax* populations deplete food resources (e.g., collagen and cholesterol) within the penetration depths of their root systems (millimeters to a few centimeters) and then die out, allowing substantial bone mass, lipid reservoirs, and sulfophilic communities to persist for more than 10 years, particularly on the lipid-rich skull bones and thoracic/caudal vertebrae (Higgs et al. 2011b).

Phylogenetic evidence for the origin and diversification of whale-fall, vent, and seep faunas.

Whale-fall communities have proven significant in generating new hypotheses on the evolutionary origins of the faunas of deep-sea reducing habitats. The discovery of chemolithoautotrophic communities and some vent/seep species at whale falls immediately suggested a potential ecological role as dispersal stepping stones for sulfide-dependent species in the deep sea (Smith et al. 1989, Smith & Baco 2003). But could whale falls also have influenced the dispersal and speciation of the vent/seep faunas over evolutionary time?

Whale falls could have affected the evolution of the deep-sea reducing-habitat faunas in at least two ways. First, they could have served as intermediate habitats, and hence evolutionary stepping stones to new habitat types, by facilitating colonization (and subsequent adaptive radiation) in habitat types not previously exploited by a clade. Second, they could have driven evolution by providing ecological stepping stones to isolated habitats for which a species was already adapted, expanding its geographic range and facilitating speciation in remote locations (Bush 1975). The first phylogenetic studies of whale-fall mollusks provided controversial evidence consistent with both mechanisms: A wood/whale-fall mussel appeared basally in the phylogeny of the vent/seep mytilid clade (Distel et al. 2000), and vent/seep vesicomyid clams appeared to have diversified when large whales first appeared in the fossil record (Baco et al. 1999).

Phylogenetic studies of the whale-fall fauna since 2003 have focused on the mollusks (mytilids and vesicomyid clams) and polychaetes (mostly siboglinids, dorvilleids, chrysopetalids, and polynoids). Mytilids in the subfamily Bathymodiolinae are a diverse, characteristic taxon of deep-sea chemosynthetic habitats (Van Dover 2000) and have been targeted in a substantial number of evolutionary stepping-stone studies (Samadi et al. 2007; Lorion et al. 2009, 2010, 2012; Miyazaki et al. 2010). The most recent and most comprehensive such evolutionary study showed that the ancestral bathymodiolin habitat almost certainly consisted of organic falls, including whale falls (Thubaut et al. 2013). However, the picture is no longer as simple as the single evolutionary step from wood/bone to vent/seep habitats postulated by Distel et al. (2000); instead, bathymodiolin mussels have invaded vent habitats independently in at least four lineages (Thubaut et al. 2013). These studies are consistent with organic falls, including whale falls, acting as a sort of biodiversity generator, providing evolutionary stepping stones for multiple lineages to new, environmentally challenging vent/seep habitats where adaptive radiations subsequently occurred.

There have been fewer follow-up phylogenetic studies to Baco et al. (1999) on vesicomyids at whale falls and other chemosynthetic habitats. The most comprehensive phylogenetic study (Decker et al. 2012) indicated that vesicomyids from whale falls do not form an obvious basal vesicomyid clade, meaning that there is no molecular evidence that whale falls functioned as evolutionary stepping stones to new deep-sea reducing habitats for these species, in contrast to the bathymodiolins. However, current molecular evidence does suggest a diversification of the main vesicomyid clades at ~30 Ma (Vrijenhoek 2013), i.e., coincident with the diversification of oceangoing whales, which is consistent with whale falls possibly having facilitated diversification by providing ecological stepping stones to isolated vent/seep habitats.

Van Dover et al. (2002) evaluated the biogeography of deep-sea vent/seep species and presented a phylogenetic tree of the annelid clade Siboglinidae. Owing to the basal position of seep-dwelling species, they hypothesized that "modern vestimentiferans diversified in cold seeps" (p. 1254) a view also supported by later phylogenetic analyses (Schulze & Halanych 2003). These established ideas were radically shaken by the description and first phylogenetic assessment of the bone-eating polychaete genus *Osedax*, which was considered to be a sister taxon to the vent/seep-dwelling vestimentiferans and the wood/seep-dwelling *Sclerolinum* clade, all of which were derived from the frenulate pogonophorans (Rouse et al. 2004). The addition of further *Osedax* species to multigene

phylogenetic analyses has gradually weakened the support for a vestimentiferan/*Sclerolinum* sister taxon relationship with *Osedax* (Glover et al. 2005b, Fujikura et al. 2006).

A large number of putative new *Osedax* species have since been informally described or discussed in the literature, in some cases with supporting data available at GenBank (Vrijenhoek et al. 2009). The inclusion of these new taxa and descriptions of further species (Rouse et al. 2008, Glover et al. 2013) have improved the resolution of relationships within the *Osedax* clade and now suggest that *Osedax* is the sister taxon to the frenulates rather than to the vestimentiferans (Glover et al. 2013). Evidence regarding the timing of the adaptive radiation of *Osedax* is still poor; based on a range of mitochondrial *COI* gene substitution rates, *Osedax* may have evolved at any time from the late Cretaceous to the late Eocene (Vrijenhoek et al. 2009). If *Osedax* evolved before the evolution of large whales, then this clade likely lived on the bones of other large carcass falls, such as those of plesiosaurs and large fish (Rouse et al. 2011). In any event, the global nature and high species diversity of *Osedax* suggest that whale falls have been important biodiversity generators in the siboglinid clade (**Figure 3*c***).

Among other annelids, dorvilleid polychaetes in the genus *Ophryotrocha* are abundant and diverse at whale falls (**Supplemental Table 3**) and are also well known from a range of organic- and sulfide-rich marine ecosystems. Whale-fall *Ophryotrocha* worms have been widely recorded, including at the isolated embayment of Deception Island, Antarctica (Taboada et al. 2013). Phylogenetic studies have shown that species occupying whale falls, wood falls, hydrothermal vents, and the sediments beneath fish farms are closely related; however, these species have probably invaded and radiated in these habitats on several occasions from shallow-water ancestors (Wiklund et al. 2009a, 2012). Species in the polychaete scale-worm family Polynoidae are also abundant and diverse at hydrothermal vents and whale falls, and clearly some species colonize both vent and whale-fall habitats (Glover et al. 2005a). Thus, whale-fall stepping stones may well have occurred for the polynoids over evolutionary time.

A final group of annelids targeted for phylogenetic study has been the hesionids. A species description and analysis suggested that a hesionid whale-fall species from Monterey Bay is closely related to the ice worms (*Sirsoe methanicola*) found at methane hydrates in the Gulf of Mexico (Pleijel et al. 2008). This is the first known evolutionary link between species living directly on methane hydrates and whale falls.

In addition to studies of bivalves and annelids, there has been a single phylogenetic study of two new bone-eating gastropod species in the new genus *Rubyspira* (Johnson et al. 2010). Work on these snails suggests that whale falls may also have helped to preserve lineages subject to extinction events in the late Cretaceous and early Cenozoic.

Supplemental Material

Figure 3

Hypothesized roles of whale-fall habitats in the evolution of mytilids, vesicomyids, and siboglinid annelids in the deep sea. (*a*) Under the evolutionary stepping-stone hypothesis, the stem-group habitat (①) comprises organic falls in the form of whale bones and sunken wood. The stem group then colonizes seep and/or vent habitats and subsequently undergoes adaptive radiations in all types of habitats (③). Current evidence suggests that this scenario likely applies to bathymodiolin mussels. (*b*) Under the ecological stepping-stone hypothesis, the stem-group habitat (①) is seeps or vents, and whale falls facilitate dispersal (②) to remote, unoccupied vent or seep habitats, where speciation subsequently can take place (③). Current evidence suggests that this scenario is plausible for vesicomyid clams. (*c*) Under the hot spots of adaptive radiation hypothesis, the stem-group habitat is seeps or vents (①), wherein radiations initially occur (②). After the evolution of whales with large bones, colonization and adaptive radiation within this new whale-fall habitat take place (③), resulting in high levels of speciation. Current evidence suggests that this is the most likely scenario for siboglinid annelids and possibly some clades of dorvilleid annelids. Photographs are from the National Oceanic and Atmospheric Administration (panels *a* and *b*) and A.G. Glover (panel *c*).
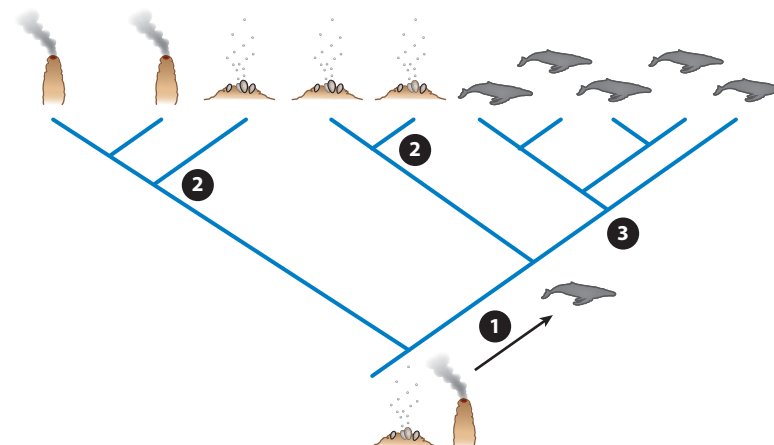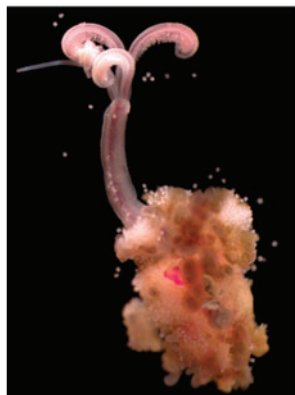
a Whale falls as evolutionary stepping stones

Sunken wood   Vent habitat

Whale bones   Seep habitat
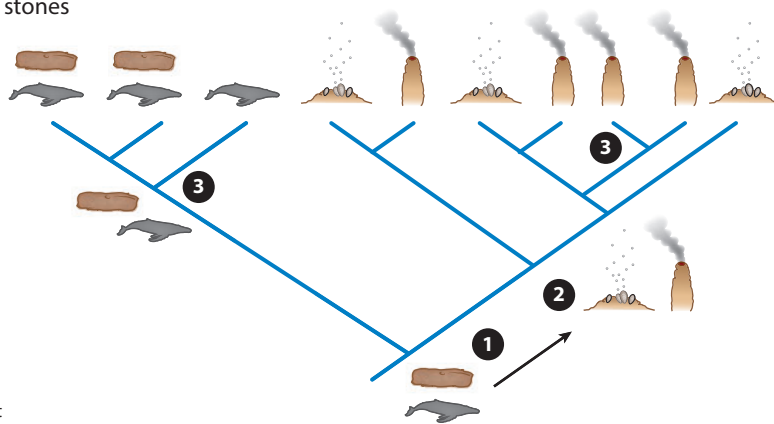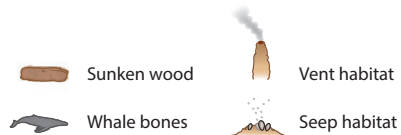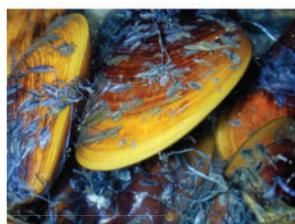
b Whale falls as ecological stepping stones
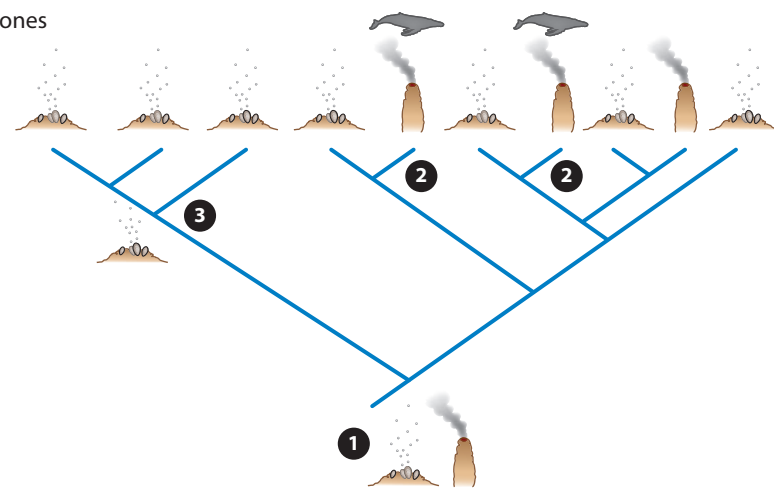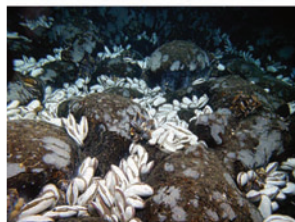
c Whale falls as hot spots of adaptive radiation

Overall, there is reasonable evidence for three potential evolutionary scenarios with regard to whale falls (see **Figure 3**). The evolutionary stepping-stone hypothesis (**Figure 3a**) is likely correct for the bathymodiolins, the ecological stepping-stone hypothesis (**Figure 3b**) is plausible for the vesicomyids, and the hot spots of adaptive radiation hypothesis (**Figure 3c**) is the most likely scenario for siboglinid annelids and possibly some clades of dorvilleid annelids.

Paleoecology of whale falls. The past decade has seen considerable progress in the study of ancient whale-fall communities and their relationships to the evolution of large whales. These advances have been facilitated by an increased understanding of the ability of ancient whale falls to support specialized seafloor communities, the discovery of numerous ancient whale-fall sites that provided much broader temporal and geographical coverage in the fossil record, and an increasing interest in the microbial component of fossil whale-fall ecosystems (Danise et al. 2012) (**Figure 1**, **Supplemental Table 1**).

The evolution of whales as sources of novel seafloor habitats. The first cetaceans, known as archaeocetes, probably evolved ~54 Ma (Uhen 2010), but it was not until the late middle Eocene (~37 Ma) that the first oceangoing cetaceans, the pelagiceti, appeared (Uhen 2008). Some of the first fully aquatic archaeocetes, such as *Basilosaurus*, had solid long bones and a dense skeleton adapted for shallow diving (Madar 1998, de Ricqlès & de Buffrénil 2001); because this skeletal ballast would have been burdensome for species living in deep water (Taylor 2000), *Basilosaurus* was likely restricted to shallow marine environments (de Buffrénil et al. 1990, Madar 1998). The skeletons of some larger Basilosaurinae archaeocetes exceeded 15 m (Gingerich 1998) and created reef-like habitats in shallow water for a diverse chondrichthyan fauna (Lancaster 1986, Underwood et al. 2011).

Only the basilaurid subfamily Dorudontinae shifted toward a pelagic, deep-diving lifestyle. The skeletons of these basilaurids exhibit a highly reduced bone density, achieved by increasing the proportion of cancellous (spongy) bone (Madar 1998, Gray et al. 2007). These structural adaptations greatly increased the volume of marrow in the bone, which could have increased the overall lipid content of the skeleton (Higgs et al. 2011b). There has been little consideration of the adaptive role of bone lipids in whales, but lipid-rich bone marrow seems to have provided both additional buoyancy and enhanced pressure resistance (Pond 1978), facilitating deep diving. It is difficult to know when the physiological shift toward lipid deposition in the skeleton took place, but clearly the structural precedent for lipid-rich skeletons had already evolved by the late Eocene (~37 Ma). The early pelagic dorudontids therefore probably provided the first abundant, lipid-rich skeletons at deepwater whale falls.

Most early cetaceans were relatively small in size (Lambert et al. 2010, Pyenson & Sponberg 2011), with dorudontids typically only 5 m in length (Gingerich 1998). There were some notable exceptions (Fordyce & Muizon 2001), including the early Oligocene (~34 Ma) mysticete *Llanocetus denticrenatus*, which reached 9 m (Fordyce 2003). The gigantism of modern mysticetes—and hence the ability to produce truly massive whale falls—appears to have evolved as a result of a shift to bulk filter feeding that began in the middle Oligocene (~31 Ma) (Fitzgerald 2006). By the late Miocene, mysticetes comparable in size to modern blue whales had evolved (Barnes et al. 1987).

Fossil whale-fall communities. Many elements of modern whale-fall communities are recognizable in the fossil record from the earliest sites (**Figures 1** and **4**, **Supplemental Table 1**). These include mobile scavengers such as sharks and whelks, which are associated with most fossil whale falls. The deposit-feeding nuculids and nuculanids commonly live at vent and seep habitats (Kiel
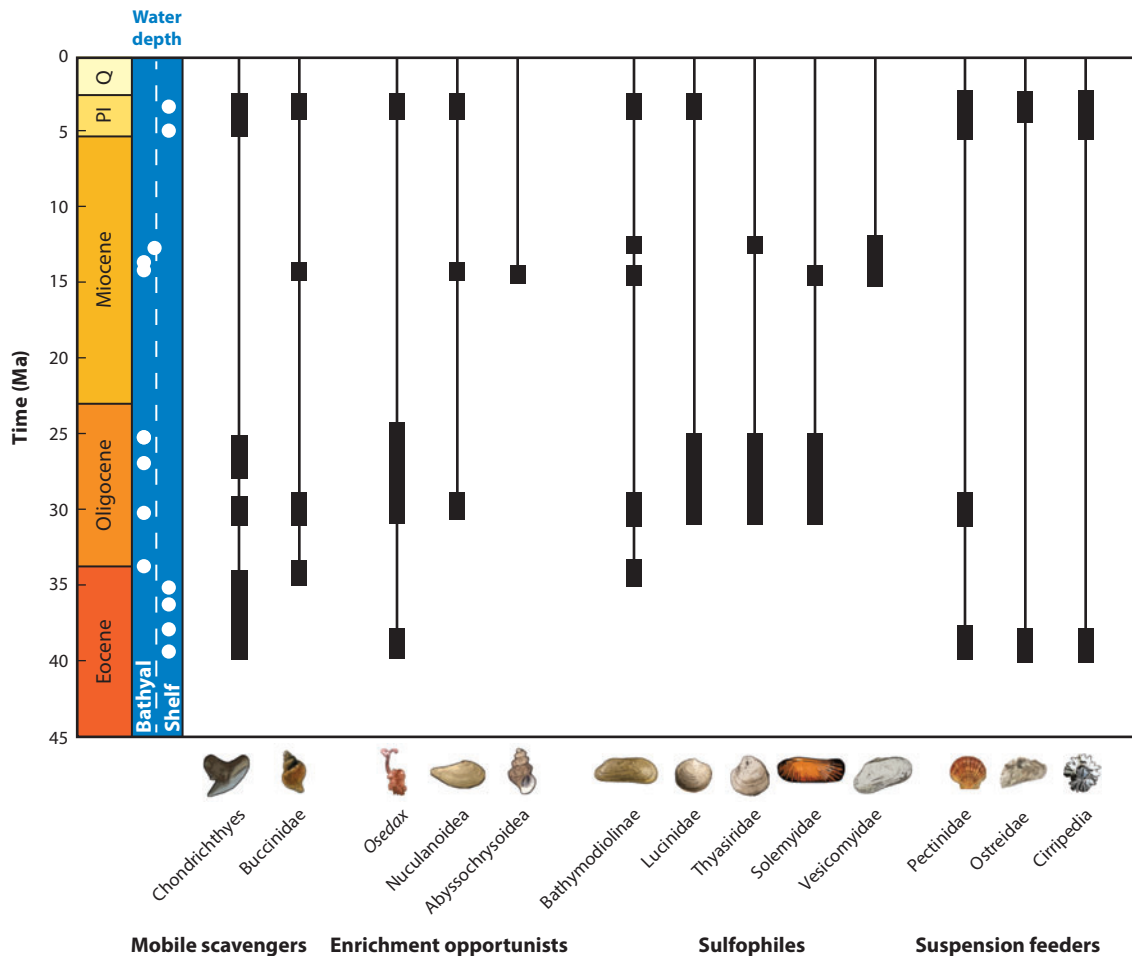
Figure 4

Whale-fall communities in the fossil record. The solid lines indicate the time ranges for selected whale-fall taxa, with the thicker bars indicating the ranges known from the fossils listed in **Supplemental Table 2**. The white dots in the blue bar indicate the approximate water depths of the marine habitats in which the fossil whale-fall communities lived (shelf is 0–200 m; bathyal is >200 m). Abbreviations: Pl, Pliocene; Q, Quaternary.

▶ Supplemental Material

2010) and are consistently found at fossil whale falls, where they were probably exploiting the enriched sediments. Bacterial grazers such as abyssochrysoid gastropods have been found on whale skeletons only from the Miocene and the present, but their association with a plesiosaurid skeleton from the Cretaceous (Kaim et al. 2008) suggests an earlier adaptation to large carcass falls. Traces of *Osedax* worms have been found in whale bones from the early Oligocene onward (Kiel et al. 2010, Higgs et al. 2012). Most bivalve taxa with chemolithoautotrophic symbionts found at modern deep-sea whale-fall communities are also found from the earliest Eocene-Oligocene whale falls onward, with the exception of the vesicomyids (first found on whale falls in the Miocene). The trophically diverse sulfophilic stage is also represented by a suite of predatory naticid and scaphopod mollusks from the earliest whale falls onward. Suspension feeders such as the pectinoids, potentially characteristic of the reef stage, have been consistently found at fossil whale

falls (both shallow and deep), where they probably took advantage of enhanced flow around the skeleton. Attached reef-stage organisms such as oysters and barnacles are also common in shallow whale-fall fossils.

The lack of vesicomyids at Eocene-Oligocene whale falls led to the suggestion that these whale carcasses were either too small or too lipid-poor to produce the sulfide levels required to support a sulfophilic stage (Kiel & Goedert 2006). Later finds of small carcasses (≤4 m) with vesicomyid bivalves (Amano et al. 2007, Pyenson & Haasl 2007) suggested that it was an increase in the lipid content of the skeletons, rather than body size per se, that led to the development of sulfophilic whale-fall communities (Kiel 2008). However, evidence of microbial sulfate reduction in Eocene whale bones indicates that even early whale skeletons held lipid reserves that generated hydrogen sulfide upon decomposition (Shapiro & Spangler 2009).

Evolutionary insights from the whale-fall fossil record. The record of chemolithoautotrophic symbiotic associations at fossil whale falls can help to elucidate the role of whale falls as ecological dispersal and evolutionary stepping stones for the vent/seep faunas (see above). Vesicomyid bivalves appeared in the fossil record at cold seeps in the Eocene-Oligocene before their first observation at whale falls in the Miocene, suggesting that whale falls did not provide evolutionary stepping stones for the initial colonization of seep habitats by vesicomyids (Amano & Kiel 2007). However, the small sample size and geographic distribution of the whale-fall fossil record make negative evidence weak. The major radiation of fossil vesicomyids in the Oligocene-Miocene (Amano & Little 2005, Amano & Kiel 2007, Vrijenhoek 2013) was synchronous with the evolution of large oceangoing whales with apparently lipid-rich bones, preventing rejection of whale falls serving as ecological stepping stones for generalized vesicomyids and thereby facilitating the widespread dispersal and subsequent speciation in vent/seep habitats. It is also noteworthy that approximately one-third (13/36) of all molluscan genera found at cold seeps appeared in the fossil record in the late Eocene and Oligocene in a burst of radiations synchronous with the appearance and diversification of oceangoing cetaceans (Kiel & Little 2006). This may also have been a time of accelerated methane seepage (Kiel 2009), yielding an increase in the overall availability of reducing habitats, with whale falls potentially facilitating dispersal to new seep regions. Molecular phylogenies of the bathymodiolin mussels do suggest that wood/whale-fall specialists are ancestral to seep lineages (Lorion et al. 2013, Thubaut et al. 2013); the appearances of bathymodiolins at whale/wood falls and at seeps are stratigraphically very close in the fossil record, suggesting a rapid colonization of seep habitats from organic substrates (Kiel & Amano 2013).

SUMMARY POINTS

1. Because of whales' enormous body sizes, efficient sinking, and high lipid content in both soft tissue and bones, whale falls are sites of intense and persistent organic and sulfide enrichment at the deep-sea floor.

2. The microbial degradation of whale-fall biomass in the deep sea is dominated by sulfate reduction and methanogenesis, which provide reduced chemical end-members (sulfide and methane) for chemosynthetic processes in free-living and endosymbiotic microorganisms.

3. Large, lipid-rich bones of adult whales provide the longest-lasting source of sulfide and methane as a consequence of gradual lipid degradation from the peripheries to the centers of the bones.

4. Whale-fall communities can pass through four stages of ecological succession, characterized respectively by mobile scavengers, enrichment opportunists, sulfophiles, and suspension feeders. The duration and overlap of these stages vary with carcass size, water depth, and other environmental parameters.

5. Extreme food limitation in deep-sea ecosystems has led to the development of a diverse and specialized deep-sea whale-fall fauna (including bone eaters and chemolithoautotrophic assemblages); whale falls in the relatively food-rich conditions of shallow water are exploited primarily by more generalized heterotrophic species. This pattern resembles the contrasts between deep- and shallow-water environments observed in vent and seep faunas.

6. All functional groups characteristic of modern whale-fall succession occur at fossil whale falls beginning ~30 Ma.

7. Molecular studies suggest that whale falls have served as hot spots of speciation and evolutionary novelty for a specialized fauna and may also have provided evolutionary and/or ecological stepping stones for vent/seep faunal lineages. The fossil record is consistent with these interpretations of molecular phylogeny.

FUTURE ISSUES

1. Whale-fall community colonization and succession remain poorly evaluated in modern shallow-water habitats, the Arctic Ocean, and the vast abyssal regions constituting most of the ocean floor. Studies of natural and experimental whale-fall communities are sorely needed in these areas.

2. The effects of ecosystem engineers, in particular bone-eating *Osedax* annelids, on microbial colonization and metabolism as well as on faunal succession at whale falls are poorly understood. Controlled whale-bone implantation experiments are needed to explore how the abundance and diversity of bone-eating *Osedax* species interact with whale-bone size and lipid content to control the nature and rates of microbial processes and the patterns of metazoan community succession, biodiversity, and ecosystem function.

3. Our understanding of the paleo-biogeography of whale-fall communities is still sample limited. Studies of fossil whale-fall assemblages across many more regions and depth facies will provide important insights into whale-fall community ecology and evolution in ancient oceans.

4. The biogeography and connectivity of modern whale-fall communities also remain poorly understood because of the paucity of data from many ocean depths (especially abyssal and hadal depths) and from some ocean basins and regions (especially central gyres). Studies with controlled seafloor implantations of whale bones across multiple depths and regions could rapidly advance our understanding of the connectivity, evolutionary novelty, and biogeography of whale-fall biota throughout the world ocean.

DISCLOSURE STATEMENT

ACKNOWLEDGMENTS

LITERATURE CITED

Allison PA, Smith CR, Kukert H, Deming JW, Bennett BA. 1991. Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the bathyal Santa Catalina Basin. *Paleobiology* 17:78–89

Amano K, Kiel S. 2007. Fossil vesicomyid bivalves from the North Pacific region. *Veliger* 49:270–93

Amano K, Little CTS. 2005. Miocene whale-fall community from Hokkaido, northern Japan. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 215:345–56

Amano K, Little CTS, Inoue K. 2007. A new Miocene whale-fall community from Japan. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 247:236–42

Amon DJ, Glover AG, Wiklund H, Marsh L, Linse K, et al. 2013. The discovery of a natural whale fall in the Antarctic deep sea. *Deep-Sea Res. II* 92:87–96

Amon DJ, Wiklund H, Dahlgren TG, Copley JT, Smith CR, et al. 2014. Molecular taxonomy of *Osedax* (Annelida: Siboglinidae) in the Southern Ocean. *Zool. Scr.* 43:405–17

Baco AR, Smith CR, Peek AS, Roderick GK, Vrijenhoek RC. 1999. The phylogenetic relationships of whale-fall vesicomyid clams based on mitochondrial COI DNA sequences. *Mar. Ecol. Prog. Ser.* 182:137–47

Baco-Taylor AR. 2002. *Food-web structure, succession and phylogenetics on deep-sea whale skeletons*. PhD Thesis, Univ. Hawaii, Honolulu

Barnes LG, Raschke RE, Brown JE. 1987. A fossil baleen whale. *Whalewatcher* 21:7–10

Beal EJ, House CH, Orphan VJ. 2009. Manganese- and iron-dependent marine methane oxidation. *Science* 325:184–87

Boetius A, Ravenschlag K, Schubert CJ, Rickert D, Widdel F, et al. 2000. A marine microbial consortium apparently mediating anaerobic oxidation of methane. *Nature* 407:623–26

Bolotin J, Hrs-Brenko M, Tutman P, Glavić N, Kožul V, et al. 2005. First record of *Idas simpsoni* (Mollusca: Bivalvia: Mytilidae) in the Adriatic Sea. *J. Mar. Biol. Assoc. UK* 85:977–78

Bottcher ME, Thamdrup B. 2001. Anaerobic sulfide oxidation and stable isotope fractionation associated with bacterial sulfur disproportionation in the presence of MnO_2. *Geochim. Cosmochim. Acta* 65:1573–81

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 Res. I* 54:1773–91

Britton JC, Morton B. 1994. Marine carrion and scavengers. *Oceanogr. Mar. Biol. Annu. Rev.* 32:369–434

Bush GL. 1975. Modes of animal speciation. *Annu. Rev. Ecol. Syst.* 6:339–64

Butman CA, Carlton JT, Palumbi SR. 1995. Whaling effects on deep-sea biodiversity. *Conserv. Biol.* 9:462–64

Carney RS. 2005. Zonation of deep-biota on continental margins. *Oceanogr. Mar. Biol. Annu. Rev.* 43:211–78

Corliss JB, Dymond J, Gordon LI, Edmond JM, von Herzen RP, et al. 1979. Submarine thermal springs on the Galapagos Rift. *Science* 203:1073–83

Dahlgren TG, Glover AG, Baco A, Smith CR. 2004. Fauna of whale falls: systematics and ecology of a new polychaete (Annelida: Chrysopetalidae) from the deep Pacific Ocean. *Deep-Sea Res. I* 51:1873–87

Dahlgren TG, Wiklund H, Kallstrom B, Lundalv T, Smith CR, Glover AG. 2006. A shallow-water whale-fall experiment in the north Atlantic. *Cah. Biol. Mar.* 47:385–89

Dando PR, Dixon DR, Southward AJ, Southward EC, Crawford A, Crawford M. 1992. Shipwrecked tube-worms. *Nature* 356:667

Danise S, Cavalazzi B, Dominici S, Westall F, Monechi S, Guioli S. 2012. Evidence of microbial activity from a shallow water whale fall (Voghera, northern Italy). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 317:13–26

Danise S, Dominici S. 2014. A record of fossil shallow-water whale falls from Italy. *Lethaia* 47:229–43

de Buffrénil V, de Ricqlès A, Ray C, Domning D. 1990. Bone histology of the ribs of the Archaeocetes (Mammalia: Cetacea). *J. Vertebr. Paleontol.* 10:455–66

de Ricqlès A, de Buffrénil V. 2001. Bone histology, heterochronies and the return of tetrapods to life in water: Where are we? In *Secondary Adaptation of Tetrapods to Life in Water*, ed. JM Mazin, V de Buffrénil, pp. 289–310. Munich: Friedrich Pfeil

Decker C, Olu K, Cunha RL, Arnaud-Haond S. 2012. Phylogeny and diversification patterns among vesi-comyid bivalves. *PLoS ONE* 7:e33359

Dell RK. 1987. Mollusca of the family Mytilidae (Bivalvia) associated with organic remains from deep water off New Zealand, with revisions of the genera *Adipicola* Dautzenborg, 1927 and *Idasola* Iredale, 1915. *Natl. Mus. N. Z. Rec.* 3:17–36

Dell RK. 1995. New species and records of deep-water mollusca from off New Zealand. *Tuhinga* 2:1–26

Deming J, Reysenbach AL, Macko SA, Smith CR. 1997. The microbial diversity at a whale fall on the seafloor: bone-colonizing mats and animal-associated symbionts. *Microsc. Res. Tech.* 37:162–70

Distel DL, Baco AR, Chuang E, Morrill W, Cavanaugh C, Smith CR. 2000. Marine ecology: Do mussels take wooden steps to deep-sea vents? *Nature* 403:725–26

Dominici S, Cioppi E, Danise S, Betocchi U, Gallai G, et al. 2009. Mediterranean fossil whale falls and the adaptation of mollusks to extreme habitats. *Geology* 37:815–18

Dubilier N, Bergin C, Lott C. 2008. Symbiotic diversity in marine animals: the art of harnessing chemosyn-thesis. *Nat. Rev. Microbiol.* 6:725–40

Ettwig KF, Butler MK, Le Paslier D, Pelletier E, Mangenot S, et al. 2010. Nitrite-driven anaerobic methane oxidation by oxygenic bacteria. *Nature* 464:544–50

Feldman RA, Shank TM, Black MB, Baco AR, Smith CR, Vrijenhoek RC. 1998. Vestimentiferan on a whale fall. *Biol. Bull.* 194:116–19

Fitzgerald E. 2006. A bizarre new toothed mysticete (Cetacea) from Australia and the early evolution of baleen whales. *Proc. R. Soc. B* 273:2955–63

Fordyce RE. 2003. Early crown-group Cetacea in the Southern Ocean: the toothed archaic mysticete *Llanoce-tus. J. Vertebr. Paleontol.* 23(Suppl. 3):50A

Fordyce RE, Muizon CD. 2001. Evolutionary history of cetaceans: a review. In *Secondary Adaptation of Tetrapods to Life in Water*, ed. JM Mazin, V de Buffrénil, pp. 169–233. Munich: Friedrich Pfeil

Fujikura K, Fujiwara Y, Kawato M. 2006. A new species of *Osedax* (Annelida: Siboglinidae) associated with whale carcasses off Kyushu, Japan. *Zool. Sci.* 23:733–40

Fujioka K, Wada H, Okano H. 1993. Torishima whale deep-sea animal community assemblage—new finding by "Shinkai 6500." *J. Geogr.* 102:507–17

Fujiwara Y, Kawato M, Noda C, Kinoshita G, Yamanaka T, et al. 2010. Extracellular and mixotrophic symbiosis in the whale-fall mussel *Adipicola pacifica*: a trend in evolution from extra- to intracellular symbiosis. *PLoS ONE* 5:e11808

Fujiwara Y, Kawato M, Yamamoto T, Yamanaka T, Sato-Okoshi W, et al. 2007. Three-year investigations into sperm whale-fall ecosystems in Japan. *Mar. Ecol.* 28:219–32

Gibbs PE. 1987. A new species of *Phascolosoma* (Sipuncula) associated with a decaying whale's skull trawled at 880 m depth in the South-west Pacific. *N.Z. J. Zool.* 14:135–37

Gingerich P. 1998. Paleobiological perspectives on Mesonychia, Archaeoceti and the origin of whales. In *The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea*, ed. JGM Thewissen, pp. 423–64. New York: Plenum

Girguis PR, Cozen AE, Delong EF. 2005. Growth and population dynamics of anaerobic methane-oxidizing archaea and sulfate-reducing bacteria in a continuous-flow bioreactor. *Appl. Environ. Microbiol.* 71:3725–33

Glover AG, Goetze E, Dahlgren TG, Smith CR. 2005a. Morphology, reproductive biology and genetic structure of the whale-fall and hydrothermal-vent specialist, *Bathykurila guaymasensis* Pettibone, 1989 (Annelida: Polynoidae). *Mar. Ecol.* 26:223–34

Glover AG, Kallstrom B, Smith CR, Dahlgren TG. 2005b. World-wide whale worms? A new species of *Osedax* from the shallow north Atlantic. *Proc. R. Soc. B* 272:2587–92

Glover AG, Kemp KM, Smith CR, Dahlgren TG. 2008. On the role of bone-eating worms in the degradation of marine vertebrate remains. *Proc. R. Soc. B* 275:1959–61

Glover AG, Wiklund H, Taboada S, Avila C, Cristobo J, et al. 2013. Bone-eating worms from the Antarctic: the contrasting fate of whale and wood remains on the Southern Ocean seafloor. *Proc. R. Soc. B* 280:20131390

Goedert JL, Squires RL, Barnes LG. 1995. Paleoecology of whale-fall habitats from deep-water Oligocene rocks, Olympic Peninsula, Washington State. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 118:151–58

Goffredi SK, Johnson SB, Vrijenhoek RC. 2007. Genetic diversity and potential function of microbial symbionts associated with newly-discovered species of *Osedax* polychaete worms. *Appl. Environ. Microbiol.* 73:2314–23

Goffredi SK, Orphan VJ. 2010. Bacterial community shifts in taxa and diversity in response to localized organic loading in the deep sea. *Environ. Microbiol.* 12:344–63

Goffredi SK, Orphan VJ, Rouse GW, Jahnke L, Embaye T, et al. 2005. Evolutionary innovation: a bone-eating marine symbiosis. *Environ. Microbiol.* 7:1369–78

Goffredi SK, Paull CK, Fulton-Bennett K, Hurtado LA, Vrijenhoek RC. 2004. Unusual benthic fauna associated with a whale fall in Monterey Canyon, California. *Deep-Sea Res. I* 51:1295–306

Goffredi SK, Wilpiszeski R, Lee R, Orphan V. 2008. Temporal evolution of methane cycling and phylogenetic diversity of archaea in sediments from a deep-sea whale-fall in Monterey Canyon, California. *ISME J.* 2:204–20

Gray N-M, Kainec K, Madar S, Tomko L, Wolfe S. 2007. Sink or swim? Bone density as a mechanism for buoyancy control in early cetaceans. *Anat. Rec.* 290:638–53

Gulland FMD, Pérez-Cortés MH, Urbán RJ, Rojas-Bracho L, Ylitalo G, et al. 2005. *Eastern North Pacific gray whale (Eschrichtius robustus) unusual mortality event, 1999–2000.* NOAA Tech. Memo. NMFS-AFSC-150, Alaska Fish. Sci. Cent., Natl. Oceanogr. Atmos. Adm., Seattle, WA

Hachiya K. 1992. A unique community in the reduced environment found from the Morozaki Group. *Kaseki no Tomo* 39:37–41

Hanson RS, Hanson TE. 1996. Methanotrophic bacteria. *Microbiol. Rev.* 60:439–71

Hecker B. 1985. Fauna from a cold sulfur-seep in the Gulf of Mexico: comparison with hydrothermal vent communities and evolutionary implications. *Bull. Biol. Soc. Wash.* 6:465–73

Heezen BC, Hollister CD. 1971. *The Face of the Deep*. Oxford, UK: Oxford Univ. Press

Higgs ND, Gates A, Jones DOB. 2014a. Fish food in the deep sea: revisiting the role of large food-falls. *PLoS ONE* 9:e96016

Higgs ND, Glover AG, Dahlgren TG, Little CTS. 2010. Using computed-tomography to document borings by *Osedax mucofloris* in whale bone. *Cah. Biol. Mar.* 51:401–5

Higgs ND, Glover AG, Dahlgren TG, Little CTS. 2011a. Bone-boring worms: characterizing the morphology, rate, and method of bioerosion by *Osedax mucofloris* (Annelida, Siboglinidae). *Biol. Bull.* 221:307–16

Higgs ND, Glover AG, Dahlgren TG, Smith CR, Fujiwara Y, et al. 2014b. The morphological diversity of *Osedax* worm borings (Annelida: Siboglinidae). *J. Mar. Biol. Assoc. UK* 94:1429–39

Higgs ND, Little CTS, Glover AG. 2011b. Bones as biofuel: a review of whale bone composition with implications for deep-sea biology and palaeoanthropology. *Proc. R. Soc. B* 278:9–17

Higgs ND, Little CTS, Glover AG, Dahlgren TG, Smith CR, Dominici S. 2012. Evidence of *Osedax* worm borings in Pliocene (~3 Ma) whale bone from the Mediterranean. *Hist. Biol.* 24:269–77

Johnson SB, Waren A, Lee R, Yano Y, Kaim A, et al. 2010. *Rubyspira*, new genus and two new species of bone-eating deep-sea snails with ancient habitats. *Biol. Bull.* 219:166–77

Jones WJ, Johnson SB, Rouse GW, Vrijenhoek RC. 2008. Marine worms (genus *Osedax*) colonize cow bones. *Proc. R. Soc. B* 275:387–91

Jørgensen BB, Nelson DC. 2004. Sulfide oxidation in marine sediments: Geochemistry meets microbiology. *Geol. Soc. Am. Spec. Pap.* 379:63–81

Kaim A, Kobayashi Y, Echizenya H, Jenkins RG, Tanabe K. 2008. Chemosynthesis-based associations on Cretaceous plesiosaurid carcasses. *Acta Palaeontol. Pol.* 53:97–104

Katz S, Klepal W, Bright M. 2010. The skin of *Osedax* (Siboglinidae, Annelida): an ultrastructural investigation of its epidermis. *J. Morphol.* 271:1272–80

Katz S, Klepal W, Bright M. 2011. The *Osedax* trophosome: organization and ultrastructure. *Biol. Bull.* 220:128–39

Kiel S. 2008. Fossil evidence for micro- and macrofaunal utilization of large nekton falls: examples from early Cenozoic deep-water sediments in Washington State, USA. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 267:161–74

Kiel S. 2009. Global hydrocarbon seep-carbonate precipitation correlates with deep-water temperatures and eustatic sea-level fluctuations since the Late Jurassic. *Terra Nova* 21:279–84

Kiel S. 2010. The fossil record of vent and seep molluscs. In *The Vent and Seep Biota: Aspects from Microbes to Ecosystems*, ed. S Kiel, pp. 255–78. New York: Springer

Kiel S, Amano K. 2013. The earliest bathymodiolin mussels: an evaluation of Eocene and Oligocene taxa from deep-sea methane seep deposits in Western Washington State, USA. *J. Paleontol.* 87:589–602

Kiel S, Goedert JL. 2006. Deep-sea food bonanzas: early Cenozoic whale-fall communities resemble wood-fall rather than seep communities. *Proc. R. Soc. B* 273:2625–31

Kiel S, Goedert JL, Kahl WA, Rouse GW. 2010. Fossil traces of the bone-eating worm *Osedax* in early Oligocene whale bones. *Proc. Natl. Acad. Sci. USA* 107:8656–59

Kiel S, Kahl WA, Goedert JL. 2011. *Osedax* borings in fossil marine bird bones. *Naturwissenschaften* 98:51–55

Kiel S, Little CTS. 2006. Cold-seep mollusks are older than the general marine mollusk fauna. *Science* 313:1429–31

King NJ, Bailey DM, Priede IG, Browman HI. 2007. Role of scavengers in marine ecosystems. *Mar. Ecol. Prog. Ser.* 350:175–78

Krogh A. 1934. Conditions of life at great depths in the ocean. *Ecol. Monogr.* 4:430–39

Lambert O, Bianucci G, Post K, de Muizon C, Salas-Gismondi R, et al. 2010. The giant bite of a new raptorial sperm whale from the Miocene epoch of Peru. *Nature* 466:105–8

Lancaster WC. 1986. The taphonomy of an archaeocete skeleton and its associated fauna. In *Montgomery Landing Site, Marine Eocene (Jackson) of Central Louisiana*, ed. JA Schiebout, W van den Bold, pp. 119–31. Austin, TX: Gulf Coast Assoc. Geol. Soc.

Lockyer C. 1976. Body weights of some species of large whales. *J. Cons. Int. Explor. Mer* 36:259–73

Lorion J, Buge B, Cruaud C, Samadi S. 2010. New insights into diversity and evolution of deep-sea Mytilidae (Mollusca: Bivalvia). *Mol. Phylogenet. Evol.* 57:71–83

Lorion J, Duperron S, Gros O, Cruaud C, Samadi S. 2009. Several deep-sea mussels and their associated symbionts are able to live both on wood and on whale falls. *Proc. R. Soc. B* 276:177–85

Lorion J, Halary S, Nascimento J, Samadi S, Couloux A, Duperron S. 2012. Evolutionary history of *Idas* sp. Med (Bivalvia: Mytilidae), a cold seep mussel bearing multiple symbionts. *Cah. Biol. Mar.* 53:77–87

Lorion J, Kiel S, Faure B, Kawato M, Ho SYW, et al. 2013. Adaptive radiation of chemosymbiotic deep-sea mussels. *Proc. R. Soc. B* 280:20131243

Lundsten L, Paull CK, Schlining KL, McGann M, Ussler W III. 2010a. Biological characterization of a whale fall near Vancouver Island, British Columbia, Canada. *Deep-Sea Res. I* 57:918–22

Lundsten L, Schlining KL, Frasier K, Johnson SB, Kuhnz LA, et al. 2010b. Time-series analysis of six whale-fall communities in Monterey Canyon, California, USA. *Deep-Sea Res. I* 57:1573–84

Madar S. 1998. Structural adaptations of early Archaeocete long bones. In *The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea*, ed. JGM Thewissen, pp. 353–78. New York: Plenum

McLean JH. 1992. Cocculiniform limpets (Cocculinidae and Pyropeltidae) living on whale bone in the deep sea off California. *J. Molluscan Stud.* 58:401–14

Milessi AC, Sellanes J, Gallardo VA, Lange CB. 2005. Osseous skeletal material and fish scales in marine sediments under the oxygen minimum zone off northern and central Chile. *Estuar. Coast. Shelf Sci.* 64:185–90

Miyamoto N, Yamamoto T, Yusa Y, Fujiwara Y. 2013. Postembryonic development of the bone-eating worm *Osedax japonicus*. *Naturwissenschaften* 100:285–89

Miyazaki JI, Martins LO, Fujita Y, Matsumoto H, Fujiwara Y. 2010. Evolutionary process of deep-sea *Bathymodiolus* mussels. *PLoS ONE* 5:e10363

Naganuma T, Wada H, Fujioka K. 1996. Biological community and sediment fatty acids associated with the deep-sea whale skeleton at the Torishima seamount. *J. Oceanogr.* 52:1–15

Nauhaus K, Albrecht M, Elvert M, Boetius A, Widdel F. 2007. In vitro cell growth of marine archaeal-bacterial consortia during anaerobic oxidation of methane with sulfate. *Environ. Microbiol.* 9:187–96

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 Sci. J.* 44:181–88

Pedrós-Alió C. 2012. The rare bacterial biosphere. *Annu. Rev. Mar. Sci.* 4:449–66

Pelorce J, Poutiers JM. 2009. Une nouvelle espèce de Bathymodiolinae (Mollusca, Bivalvia, Mytilidae) associée à des os de baleine coulés en Méditerranée. *Zoosystema* 31:975–85

Pershing AJ, Christensen LB, Record NR, Sherwood GD, Stetson PB, Humphries S. 2010. The impact of whaling on the ocean carbon cycle: Why bigger was better. *PLoS ONE* 5:e12444

Pleijel F, Rouse GW, Ruta C, Wiklund H, Nygren A. 2008. *Vrijenhoekia balaenophila*, a new hesionid polychaete from a whale fall off California. *Zool. J. Linn. Soc.* 152:625–34

Pond C. 1978. Morphological aspects and the ecological and mechanical consequences of fat deposition in wild vertebrates. *Annu. Rev. Ecol. Syst.* 9:519–70

Puig P, Palanques A, Martín J. 2014. Contemporary sediment-transport processes in submarine canyons. *Annu. Rev. Mar. Sci.* 6:53–77

Pyenson ND, Haasl DM. 2007. Miocene whale fall from California demonstrates that cetacean size did not determine the evolution of modern whale-fall communities. *Biol. Lett.* 3:709–11

Pyenson ND, Sponberg SN. 2011. Reconstructing body size in extinct crown Cetacea (Neoceti) using allometry, phylogenetic methods and tests from the fossil record. *J. Mamm. Evol.* 18:269–88

Reisdorf AG, Bux R, Wyler D, Benecke M, Klug C, et al. 2012. Float, explode or sink: postmortem fate of lung-breathing marine vertebrates. *Palaeobiodivers. Palaeoenviron.* 92:67–81

Roman J, Estes JA, Morissette L, Smith CR, Costa D, et al. 2014. Whales as marine ecosystem engineers. *Front. Ecol. Environ.* 12:377–85

Rouse GW, Goffredi SK, Johnson SB, Vrijenhoek RC. 2011. Not whale-fall specialists, *Osedax* worms also consume fishbones. *Biol. Lett.* 7:736–39

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

Rouse GW, Wilson NG, Goffredi SK, Johnson SB, Smart T, et al. 2009. Spawning and development in *Osedax* boneworms (Siboglinidae, Annelida). *Mar. Biol.* 156:395–405

Rouse GW, Worsaae K, Johnson SB, Jones WJ, Vrijenhoek RC. 2008. Acquisition of dwarf male "harems" by recently settled females of *Osedax roseus* n. sp. (Siboglinidae; Annelida). *Biol. Bull.* 214:67–82

Rowe GT, Wei C, Nunnally C, Haedrich R, Montagna P, et al. 2008. Comparative biomass structure and estimated carbon flow in food webs in the deep Gulf of Mexico. *Deep-Sea Res. II* 55:2699–711

Samadi S, Quemere E, Lorion J, Tillier A, Von Cosel R, et al. 2007. Molecular phylogeny in mytilids supports the wooden steps to deep-sea vents hypothesis. *C. R. Biol.* 330:446–56

Schander C, Rapp HT, Dahlgren TG. 2010. *Osedax mucofloris* (Polychaeta, Siboglinidae), a bone-eating marine worm new to Norway. *Fauna Nor.* 30:5–8

Schuller D, Kadko D, Smith CR. 2004. Use of ^{210}Pb/^{226}Ra disequilibria in the dating of deep-sea whale falls. *Earth Planet. Sci. Lett.* 218:277–89

Schulze A, Halanych KM. 2003. Siboglinid evolution shaped by habitat preference and sulfide tolerance. *Hydrobiologia* 496:199–205

Shapiro RS, Spangler E. 2009. Bacterial fossil record in whale falls: petrographic evidence of microbial sulfate reduction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 274:196–203

Smith CR. 1992. Whale falls: chemosynthesis on the deep seafloor. *Oceanus* 35:74–78

Smith CR. 2006. Bigger is better: the role of whales as detritus in marine ecosystems. In *Whales, Whaling and Ocean Ecosystems*, ed. JA Estes, P DeMaster, DF Doak, TM Williams, RL Brownell Jr, pp. 286–300. Berkeley: Univ. Calif. Press

Smith CR, Baco AR. 2003. Ecology of whale falls at the deep-sea floor. *Oceanogr. Mar. Biol. Annu. Rev.* 41:311–54

Smith CR, Baco AR, Glover AG. 2002. Faunal succession on replicate deep-sea whale falls: time scales and vent-seep affinities. *Cah. Biol. Mar.* 39:345–46

Smith CR, Bernardino AF, Baco A, Hannides AK, Altamira I. 2014. The seven-year enrichment: macrofaunal succession in deep-sea sediments around a 30-tonne whale fall in the Northeast Pacific. *Mar. Ecol. Prog. Ser.* In press. doi: 10.3354/meps10955

Smith CR, de Leo F, Bernardino AF, Sweetman AK, Arbizu PM. 2008. Abyssal food limitation, ecosystem structure and climate change. *Trends Ecol. Evol.* 23:518–28

Smith CR, Demopoulos AWJ. 2003. The deep Pacific Ocean floor. In *Ecosystems of the World*, ed. PA Tyler, pp. 181–220. Amsterdam: Elsevier

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

Smith KE, Thatje S, Singh H, Amsler MO, Vos SC, et al. 2014. Discovery of a recent, natural whale fall on the continental slope off Anvers Island, western Antarctic Peninsula. *Deep-Sea Res. I* 90:76–80

Sogin ML, Morrison G, Huber J, Welch D, Huse S, et al. 2006. Microbial diversity in the deep sea and the underexplored "rare biosphere." *Proc. Natl. Acad. Sci. USA* 103:12115–20

Squires RL. 1991. Whale carcasses. *Nature* 349:574

Taboada S, Wiklund H, Glover A, Dahlgren T, Cristobo J, Avila C. 2013. Two new Antarctic *Ophryotrocha* (Annelida: Dorvilleidae) described from shallow-water whale bones. *Polar Biol.* 36:1031–45

Tarasov VG, Gebruk A, Mironov AN, Moskalev LI. 2005. Deep-sea and shallow-water hydrothermal vent communities: two different phenomena? *Chem. Geol.* 224:5–39

Taylor MA. 2000. Functional significance of bone ballastin in the evolution of buoyancy control strategies by aquatic tetrapods. *Hist. Biol.* 14:15–31

Thamdrup B, Finster K, Hansen JW, Bak F. 1993. Bacterial disproportionation of elemental sulfur coupled to chemical reduction of iron and manganese. *Appl. Environ. Microbiol.* 59:101–8

Thiel V, Blumenberg M, Kiel S, Leefmann T, Liebenau K, et al. 2014. Occurrence and fate of fatty acyl biomarkers in an ancient whale bone (Oligocene, El Cien Formation, Mexico). *Org. Geochem.* 68:71–81

Thubaut J, Puillandre N, Faure B, Cruaud C, Samadi S. 2013. The contrasted evolutionary fates of deep sea chemosynthetic mussels (Bivalvia, Bathymodiolinae). *Ecol. Evol.* 3:4748–66

Tresguerres M, Katz S, Rouse GW. 2013. How to get into bones: proton pump and carbonic anhydrase in *Osedax* boneworms. *Proc. R. Soc. B* 280:20130625

Treude T, Smith CR, Wenzhàfer F, Carney E, Bernardino AF, et al. 2009. Biogeochemistry of a deep-sea whale fall: sulfate reduction, sulfide efflux and methanogenesis. *Mar. Ecol. Prog. Ser.* 382:1–21

Tringe SG, von Mering C, Kobayashi A, Salamov AA, Chen K, et al. 2005. Comparative metagenomics of microbial communities. *Science* 308:554–57

Uhen MD. 2008. New protocetid whales from Alabama and Mississippi, and a new cetacean clade, Pelagiceti. *J. Vertebr. Paleontol.* 28:589–93

Uhen MD. 2010. The origin(s) of whales. *Annu. Rev. Earth Planet. Sci.* 38:189–219

Underwood CJ, Ward DJ, King C, Antar SM, Zalmout IS, Gingerich PD. 2011. Shark and ray faunas in the Middle and Late Eocene of the Fayum Area, Egypt. *Proc. Geol. Assoc.* 122:47–66

Van Dover CL. 2000. *The Ecology of Deep-Sea Hydrothermal Vents*. Princeton, NJ: Princeton Univ. Press

Van Dover CL, German CR, Speer KG, Parson LM, Vrijenhoek RC. 2002. Evolution and biogeography of deep-sea vent and seep invertebrates. *Science* 295:1253–57

Verna C, Ramette A, Wiklund H, Dahlgren TG, Glover AG, et al. 2010. High symbiont diversity in the bone-eating worm *Osedax mucofloris* from shallow whale falls in the North Atlantic. *Environ. Microbiol.* 12:2355–70

Vrijenhoek RC. 2013. On the instability and evolutionary age of deep-sea chemosynthetic communities. *Deep-Sea Res. II* 92:189–200

Vrijenhoek RC, Collins P, Van Dover CL. 2008. Bone-eating marine worms: habitat specialists or generalists? *Proc. R. Soc. B* 275:1963–64

Vrijenhoek RC, Johnson SB, Rouse GW. 2009. A remarkable diversity of bone-eating worms (*Osedax*; Siboglinidae; Annelida). *BMC Biol.* 7:74

Wada H, Naganuma T, Fujioka K, Ditazato H, Kawamura K, Akazawa Y. 1994. The discovery of the Tor-ishima whale bone animal community and its meaning: the results of revisit dives by the "Shinkai 6500." *JAMSTEC Deep-Sea Res.* 10:38–47

Waren A. 1996. New and little known Mollusca from Iceland and Scandinavia. Part 3. *Sarsia* 81:197–245

Wiklund H, Altamira I, Glover AG, Smith CR, Baco A, Dahlgren TG. 2012. Systematics and biodiversity of *Ophryotrocha* (Annelida, Dorvilleidae) with descriptions of six new species from deep-sea whale-fall and wood-fall habitats in the north-east Pacific. *Syst. Biodivers.* 2012:243–59

Wiklund H, Glover AG, Dahlgren TG. 2009a. Three new species of *Ophryotrocha* (Annelida: Dorvilleidae) from a whale fall in the Northeast Atlantic. *Zootaxa* 2228:43–56

Wiklund H, Glover AG, Johannessen PJ, Dahlgren TG. 2009b. Cryptic speciation at organic-rich marine habitats: a new bacteriovore annelid from whale-fall and fish farms in the North-East Atlantic. *Zool. J. Linn. Soc.* 155:774–85

Woodward SP. 1854. *A Manual of the Mollusca; or, Rudimentary Treatise on Recent and Fossil Shells*. London: Weale

Contents

Errata

An online log of corrections to *Annual Review of Marine Science* articles may be found
at http://www.annualreviews.org/errata/marine