ECOLOGY OF WHALE FALLS AT THE DEEP-SEA FLOOR

CRAIG R. SMITH[1] & AMY R. BACO[1,2]

[1]*Department of Oceanography, University of Hawaii at Manoa, 1000 Pope Road, Honolulu, HI, 96822, USA*
e-mail: csmith@soest.hawaii.edu
[2]*present address: Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA*
e-mail: abaco@whoi.edu

Abstract   The falls of large whales (30–160 t adult body weight) yield massive pulses of labile organic matter to the deep-sea floor. While scientists have long speculated on the ecological roles of such concentrated food inputs, observations have accumulated since the 1850s to suggest that deep-sea whale falls support a widespread, characteristic fauna. Interest in whale-fall ecology heightened with the discovery in 1989 of a chemoautotrophic assemblage on a whale skeleton in the northeast Pacific; related communities were soon reported from whale falls in other bathyal and abyssal Pacific and Atlantic sites, and from 30 mya (million years ago) in the northeast Pacific fossil record. Recent time-series studies of natural and implanted deep-sea whale falls off California, USA indicate that bathyal carcasses pass through at least three successional stages:

(1)   a *mobile-scavenger stage* lasting months to years, during which aggregations of sleeper sharks, hagfish, rat-tails and invertebrate scavengers remove whale soft tissue at high rates (40–60 kg d^{-1});
(2)   an *enrichment opportunist stage* (duration of months to years) during which organically enriched sediments and exposed bones are colonised by dense assemblages (up to 40 000 m^{-2}) of opportunistic polychaetes and crustaceans;
(3)   a *sulphophilic* ("or sulphur-loving") *stage* lasting for decades, during which a large, species-rich, trophically complex assemblage lives on the skeleton as it emits sulphide from anaerobic breakdown of bone lipids; this stage includes a chemoautotrophic component deriving nutrition from sulphur-oxidising bacteria. Local species diversity on large whale skeletons during the sulphophilic stage (mean of 185 macrofaunal species) is higher than in any other deep-sea hard substratum community.

Global species richness on whale falls (407 species) is also high compared with cold seeps and rivals that of hydrothermal vents, even though whale-fall habitats are very poorly sampled. Population-level calculations suggest that whale falls are relatively common on the deep-sea floor, potentially allowing macrofaunal species to specialise on these habitat islands; to date, 21 macrofaunal species are known only from whale falls and may be whale-fall specialists. Nonetheless, whale falls also share 11 species with hydrothermal vents and 20 species with cold seeps, and thus may provide dispersal stepping stones for a subset of the vent and seep faunas. Molecular evidence also suggests that whale falls provided evolutionary stepping stones for the bathymodiolin mussel lineage to move down the continental slope and into deep-sea vent and

seep habitats. Finally, whale-fall bacteria have proven to be a novel source of cold-adapted enzymes of potential utility in cold-water detergents. Despite these scientific advances, major gaps persist in our understanding of the microbial processes, reproductive strategies, population genetics, and biogeography of whale-fall communities.

Scientific history of whale-fall ecology

Whales are the giants of the ocean, with the eight largest cetacean species attaining body weights of 30 t to 160 t (Lockyer 1976). A sunken whale carcass provides a massive food fall to the normally organic-poor deep-sea floor; for example, the organic carbon contained in a 40-t whale ($\sim 2 \times 10^6$ g C) is equivalent to that typically sinking from the euphotic zone to a hectare of abyssal sea floor over 100 yr to 200 yr (e.g. Smith & Demopoulos 2003). The sediments directly underlying a sunken whale carcass (which covers roughly 50 m^2) experience an initial pulse of labile organic material equivalent to $\sim$2000 yr of background organic-carbon flux.

In part because of the massive size of whales, scientists have long speculated on the ecological effects of whale carcasses sinking to the deep-ocean floor. In 1934, Krogh commented that "whalebone whales represent the maximum energetic efficiency attained in the ocean" by feeding low on the oceanic food web and attaining enormous size. He speculated that the dead bodies of large animals (including whales) may "constitute the ultimate food for abyssal fauna" (Krogh 1934b). In particular, Krogh (1934a) calculated for the Southern Ocean that the flux of whale-fall biomass to the sea floor may be $\sim$0.5 g m^{-2} yr^{-1} (Krogh 1934a,b), and decided that it is "practically certain that the bottom fauna must obtain a more than negligible amount of food from fairly large animals sinking down from the surface." In considering food sources for the deep sea, Bruun (1956) noted that whale ear bones are often trawled or dredged from the abyssal sea floor, and that a dead whale of 50 t "must attract scavengers for a long time and thus form a local focus of abundant food for predators." Stockton & DeLaca (1982) speculated similarly that very large food falls, such as dead cetaceans, might yield localised development of dense communities at the deep-sea floor, possibly with an unusual (or "characteristic") species structure. They suggested that the rise and fall of such localised benthic populations might take "many years."

In parallel with whale-fall speculations, evidence has accumulated in the taxonomic literature for nearly 150 yr that deep-sea whale remains support a widespread, characteristic fauna (Fig. 1). In 1854, S. P. Woodward described a small mytilid mussel (now known as *Adipicola pelagica*) living in whale blubber found floating off the Cape of Good Hope, South Africa (Dell 1987). This species was again reported in 1927 from whale debris in the North Atlantic, and in 1964 living in abundance on a whale skull recovered from 439 m off South Africa (Dell 1987). Dell (1987) concluded that *A. pelagica* is distributed from the Azores to South Africa living attached to whale remains at the deep-sea floor (400–1800 m); its occasional recovery in surface waters results from debris floating up from carcasses rotting at the sea floor. Another species of mytilid, *"Adula"* (now *Adipicola*) *simpsoni* was noted by Tebble (1966) to live in abundance in "a quite exceptional habitat," (i.e. on weathered whale skulls trawled from the sea floor off Scotland, Ireland and the Orkney Islands). From the south Pacific, Marshall (1987) and Gibbs (1987) described, respectively, a new family of limpets (Osteopeltidae) and a sipunculid species (*Phascolosoma saprophagicum*)
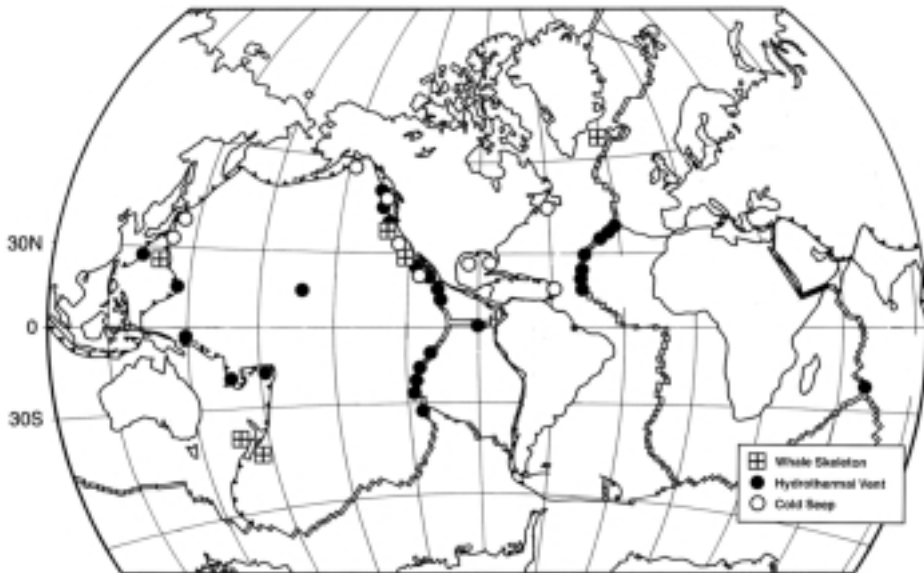
Figure 1   Location of known deep-sea whale-fall sites studied in the world ocean, as well as the locations of known hydrothermal vents, and cold seeps at the deep-sea floor (Lonsdale 1979, Sibuet and Olu 1998, Van Dover et al. 2002). Note that the whale-skeleton symbol at ~30°N in the northeast Pacific represents five deep-sea whale skeletons studied off southern California.

living in abundance on oily whale skulls trawled from 800–955 m on the Chatham Rise, near New Zealand. Both of these new taxa were surmised to feed on whale bones, with *P. saprophagicum* ingesting whale-bone oil (Gibbs 1987) and the osteopeltid limpet grazing on bacteria decaying the bones (Marshall 1987). Marshall and Gibbs also noted that the Chatham Rise skulls were encrusted with thousands of two unrecorded species of mytilid bivalves (Marshall 1987) and supported a "a rich fauna of mussels, gastropods, harpacticoid copepods, polychaetes and sipunculans." Finally, in 1989 Warén reported a second osteopeltid limpet from whale bone trawled off Iceland (Warén 1989). This series of finds spurred Dell (1987) to note insightfully that the fauna of large organic debris at the deep-sea floor (including whale remains) was likely to become better known in the future due to increasing commercial trawling in deep water.

   In 1989, ecological understanding of whale-fall communities advanced substantially with the recognition that deep-sea whale skeletons may harbour chemoautotrophic assemblages (Smith et al. 1989). Based on the first submersible observations and quantatitive samples of a deep-sea whale fall, Smith et al. (1989) reported large communities of bacteria, vesicomyid clams, mytilid mussels and gastropods supported by an oil-rich whale skeleton at 1240 m off California, in Santa Catalina Basin. They also noted that several of these species had been recovered from three whale skulls trawled at other bathyal sites off California. Several of the abundant whale-skeleton species (including two species of vesicomyid clams and the extremely abundant mytilid *Idas washingtonia*) contained sulphur-oxidising

chemoautotrophic endosymbionts that appeared to use sulphide derived from anaerobic decomposition of concentrated bone lipids (Smith et al. 1989, Smith 1992, Deming et al. 1997). Based on the calculated abundance of whale falls and faunal similarities to hydrothermal vents, Smith et al. (1989) hypothesised that whale skeletons might provide important dispersal stepping stones for species (including some from hydrothermal vents and cold seeps) dependent on sulphide availability at the deep-sea floor.

The finds of Smith et al. (1989) were quickly followed by discoveries of chemoautotrophically based assemblages on deep-sea whale skeletons from four other bathyal sites off California (McLean 1992, Smith & Baco 1998, C. Smith unpubl. obs.), and from the western Pacific at 4000 m on the Torishima Seamount (Fujioka et al. 1993, Wada et al. 1994). The demonstration of chemoautotrophic endosymbiosis in *Idas washingtonia* (Smith et al. 1989, Deming et al. 1997) also suggested that other closely related mytilids (e.g. *Adipicola* spp., and *Idas* spp.) found on deep-sea whale bones from numerous locations off New Zealand (Dell 1987, 1996), off Japan (Y. Shiriyama, pers. comm.) and in the Atlantic (Tebble 1966, Dell 1987) might be utilising chemoautotrophy. In addition, apparently chemoautotrophic fossil communities (including *Idasola* (now *Idas*)) were discovered on fossilised whale remains from the bathyal northeast Pacific dating from the Oligocene (~30 mya) (Squires et al. 1991, Goedert et al. 1995). Concurrently, new species of invertebrates (e.g. five limpets, a mytilid and two polychaetes) were documented from whale bones recovered off New Zealand and California (Pettibone 1993, Marshall 1994, Bennett et al. 1994, Dell 1996).

When considered together, these findings suggested that chemoautotrophic assemblages, and specialised whale-bone communities, colonise whale falls over wide areas of the modern deep-sea floor (Smith 1992, Fig. 1) and have been utilising this habitat for tens of millions of years. These results also led to speculation that whale falls contribute significantly to deep-sea diversity by providing specialised habitats, and by facilitating the dispersal of some vent-seep taxa (e.g. Committee on Biological Diversity in Marine Systems 1995, Butman et al. 1995). By 1995, the ecology, biogeography and evolution of deep-sea whale-fall communities had become topics of broader interest to the oceanographic and marine biological communities, setting the stage for more detailed ecological and phylogenetic studies of whale falls.

Manipulative studies of whale falls off Southern California

Although a substantial number of deep-sea whale skeletons had been sampled (mostly accidentally) by 1995, the ecology and biogeography of whale-fall communities remained very poorly understood. In particular, very little was known concerning (a) faunal succession following the arrival of a fresh whale carcass at the deep-sea floor, (b) persistence times of whale-bone chemoautotrophic assemblages, and (c) faunal relationships between whale-fall, cold-seep and hydrothermal-vent assemblages. Such information is essential for our understanding of the dynamics of whale-fall habitat islands, the recycling of large parcels of labile organic matter, and the ecology and evolution of sulphophiles and opportunistic species at the deep-sea floor.

With funding ultimately derived from a variety of sources (the U.S. National Science Foundation, the National Undersea Research Center – Alaska, The National Geographic Society, and the British Broadcasting Corporation), in 1992 the University of Hawaii initi-

ated experimental studies of whale-fall communities at the bathyal sea floor. Overall goals were to (a) evaluate deep-sea community response to intense pulses of organic enrichment such as that resulting from a whale fall, and (b) elucidate the importance of whale falls as organic and sulphide-rich habitat islands at the deep-sea floor (Smith et al., in press). The general approach involved use of manned submersibles (e.g. the DSRV ALVIN) and Remotely Operated Vehicles (ROV's) to conduct time-series studies of natural and experimentally implanted whale carcasses at the ocean floor. Whale carcasses for experimental emplacement were obtained through NOAA's Marine Mammals Stranding Network, which monitors the stranding of marine mammals along all USA coasts. When a suitable carcass became available for deep-sea emplacement off California, a team of scientists flew to the site from the University of Hawaii, towed the carcass to an appropriate drop site using a vessel of opportunity, and then sank the carcass to the sea floor. Because dead whales used in experiments had remained at the sea surface after death and thus had generated decompositional gases (Allison et al. 1991), substantial amounts of steel ballast (600–2700 kg) were used to sink each carcass. Because of the high costs and logistical difficulties of sinking dead whales, a limited number of carcasses (n = 3) could be implanted at the sea floor for experimental study (Table 1). These three experimental whale falls, along with two natural skeletons discovered by chance off southern California (Fig. 2), were then visited at time periods ranging from 1 wk to 46 yr after estimated carcass arrival at the sea floor (Fig. 3). The resulting data provided the basis for the ecological and biogeographic syntheses below.

Patterns of succession on southern California whale falls

Patterns of succession on whale carcasses are of broad ecological interest because they provide insights into deep-sea community response to extreme point-source enrichment, both natural (e.g. from whale falls) and anthropogenic. When the whale-fall experiments were initiated, ecologists had detailed understanding of the effects of organic-loading on shallow-water benthos (e.g. Pearson & Rosenberg 1978, Rhoads et al. 1978, Weston 1990, Zmarzly et al. 1994) but could only speculate on the community effects of intense organic loading, in the form of a whale fall, at the deep-sea floor (e.g. Krogh 1934a, Bruun 1956, Stockton & Delaca 1982, Smith 1985, Bennett et al. 1994). The timescales over which 5–35 t of solid, labile organic material might become assimilated into the seafloor community were unconstrained (Stockton & DeLaca 1982) as were the periods of local community recovery after dissipation of enrichment from a whale fall (although deep-sea successional studies on small scales suggested recovery times ≥2 yr (Grassle & Morse-Porteous 1987, Smith & Hessler 1987, Kukert & Smith 1992, Snelgrove et al. 1994)). Both issues are of relevance to deep-sea patch dynamics and carbon flux (Stockton & Delaca 1982; Smith 1985, 1986; Snelgrove et al. 1992, 1994, Etter & Caswell 1994, Butman et al. 1995, 1996), and to predicting the effects of analogous anthropogenic organic enrichment in the deep sea (e.g. relocation of sewage sludge, fishery discards, and disposal of animal and medical wastes (Gage & Tyler 1991)).

Based on previous studies of deep-sea scavengers, analogies with shallow-water organic-enrichment communities, and initial whale-skeleton finds, fresh whale falls at the bathyal sea floor off California were expected to pass through four overlapping stages of ecological succession (Bennett et al. 1994, Smith et al. 1998):

Table 1 Natural and experimentally implanted whale carcasses studied off California by the University of Hawaii research effort.

| Site	Whale species	Estimated carcass wt (10^3 kg)	Time of arrival at sea floor	Water depth (m)	Year(s) sampled	Latitude (N)	Longitude (W)
Santa Catalina Basin (natural)	Blue or fin	~60	~1948	1240	1988, 1991, 1995, 1999	33°12′	118°30′
San Nicolas slope (natural)	Balaenopterid?	~40	1980–90?	960	1995	33°20′	119°59′
San Clemente Basin (implanted)	Gray	10	1992	1960	1995, 2000	32°26′	118°9′
San Diego Trough (implanted)	Gray	5	1996	1220	1996, 1998, 1999	32°35′	117°30′
Santa Cruz Basin (implanted)	Gray	35	1998	1675	1998, 1999	33°30′	119°22′
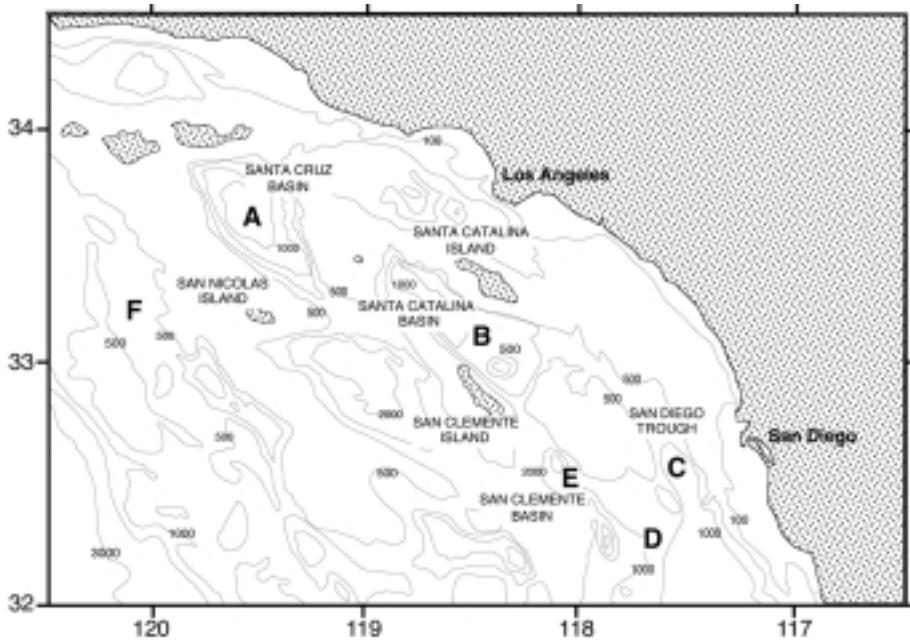
Figure 2   Location of whale falls (sites A, B, C, E and F) studied off southern California. The location of the San Clemente Seep (site D) is also indicated. Depth contours are in metres, the ordinate is in degrees north latitude, and the abscissa in degrees west longitude.

(1)   A *mobile-scavenger stage,* during which soft tissue would be removed from the carcass by dense aggregations of large, active necrophages (cf. Dayton & Hessler 1972, Isaacs & Schwartzlose 1975b, Hessler et al. 1978, Smith 1985).

(2)   An *enrichment-opportunist stage,* during which dense assemblages of hetero-trophic macrofauna (especially polychaetes and crustaceans) would colonise the bones and organically-enriched sediments surrounding the whale fall (cf. Turner 1977, Pearson & Rosenberg 1978, Levin et al. 1994).

(3)   A *sulphophilic (*or *"sulphur-loving")* stage, during which a chemoautotrophic assemblage would colonise the bones as they emitted sulphide during anaerobic bacterial decomposition of bone lipids. Methane might also be released during whale-tissue decay (Allison et al. 1991, Naganuma et al. 1996), fostering free-living or endosymbiotic bacterial methanotrophs.

(4)   A *reef stage*, occurring after the depletion of whale organic material, during which the mineral remnants of whale skeletons would be colonised primarily by suspension feeders exploiting flow enhancement (e.g. Jumars & Gallagher 1982) and hard substrata.

Time-series studies of five carcasses at the bathyal sea floor, two natural whale falls and three experimentally implanted whale carcasses (Table 1, Fig. 2), provide strong evidence of the first three successional stages (Bennett et al. 1994, Smith et al. 1998, Baco-Taylor 2002, Smith et al. 2002, Baco & Smith, unpubl. data). The structure and duration of these stages are discussed below.
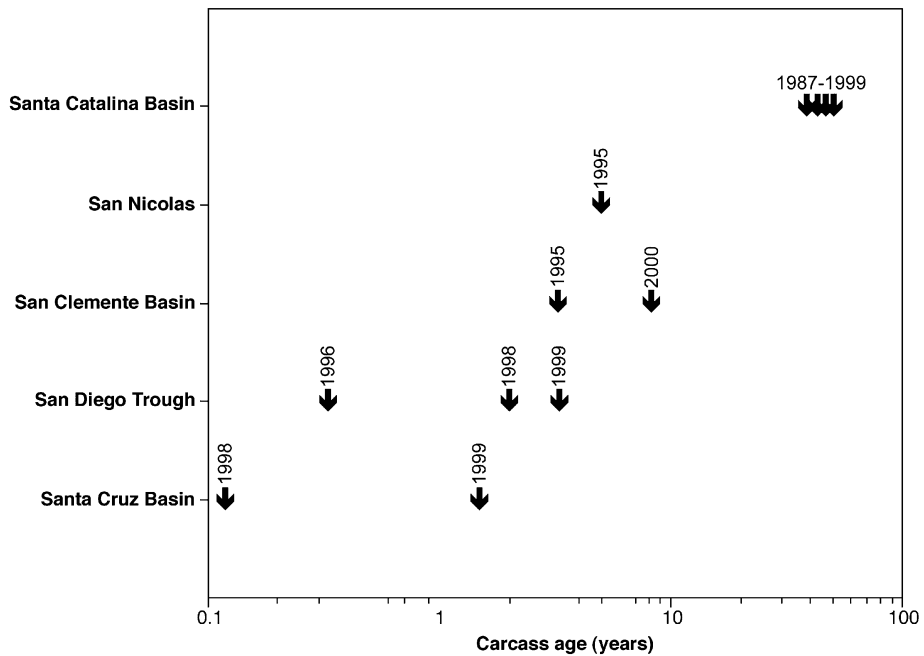
Figure 3 Times since arrival at the sea floor at which whale-fall sites off southern California have been sampled. For the San Nicolas carcass, an arrival of 1990 is used because this is the latest likely arrival time.

The mobile-scavenger stage

Carcasses studied at times of 0.5–1.5 months after arrival at the sea floor (n = 2) exhibited clear evidence of a *mobile-scavenger stage*. Both carcasses were largely intact but were covered with hundreds of hagfishes (predominantly *Eptatretus deani* but including *Mixine circifrons*) consuming soft tissue (Table 2). Sleeper sharks (*Somniosus pacificus*), ranging in size from approximately 1.5 m to 3.5 m, were observed feeding voraciously on one carcass and in the vicinity of the other (Smith at al. 2002). Observed feeding activities and bite marks suggested that *S. pacificus* had removed more soft tissue from the carcass at 1.5 months than had any other species. Other notable scavengers at 0.5–1.5 months included huge numbers of small (~0.5 cm long) lysianassid amphipods (Santa Cruz Basin carcass) and small numbers of large lithodid crabs, possibly *Paralomis multispina* (San Diego Trough carcass) (Table 2). Assuming hagfish densities similar to those estimated for the 1300-m deep Santa Catalina Basin (370 km^{-2}; Smith 1985, Martini 1998), after 0.5 months to 1.5 months, the whale carcasses had drawn *Eptatretus deani* from minimum areas of ~1–2 km^2 (or a radius of 0.6–0.8 km).

By 4 months for the 5000-kg San Diego Trough carcass, and by 18 months for the 35 000-kg Santa Cruz Basin carcass, >90% of whale soft tissue had been removed, with only a small number of megafaunal scavengers remaining, indicating that the *mobile-scavenger stage* was drawing to a close (Smith et al. 2002). Thus, the duration of the *mobile-scavenger*

stage for megafauna at 1200–1800 m off California appears to range from the order of 4–5 months to 1.5–2.0 yr, depending on carcass size. Assuming that the soft tissue of a whale carcass constitutes about 90% of its total wet weight (cf. Robineau & de Buffrénil 1993), bathyal scavenger assemblages off California remove tissue from whale carcasses at rates of roughly 40–60 kg day^{-1}. These scavenging rates are approximately an order of magnitude higher than recorded on much smaller carcass falls (1–4 kg) off California (Smith 1985). Nonetheless, the scavenging rates for small and large parcels at bathyal depths off southern California are all well fitted by a single logarithmic curve, in contrast to scavenging rates from the abyssal North Atlantic (Jones et al. 1998) (Fig. 4). The location of the whale-fall points on the logarithmic curve suggest that the whale-fall implantations are close to saturating the scavenging capacity of California bathyal ecosystems (i.e. whale falls (or other falls of labile organic material) that are larger in mass than 35 000 kg are likely to be scavenged at similar rates). If this is true, the *mobile-scavenger stage* for an adult blue-whale carcass of 100 000 kg at bathyal depths off southern California may last ~5 yr. Based on the relatively low scavenging rates for small cetaceans obtained by Jones et al. (1998), the mobile scavenger stage may last much longer for large whale falls in the abyssal North Atlantic.

It is interesting to note that while megafaunal scavengers had largely dispersed from the San Diego Trough at 4 months and the Santa Cruz carcass at 1.5 yr, highly mobile macrofauna thought to be scavengers, in particular calanoid copepods (K. Wishner, pers. comm.) were very abundant on the whale bones at this time (Baco-Taylor 2002, Baco & Smith, unpubl. data). Thus, it seems likely that the *mobile-scavenger stage* itself undergoes a temporal succession as the remaining fragments of soft tissue attached to the carcass diminish in size, and are in turn exploited by species of scavengers of successively smaller body size (e.g. starting with sleeper sharks, hagfishes and macrourids, passing through lysianassid amphipods, and ending with calanoid copepods).

The enrichment-opportunist stage

An *enrichment-opportunist stage*, during which dense assemblages of heterotrophic macrobenthos colonise organic-rich sediments and bones, was evident on carcasses visited at times of 4 months to 1.5 yr after arrival at the sea floor (the 5000-kg San Diego Trough carcass and the 35 000-kg Santa Cruz Basin carcass, respectively). This stage appears to begin in organically-enriched sediments surrounding the skeleton but eventually includes the bone epifauna as well.

The organically-enriched sediments within 1–3 m of each carcass were colonised by extremely high densities of macrofauna (Fig. 5). Around the San Diego Trough skeleton, a bed of free-living, centimetre-long polychaetes (*Vigtorniella* n. sp. and two undescribed species of dorvilleids; Dahlgren et al., unpubl. data, B. Hilbig, pers. comm.) undulated in the near-bottom flow, resembling a field of white grass; the bones themselves harboured high densities of dorvilleid polychaetes (Baco-Taylor 2002, Baco & Smith, unpubl. data). Large numbers of minute white gastropods (a new genus; J. McLean, pers. comm.) and juvenile bivalves colonised sediments around the Santa Cruz skeleton, and some bones of this skeleton were densely covered with writhing masses (thousands of individuals) of *Vigtorniella* n. sp. (Dahlgren et al., unpubl. data). Sediment macrofaunal densities attained 20 000–45 000 m^{-2} within 1 m of the skeletons (Fig. 5); these are the highest ever reported for macrobenthos below 1000 m depths. In contrast, species diversity was dramatically reduced within 1 m of carcasses (Fig. 5). Dominant macrofauna common to both skeletons
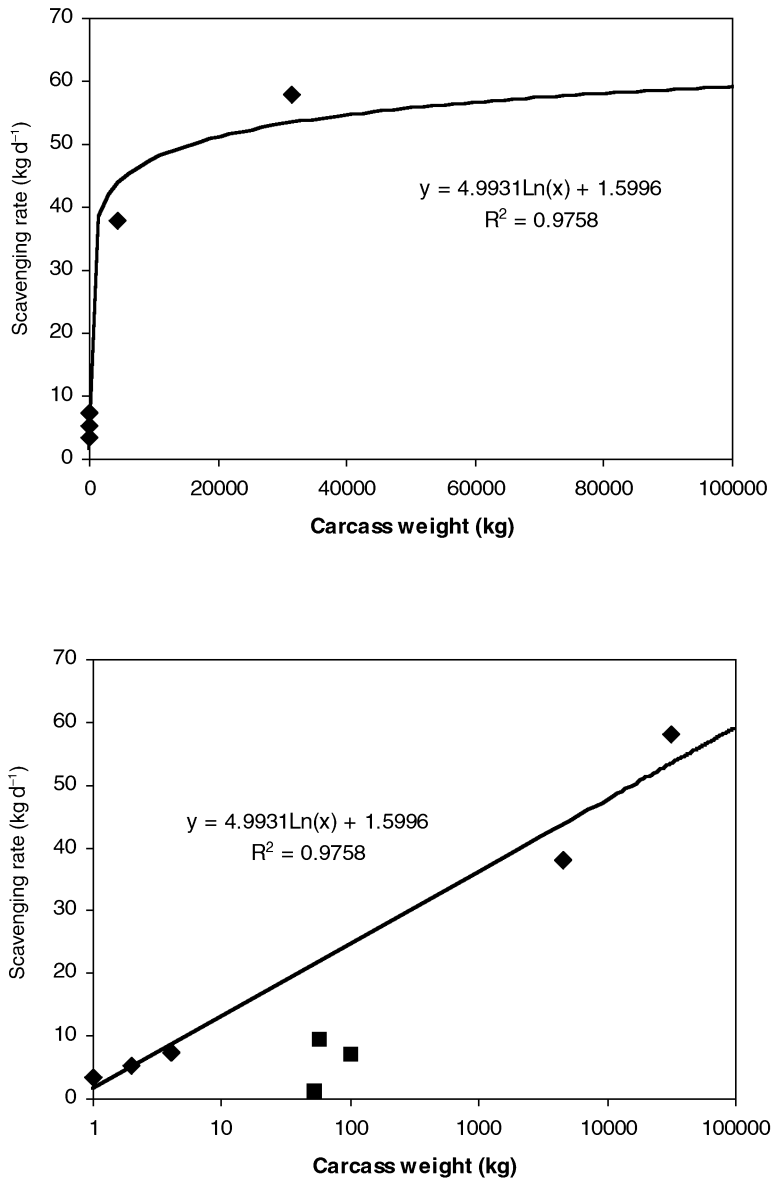
Figure 4 Top: Linear plot of scavenging rates of soft tissue from carrion falls off southern California as a function of carrion-fall mass. The equation for the plotted logarithmic curve is given. Data from Smith (1985) and Smith et al. (2002). Bottom: Log-linear plot of scavenging rates for carrion falls off southern California (diamonds) (data from Smith 1985 and Smith et al. 2002, as above) and for small cetacean carcasses in the abyssal North Atlantic (squares) (Jones et al. 1998). Note that scavenging rates for small cetacean carcasses in the abyssal North Atlantic fall well below the logarithmic curve fitted for southern California carrion falls.
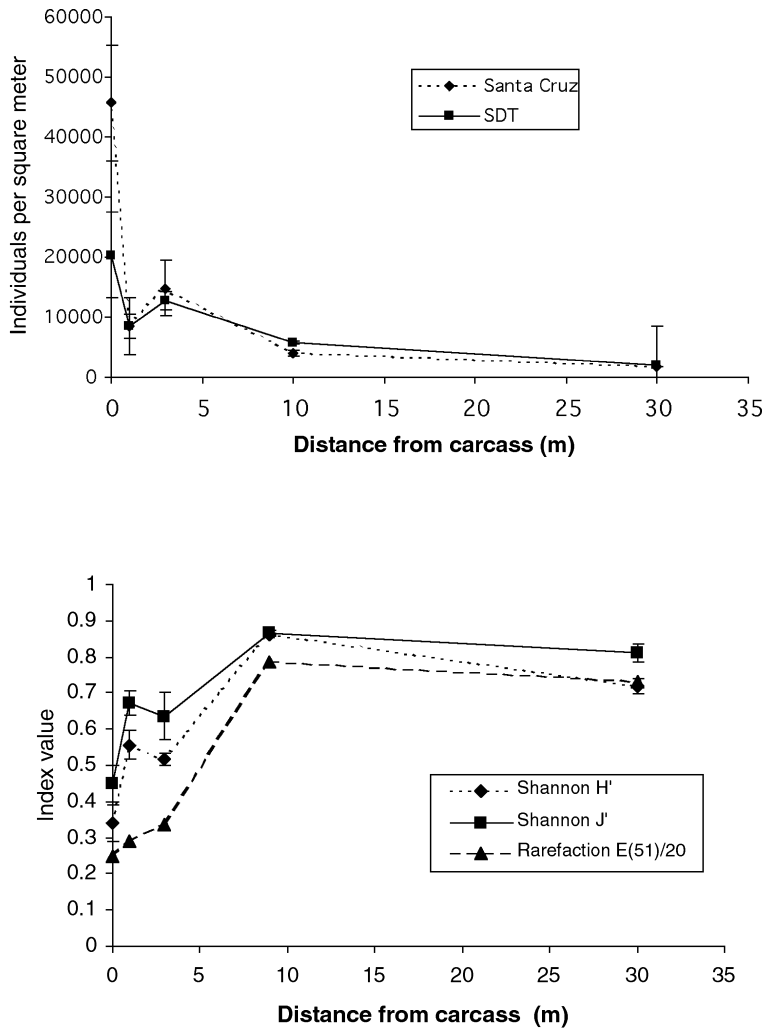
Figure 5 Top: Sediment macrofaunal densities around whale falls in the San Diego Trough (SDT) at 4 months, and in the Santa Cruz Basin at 18 months. Both carcasses are in the *enrichment-opportunist stage*. Means $\pm$ one standard error are given. Bottom: Macrofaunal species diversity, based on three diversity indices, versus distance for the Santa Cruz Basin carcass at 18 months. Rarefaction E(51)/20 is the expected number of species in a normalised sample size of 51 individuals, divided by a constant of 20 to allow all three indices to be plotted on a single y-axis. Data from Smith et al. (2002).

Table 2 Estimated total megafaunal abundance on whale carcasses at the sea floor for 0.5 and 1.5 months. Note that the original wet weight of the San Diego Trough carcass was 5000 kg, and that of the Santa Cruz carcass was 35 000 kg. Estimated abundances of lysanassid amphipods are extremely rough. From Smith et al. (2002).

Megafaunal taxon	San Diego Trough carcass (t = 0.5 months)	Santa Cruz Basin carcass (t = 1.5 months)
Eptatretus deani	∼ 300	400–800
Nezumia stelgidolepis	1–2	0
Lithodid crabs (*Paralomis multispina?*)	2–4	0
Small lysianassid amphipods	0	10^5–10^6?
Somniosus pacificus	1 observed on periphery	1–3

included *Vigtorniella* n. sp., the dorvilleid polychaete *Ophryotrocha* sp. A, and the cumacean *Cumella* sp. A, all of which exceeded densities of $3000 \, m^{-2}$ within 3 m of the carcass (Table 2). It is worth noting that the dominant species abounding in whale-enriched sediments (e.g. *Vigtorniella* n. sp., and the undescribed dorvilleids) have not been collected in the background communities. This suggests rapid recruitment and population growth for these relatively sessile species, reaching densities of $3000–10 000 \, ind. \, m^{-2}$ in <4 months.

The occurrence of a high-density, low-diversity assemblage in organically-enriched sediments near the whale carcasses is highly reminiscent of macrofaunal community patterns around point sources of organic enrichment in shallow water, for example, sewage outfalls and salmon pens (e.g. Pearson & Rosenberg 1978, Weston 1990, Zmarzly et al. 1994). In addition, there is some faunal similarity at the generic level, with dorvilleids in the genus *Ophryotrocha* responding to deep-sea whale falls and to sewer outfalls at shelf depths on the California coast (Levin & Smith 1984, Zmarzly et al. 1994). It appears that intense pulses of organic enrichment (e.g. due to whale falls, kelp falls, etc.) are common enough at bathyal depths off California to have allowed the evolution of bathyal enrichment opportunists.

The duration of the *enrichment-opportunist stage* is likely to vary substantially with whale-carcass size and is still difficult to constrain. For the 5000-kg San Diego Trough carcass, enrichment opportunists were abundant in adjacent sediments at 4 months but absent after 2 yr (Smith et al. 2002, C. Smith, unpubl. data), indicating a stage duration of <2 yr.

The sulphophilic stage

The fresh bones of large whales, for example, the vertebrae of baleanopterids, may exceed 60% lipid by weight (Allison et al. 1991, D. Schuller, unpubl. data, S. Macko, pers. comm.). Thus, whale-bone lipids may constitute roughly 5–8% of the total body mass (Allison et al. 1991, Robineau & de Buffrénil 1993), and the skeleton of a 40-ton whale carcass may hold 2000–3000 kg of lipids. Following removal of whale soft tissue by scavengers, whale-skeleton decay appears to be dominated by anaerobic microbial decomposition of the large lipid reservoirs within the bones (Smith 1992, Deming et al. 1997; Fig. 6). Sulphate reduction is particularly important, yielding an efflux of sulphide from the bones (Deming et al. 1997). As a consequence of the sulphide efflux, species exploiting sulphide-based chemo-autotrophic production, as well as species of other trophic types (bacterial grazers, bone-
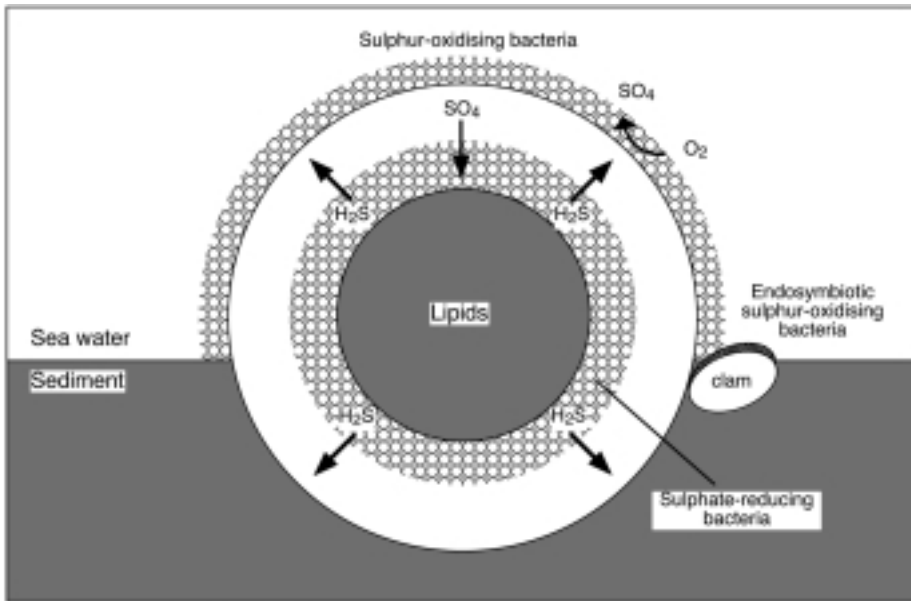
Figure 6 Schematic of cross section of a whale vertebra resting at the sea floor during the *sulphophilic stage* of succession. The predominant decompositional processes occurring within in the bones are illustrated, which include: (1) Diffusion of sulphate from sea water into the bone; (2) Sulphate reduction by anaerobic bacteria decomposing lipids in the lipid-rich bone core; (3) Diffusion of sulphide outward from the bone core, (4) Sulphide oxidation, and organic-matter synthesis, by sulphur-oxidising bacteria living on the bone surface and within the tissues (i.e. endosymbiotically) of vesicomyid clams and other invertebrates (Smith 1992, Deming et al. 1997).

lipid consumers, predators) able to tolerate elevated sulphide concentrations, are expected to colonise the whale skeleton, yielding the *sulphophilic stage* (Smith et al. 1998).

Strong evidence of a recurrent sulphophilic stage comes from carcasses at the bathyal sea floor off California for periods between 2 yr and 51 yr (n = 4 carcasses). This stage is characterised by several key components including:

(1) diverse assemblages of heterotrophic and chemoautotrophic bacteria growing on bone surfaces and within bone cracks and trabaculae (Allison et al. 1991, Deming et al. 1997),

(2) large populations (typically >10 000 ind.) of the centimetre-long mytilid *Idas washingtonia*, which harbours chemoautotrophic endosymbionts (Bennett et al. 1994, Deming et al. 1997),

(3) large populations (hundreds to thousands) of the isopod *Ilyarachna profunda* and galatheid crabs, and frequently,

(4) large populations of diverse dorvilleid polychaetes, pyropeltid and cocculinid limpets (in particular *Pyropelta musaica* and *Cocculina craigsmithi*), provannid

Table 3 Community structure on three whale skeletons during the sulphophilic stage. Estimated population sizes for each carcass are given. Time since whale-carcass arrival at the sea floor is indicated in parentheses. Data from Bennett et al. (1994), Smith & Baco (1998), Baco et al. (1999), Baco-Taylor (2002) Smith et al. (2002), and Baco & Smith (unpubl. data).

Taxon	San Clemente (3.4 yr)	San Nicolas (>5 yr)	Santa Catalina (39–51 yr)
Mytilid			
Idas washingtonia	>20 000	>10 000	>10 000
Limpets			
Cocculina craigsmithi	–	300	1100
Pyropelta corymba	–	1200	1000
Pyropelta musaica	–	280	1000
Other limpets	–	1800	1200
Snails			
Mitrella permodesta	3?	1800	1800
Provanna lomana	–	1500	–
Eulimella lomana	~1000	–	–
Juveniles and others	1800	1700	800
Crustaceans			
Illyarachna profunda	900	500	1800
Amphipods	<400	800	500
Galatheids	800	~50	~100
Misc. crustaceans	9000	8000	4000
Polychaetes			
Nereid sp. 1	~50	~50	~50
Ampharetids	50?	2500	100
Misc. polychaetes	1800	10 000	8000
Total individuals	>40 000	>40 000	>30 000
Total species	>103	>191	>180

gastropods, and the columbellid snail *Astyris permodesta* (Table 3) (Smith et al. 1989, Allison et al. 1991, Bennett et al. 1994, Deming et al. 1997, Baco-Taylor, 2002, Baco & Smith, unpubl. data).

This stage may also include vesicomyid and lucinid clams, and an occasional vestimentiferan worm, in sediments adjacent to the whale bones (Bennett et al. 1994, Feldman et al. 1998, Baco et al. 1999).

For large skeletons, several other aspects of the *sulphophilic stage* on southern California whale falls are noteworthy.

(1)   Macrofaunal communities in this stage are large (exceeding 30 000 ind. to 40 000 ind.), species rich and trophically complex (Table 3, and see sections on Trophic relationships and Biodiversity patterns, pp. 326, 329).

(2)   This successional stage may be remarkably long lasting. A well-developed, chemoautotrophic assemblage has persisted on the Santa Catalina Basin skeleton for at least 15 yr, that is, from 1987 to 2002 (Smith et al. 1989, 2002, Bennett et al. 1994, Baco-Taylor 2002, Smith & Baco, unpubl. data). In addition, radiomet-

ric dating using ^{226}Ra/^{210}Pb disequilibrium, indicates that the Santa Catalina Basin carcass in 1987 had already been at the sea floor for 39 ($\pm$4) yr (Schuller et al., in prep). Considering that experimentally implanted carcasses have developed sulphophilic communities within 2 yr of reaching the sea floor (Baco-Taylor 2002, Smith et al. 2002, Baco & Smith, unpubl. data), this suggests that large whale skeletons may support sulphophilic communities for at least 50 yr.

(3) A number of species (e.g. *Idas washingtonia, Ilyarachna profunda, Cocculina craigsmithi, Pyropelta corymba, P. musaica*) are extremely abundant on sulphide-rich whale skeletons but have rarely, or never, been collected in other habitats. These species may be whale-fall specialists that have evolved to exploit the productive and persistent habitat of sulphide-rich whale skeletons. The frequency distribution of abundances of macrofaunal species on whale skeletons in this stage also suggest the presence of a "core" group of species that have been associated with whale skeletons over evolutionary time (Bennett et al. 1994).

Although smaller whale skeletons (e.g. those of juvenile gray whales), support many species characteristic of the *sulphophilic stage* on large skeletons, stable-isotopic evidence suggests that most of the macrofaunal biomass on these small skeletons (including the dominant *Idas washingtonia*) is not derived from sulphide-based chemoautotrophic production of endosymbionts (e.g. those in *I. washingtonia*) (Baco-Taylor 2002, Baco & Smith, unpubl. data). Thus, in contrast to large whale skeletons in the *sulphophilic stage*, the macrofaunal communities on small skeletons are sulphide tolerant but do not appear to be predominantly chemoautotrophic (see Trophic relationships section, p. 326).

It should be noted that communities of animals reported on whale skeletons from other oceanic regions, for example, the North Atlantic, South Atlantic, western Pacific, and South Pacific (Tebble 1966, Dell 1987, 1995, Marshall 1987, 1994, Warén 1989, Wada et al. 1994, Naganuma et al. 1996) also appear to fall into the *sulphophilic stage*. These communities are dominated by mytilid mussels closely related to *I. washingtonia* (Distel et al. 2000, Baco-Taylor 2002, Baco et al., unpubl. data), many of which appear to derive nutrition from chemoautotrophic production (Baco-Taylor 2002, Baco et al., unpubl. data). In addition, where observed *in situ* or sampled relatively carefully, many of these communities included bacterial mats, cocculinid limpets and galatheid crabs.

The reef stage

Time-series studies of whale skeletons thus far have yielded no direct evidence of a *reef stage* dominated by suspension feeders because the *sulphophilic stage* has occurred even on very old carcasses (e.g. the Santa Catalina Basin carcass at ~50 yr) (Baco-Taylor 2002, Smith et al. 2002). However, the *sulphophilic stage* does contain a few suspension feeders, including sabellid, chaetopterid and serpulid polychaetes, likely to be exploiting enhanced flow conditions on the bones (Baco-Taylor, 2002, Baco & Smith, unpubl. data). Some of these taxa also occur in the background community on hard substrata (Bennett et al. 1994) and are likely to continue to exploit large, well calcified skeletons even after depletion of whale organic matter, yielding a *reef stage*. On large skeletons, this stage may not be reached for many decades. On smaller skeletons (e.g., those of juveniles gray whales), this stage may be curtailed by relatively rapid decomposition and dissolution of the poorly calcified bones (C. Smith, pers. obs. from the 5000 kg San Deigo Trough carcass).

Trophic relationships on Southern California whale falls

Bennett et al. (1994) cite five sources of organic matter potentially of major significance in whale-fall habitats:

(1) whale organic material (e.g. soft tissues and lipids within the bones);
(2) free-living hetero- and chemoautotrophic bacteria;
(3) endosymbiotic, sulphur-oxidising chemoautotrophic bacteria;
(4) tissue of primary consumers; and
(5) detrital particles suspended in currents or deposited in sediments around the bones.

Based on $\delta^{13}C$ and $\delta^{15}N$ values for epifauna on skeletons at the sea floor for 4 months to 51 yr, the relative importance of these sources of organic matter varies with successional stage (Baco-Taylor 2002, Baco & Smith, unpubl. data). Our synthesis is based on the assumptions that the whole bodies of consumers have (a) $\delta^{13}C$ values within -0.3‰ to $+1.9$‰ of their food material (DeNiro & Epstein 1978, Rau et al. 1983, Fry & Sherr 1984), and (b) $\delta^{15}N$ values 1.3‰ to 5.3‰ heavier than their food material (DeNiro & Epstein 1981, Minagawa & Wada 1984). Because of the relatively large change in $\delta^{15}N$ values between consumers and their food source(s) (the so called "trophic shift"), $\delta^{15}N$ values are frequently useful for delineating trophic levels within food webs.

Mobile scavenger/enrichment opportunist stage

Bone epifauna in the *mobile scavenger* and *enrichment-opportunist* stages at 4 months to 1.5 yr had $\delta^{13}C$ and $\delta^{15}N$ values indicating a single trophic level relying on whale organic material (Baco-Taylor 2002, Baco & Smith, unpubl. data). At the San Diego Trough skeleton at 4 months, the community appeared to derive its nutrition primarily from whale soft tissue. On the Santa Cruz whale community at 1.5 yr, $\delta^{13}C$ and $\delta^{15}N$ isotope values were more negative than at San Diego Trough, suggesting a greater dependence on bone lipids.

Sulphophilic stage

The communities on all whale skeletons on the sea floor for ≥ 2 yr exhibited high species overlap and appeared to fall into the *sulphophilic stage* (see above). However, stable isotopic values revealed distinct differences in trophic structure between the communities on juvenile gray whales (San Diego Trough and San Clemente Basin skeletons) and those on the skeletons of larger whales (Santa Catalina Basin and San Nicolas skeletons).

Small skeletons   The mytilid *Idas washingtonia* was the community dominant on all skeletons on the bottom for ≥ 2 yr (Bennett et al. 1994, Baco et al. 1996, Baco-Taylor 2002, Baco & Smith, unpubl. data). Deming et al. (1997) documented chemoautotrophic endosymbioses in this species from the Santa Catalina Basin skeleton based on microscopy, enzymes assays and isotope values. However, the $\delta^{13}C$ and $\delta^{15}N$ values for *I. washingtonia* from the small skeletons (San Clemente Basin and San Diego Trough) at 2–8.25 yr were much higher than the Santa Catalina Basin and San Nicolas skeletons (Fig. 7), suggesting that *I. washingonia* did not rely on chemoautotrophy at the small skeletons.
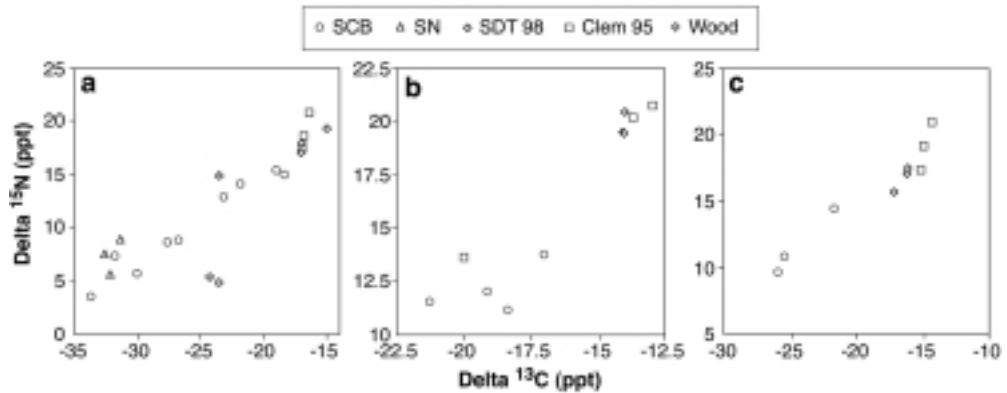
Figure 7 Variation in δ^{13}C and δ^{15}N values for species common to skeletons that have been on the bottom for ≥ 2 yr. (a) *Idas washingtonia*; (b) *Ilyarachna profunda*; (c) Amphipod sp. D. Note that for the larger skeletons (i.e. Santa Catalina Basin (SCB) and San Nicolas (SN)), all three species tend to be substantially lighter in both isotopic ratios, indicating a much greater dependence on chemoautotrophic production than on the smaller skeletons in the San Diego Trough (SDT) and San Clemente Basin (Clem) and on wood (from Baco-Taylor 2002, Baco & Smith, unpubl. data).

Rather than dependence on chemoautotrophy, most of the other species on small skeletons at 2–8.25 yr appeared to depend on bone lipids (δ^{13}C values of -20.0 to -13.0 ‰ and δ^{15}N values of 13.6‰ to 21.0‰). Even species that were found on all skeletons ≥ 2 yr, *I. washingtonia*, *Ilyarachna profunda* and Amphipod sp. D, had much higher δ^{13}C and δ^{15}N values on the San Clemente Basin and San Diego Trough skeletons than on the Santa Catalina Basin and San Nicolas skeletons (Fig. 7). Thus, in contrast to large whale skeletons in the *sulphophilic stage* (discussed below), the macrofaunal communities on small skeletons are sulphide tolerant but do not appear to be predominantly chemoautotrophic.

The San Clemente Basin and San Diego Trough skeletons were from juvenile gray whales, whose vertebrae were poorly calcified compared with adults (Jones et al. 1984). The juvenile skeletons appeared to decompose much more rapidly that than those of adults whales, releasing lipid reservoirs relatively quickly. Because of the relatively small size of juvenile bones, the bone-lipid reservoir is also likely to be much smaller in juveniles than in adult whales. The gradual anaerobic breakdown of bone lipids appears to be the source of sulphides for chemoautotrophic production on whale falls (Smith 1992, Deming et al. 1997), so the lipid reservoir will be depleted more rapidly, and sulphides available for a shorter period of time, on skeletons of younger whales. It appears that there is a minimum size/degree of calcification required for a whale skeleton to sustain chemoautotrophic communities for extended periods (i.e. years). Juvenile skeletons have not been sampled between 4 months and 2 yr so it is conceivable that during this interval, the community may be at least partially dependent on chemoautotrophic production.

Large Whale Falls Whale-fall communities in the sulphophilic stage on large skeletons (Santa Catalina Basin and San Nicolas slope) exhibited much more complex trophic

structure, utilising organic material from chemoautotrophic endosymbionts, free-living bacteria, and whale tissue (Baco-Taylor 2002, Baco & Smith, unpubl. data). The majority of the species analysed on the larger skeletons had $\delta^{13}C$ values $< -20‰$ and appear to be part of a food web dependent on chemoautotrophic sources of production. Nitrogen isotopic ratios of organisms apparently dependent on endosymbiotic chemoautotrophic production ranged from $-0.9‰$ to $14.4‰$. Assuming a trophic shift of $+3‰$ to $+5‰$ (DeNiro & Epstein 1981, Minagawa & Wada 1984), there appear to be three to five trophic levels in the whale-skeleton food web, for example, producers with chemoautotrophic endosymbionts, primary consumers, secondary consumers and scavengers (Baco-Taylor 2002, Baco & Smith, unpubl. data).

There were several species with very negative carbon isotopic values ($\delta^{13}C$ from $-36.5‰$ to $-29.6‰$), indicative of reliance on chemoautotrophic endosymbionts (Baco-Taylor 2002, Baco & Smith, unpubl. data). These species include vesicomyid clams, *Idas washingtonia*, and the polychaete dorvilleid sp. D. To date, polychaetes containing chemoautotrophic and/or nitrogen fixing bacteria have not been reported from any hydrothermal vent habitat. However, dorvilleid sp. D (characterised by paired dorsal pouch-like structures on each segment, Baco-Taylor 2002, Baco & Smith, unpubl. data) had $\delta^{15}N$ values lighter than any other whale-fall species ($-0.9‰$ to $4.0‰$) and $\delta^{13}C$ values ranging from $-31.7‰$ to $-29.6‰$. Such ^{13}C-depleted values are strongly suggestive of chemoautotrophic production, for example, via chemoautotrophic endosymbionts (e.g. Fisher et al. 1994, Deming et al. 1997). A similar dorvilleid with dorsal pouches and extremely depleted $\delta^{13}C$ values ($-90‰$ to $-35‰$) has recently been found on northern California, Oregon, and Alaska seeps (Levin et al. 2000, and in prep).

The next putative trophic level on large whale skeletons in the *sulphophilic stage* included the provannid snail *Provanna lomana*, the columbellid snail, *Astyris (Mitrella) permodesta*, and two species of ampharetid polychaetes. These four species had light isotopic values ($\delta^{13}C$ values of $-29.5‰$ to $-23.5‰$ and $\delta^{15}N$ values of $1.3‰$ to $11.1‰$) consistent with chemoautotrophic endosymbionts, predation on species with symbionts, or grazing on free-living chemoautotrophic bacteria. Deming et al. (1997) could find not evidence of sulphide-oxidising endosymbionts in *A. permodesta*.

Isotope values for the three potential secondary consumers and/or scavenging species, *Nereis anoculis*, Amphipod sp. D, and Galathaeid sp. 3 ($\delta^{13}C$ values of $-26.6‰$ to $-20.0‰$ and $\delta^{15}N$ values of $8.8‰$ to $14.4‰$), are more positive than expected if they were preying solely on species with chemoautotrophic endosymbionts and may reflect a mixed diet.

A portion of the food web on large skeletons in the *sulphophilic stage* appeared to be dependent on bacterial mats. Bacterial mat $\delta^{13}C$ ranged from $-23.4‰$ to $-19.4‰$ and $\delta^{15}N$ ranged from $-4.3‰$ to $7.4‰$. Two species which appear to feed on bacterial mats, *Pyropelta musaica* and *Ilyarachna profunda*, had $\delta^{15}N$ values ranging from $9.8‰$ to $13.8‰$, and $\delta^{13}C$ values similar to, or slightly heavier than, mat material.

In contrast to the smaller San Diego Trough, San Clemente Basin and Santa Cruz skeletons, only two species in the Santa Catalina Basin and San Nicolas communities appeared to depend on whale organic material. These were the limpet species, *Cocculina craigsmithi* and several individuals of *Pyropelta musaica*, with $\delta^{15}N$ ranging from $17.6‰$ to $19.5‰$. This small range of isotope values suggests a single trophic level, with the limpets as secondary consumers of the whale organic material.

The trophic structure of the large, old whale-skeleton communities has interesting parallels to hydrothermal-vent communities (Baco-Taylor 2002, Baco & Smith, unpubl. data).

(1) $\delta^{15}N$ values indicated at least three trophic levels ultimately supported by species with chemoautotrophic endosymbionts. East Pacific hydrothermal-vent communities have similar trophic structure, with the first level occupied by free-living bacteria, which support $\sim$2.5 trophic levels of invertebrate consumers (Van Dover & Fry 1989).

(2)   Like vent communities, the distinctly lower $\delta^{15}N$ values, $<$10‰, of the organisms apparently dependent on chemoautotrophic production and bacterial mats indicate that much of the organic nitrogen in the Santa Catalina Basin and San Nicolas whale-fall communities is of local origin (Rau 1981, Van Dover & Fry 1989).

(3)   biomass distributions on large, old skeletons indicate dominance by species harbouring chemoautotrophic endosymbionts. Bivalves with chemoautotrophic endosymbionts, *Vesicomya gigas* and *Idas washingtonia*, comprised $>$58% of the molluscan biomass collected at the Santa Catalina Basin skeleton in 1991. The three species of limpets, which are most likely dependent on production by free-living chemoautotrophic bacteria and whale organic material, constituted $<$42% of the biomass (Baco-Taylor 2002, Baco & Smith, unpubl. data). These findings are similar to those from hydrothermal vents where biomass is dominated by organisms bearing chemoautotrophic endosymbionts (Sarrazin & Juniper 1999).

Biodiversity patterns on Southern California whale falls

Diversity in whale-bone epifaunal communities varied with successional stage. The *mobile-scavenger* and *enrichment-opportunist* stages are characterised by relatively low species richness, with totals of 38 and 18 macrofaunal species, respectively (Baco-Taylor 2002). The *sulphophilic* stage appears to harbour the greatest species richness, often with $>$100 macrofaunal species per skeleton. The *sulphophilic stage* on the San Nicolas skeleton was particularly speciose, with at least 190 species of macrofauna living on the bones (Baco-Taylor 2002, Baco & Smith, in review). At all successional stages, roughly half of the known species richness (47–60%) was contributed by the polychaetes.

The diversity on the chemoautotrophic whale skeletons of San Nicolas and Santa Catalina Basin was lower than in background sediments in the vicinity of the skeletons (Baco-Taylor 2002, Baco & Smith, in review). However, the average local species richness (185 species) on these two skeletons was higher than on any other type of deep-sea hard substratum, including other reducing habitats. Despite being one of the least-studied deep-sea reducing habitats, whale falls may harbour the highest levels of global species richness; thus far, 407 species are known from whale falls, with 91% of these species coming from California whale falls alone. As more whale falls are sampled in other deep-sea regions, the total number of species known from whale falls certainly will rise dramatically. By comparison, the much more intensively studied hydrothermal vents (Tunnicliffe 1991) are thus far known to harbour $\sim$469 species worldwide, (Tunnicliffe et al. 1998) and $\sim$230 species are known from cold seeps (Sibuet & Olu 1998, Poehls et al., in prep).

The remarkable species richness on whale skeletons on local and (potentially) global scales may be explained by an unusually large number of trophic types found on whale bones including species with chemoautotrophic endosymbionts, bacterial grazers, generalised organic-enrichment respondents, whale-bone consumers, and more typical

hard-substratum detritivores such as suspension and deposit feeders (Baco-Taylor 2002, Baco & Smith, in review).

Overall structure and mechanisms of succession on Southern California whale falls

The overall structure of succession on deep-sea whale falls is longer and more complex than that on fish carcasses and other small carrion parcels in the deep sea. For carcass falls ranging up to ~50 kg in size, the *enrichment-opportunist* and *sulphophilic* stages typically appear to be absent (e.g. Smith 1985, 1986, Jones et al. 1998). Intense organic enrichment of nearby sediments does not occur because the mobile scavengers (including epibenthic forms at bathyal depths) can efficiently remove the smaller mass of soft tissue over very short timescales (typically days, Dayton & Hessler 1972, Hessler et al. 1978, Smith 1985, Jones et al. 1998). The primary effect of such food falls on the local sediment community appears to be physical disturbance resulting from the vigorous feeding and swimming activities of scavengers (Smith 1986). On scavenged fish carcasses, the remaining bones are apparently too small and contain an inadequate organic-matter reservoir to sustain the development of a sulphur-oxidising microbial assemblage; hence, the *sulphophilic* stage does not develop (Smith 1985). However, the skeletons of small cetaceans such as dolphins, as well as cow bones artificially placed on the deep-sea floor, contain large enough organic reservoirs to support mats of *Beggiatoa* (a sulphate reducing bacterium) (Kitazato & Shirayama 1996) and to sustain limited recruitment of bathymodiolin mussels with chemoautotrophic endosymbionts (Y. Shirayama, pers. comm., Baco et al., unpubl. data).

Several aspects of whale-fall community change are of relevance to the consideration of successional mechanisms. As with carrion falls in terrestrial environments (Schoenly & Reid 1987), biotic succession on southern California whale falls appears to be largely a continuum of change, with temporal overlap in the occurrence of the characteristic species from different stages. For example, on 4 month-old and 18 month-old carcasses (the San Diego Trough and Santa Cruz carcasses, respectively), components of both the *mobile-scavenger* and the *enrichment-opportunist stages* were present (Smith et al. 2002, Baco-Taylor 2002). In addition, on the Santa Cruz carcass at 18 months, components of the *sulphophilic stage* had begun to recruit, in particular *Idas washingtonia* (Baco-Taylor 2002, Baco & Smith, unpubl. data).

Nonetheless, there appear to be periods of relatively rapid faunal change on the whale falls that can be considered to be loose successional-stage boundaries. The presence of soft tissue on carcasses elicits active feeding by large aggregations of megafaunal scavengers. When this tissue is depleted (within approximately 4 months for the 5000 kg carcass and 18 months for the 35 000 kg carcass), the abundance of scavenging megafauna drops abruptly (Smith et al. 2002). Similarly, based on analyses using Bray-Curtis similarity and non-metric multidimensional scaling, Baco-Taylor (2002, Baco & Smith, unpubl. data) found abrupt differences in species structure between skeletons at the sea floor for less than, and greater than, 2 yr. Thus, 2 yr marked the approximate boundary between the *enrichment-opportunist* and *sulphophilic stages*. These intervals of relatively rapid community change occurring between periods of relative community stasis are consistent with the concept of "successional stages" (Schoenly & Reid 1987).

Successional changes on whale falls not only involve species turnover but also include

changes in both faunal mobility and trophic structure. The *mobile-scavenger stage* is dominated by very active swimmers (hagfishes, sharks, lysianiassid amphipods), the *enrichment-opportunist stage* is dominated by moderately mobile epibenthos (e.g. gastropods, dorvilleids, chrysopetalids), and the *sulphophilic stage* by sessile macrofauna (e.g. *I. washingtonia*, which attaches with byssal threads) and microbial mats (Bennett et al. 1994, Baco-Taylor 2002, Smith et al., in press, Baco & Smith, unpubl. data). Trophic structure shifts from a predominance of scavengers, through carnivore–scavenger–omnivores, to macrofauna harbouring chemoautotrophic, sulphur-oxidising endosymbionts (Baco-Taylor 2002, Smith et al. 2002, Baco & Smith, unpubl. data). In fact, it is the dramatic shifts in mobility patterns and trophic structure that has led to the names of the successional stages.

Connell & Slatyer (1977) identified three general mechanistic models to explain species turnover during successional change: (a) *facilitation,* (b) *tolerance* and (c) *inhibition*. Under *facilitation*, species arriving early in the successional sequence modify the habitat to facilitate, or "pave the way for", the colonisation of later-stage species. Under the *tolerance* model, early-stage species are less tolerant of lower resource levels than are later-stage species, and thus early species are replaced by superior competitors. In the *inhibition* model, mature individuals of species from all stages inhibit habitat utilisation by all other individuals regardless of species; early successional species dominate initially because they disperse better and/or grow faster, whereas later-stage species ultimately dominate because they live longer and accumulate as early species die off.

As originally formulated, all three of the Connell & Slatyer (1977) models rely heavily on competitive interactions. In the *facilitation* and *tolerance* models, early species are excluded (or killed) through competition with later-stage species. In the *inhibition* model, competition, particularly for space, is the primary interaction. It also should be noted that these models do not exhaust the full suite of reasonable interaction scenarios. For example, a *null* or *noninteractive* model might be considered, in which species abundances rise and fall independently of other species colonising the habitat. Such a model might apply if all species were held well below carrying capacity due to inadequate larval supply or heavy predation pressure, or if species-specific pathogens or toxic chemicals (e.g. sulphide) controlled population dynamics. In addition, there is no *a priori* reason in successional models to link the effects of early-stage species on later colonists (e.g. facilitation) with those of later colonists on early species. For example, it is quite possible (and, in fact, likely for the *mobile-scavenger* stage of whale falls) that early species facilitate the arrival of later successional species, and then disappear due to reasons other than interspecific competition.

Given this conceptual framework, which mechanisms of succession apply to whale carcasses at the deep-sea floor? Clearly, *facilitation* is a dominant mechanism in the transitions between the *mobile-scavenger* and *enrichment-opportunist* stages, and between the *enrichment-opportunist* and *sulphopilic* stages (Baco-Taylor 2002, Baco & Smith, unpubl. data). Enrichment opportunists cannot colonise bone surfaces until scavengers have stripped off the soft tissue; nor will they recruit to nearby sediments until the frenzied feeding of scavengers has broadcasted a fine rain of whale-tissue fragments over the surrounding sea floor. The mobile scavengers, however, are not ultimately excluded by competition with enrichment opportunists; the scavengers themselves deplete the carrion resource and then move off in search of other feeding opportunities (cf. Smith 1985, 1986). In turn, many species in the *sulphophilic stage*, in particular the dominant species *I. washingtonia*, benefit from the development of sulphate-reducing microbial assemblages on and within the bones (Smith et al. 1989, Smith 1992, Deming et al. 1997). Thus, the colonisation of the bones by anaerobic

microbial populations is necessary to facilitate the development of the chemoautotrophic assemblages. Once again, however, the decline of the *sulphophilic* stage is unlikely to be a consequence of competitive exclusion by later colonists (e.g. by suspension feeders). This stage necessarily declines as sulphate-reducing bacteria deplete lipid reservoirs within the whale bones, and sulphide levels drop below those required to sustain chemoautotrophic endosymbionts. Overall, facilitation appears likely to be the dominant process governing turnover of whale-fall successional stages. However, unlike Connell & Slatyer's (1977) original *facilitation* model, the facilitation by early species in whale-fall succession is not ungraciously repaid with competitive exclusion by later colonists.

Mechanisms of succession on deep-sea whale falls exhibit some similarities to those on carrion falls in terrestrial environments. As for deep-sea whale falls, facilitation may dominate successional changes in terrestrial carcasses (Connell & Slatyer 1977). In addition, a true *mobile-scavenger* stage does occur in some terrestrial habitats where large specialised necrophages (e.g. vultures) or facultative scavengers (e.g. minks, foxes, bears, wolves, hyenas) feed on carcasses as mobile adults, removing much of the soft tissue (e.g. Houston 1986, Anderson 2001). However, in many terrestrial ecosystems in North America and Europe, soft tissue persists on large carcasses for substantial periods of time (i.e. scavenging rates appear to be roughly an order of magnitude lower than observed on whale falls), and much of the soft tissue is consumed by the feeding larvae of saprophytic insects (Anderson 2001). In other words, unlike whale falls and other large carrion falls in the deep sea (e.g. Dayton & Hessler 1972, Isaacs & Schwartzlose 1975a, Smith 1985), soft-tissue reduction in many terrestrial ecosystems depends on a reproductive response by saprophytic species (e.g. blow flies, carrion beetles and dermestid beetles) as well as on the decompositional activities of microbes (bacteria and fungi) (Anderson 2001, Byrd & Castner 2001, Merritt & Wallace 2001). The lack of large mobile scavengers in many terrestrial systems is likely to be a consequence of anthropogenic extinction of large vertebrates, which could act as facultative or obligate scavengers (e.g. bears, wolves, wolverines, coyotes, foxes, vultures and condors; Pulliainen 1988, Hewson 1984, 1995, Willey & Snyder 1989, Green et al. 1997). In contrast, in marine environments, human activities may have had the opposite effect, increasing the abundance of large scavengers by enhancing carrion availability through fishery discards and trawling disturbance (Britton & Morton 1994). Thus, anthropogenic impacts may ultimately have driven the recycling of large carrion parcels along substantially different pathways in terrestrial and marine environments.

Biogeographic and evolutionary relationships of whale-fall communities

Modern relationships

Abundance of whale falls at the deep-sea floor

How common are whale falls at the deep-sea floor? Are they frequent enough now, or have they been in the past, to allow faunal dispersal (e.g. by planktonic larvae) between adjacent whale falls? Such dispersal is essential for whale falls to serve as sulphide-rich stepping

stones for species dependent on chemoautotrophy (Smith et al. 1989, Kitazato & Shirayama 1996) and to allow the evolution of whale-fall specialists (Bennett et al. 1994). The abundance of whale-fall communities within a particular successional stage will be a function of the overall frequency of whale falls, and the duration of that particular stage (roughly 0.33–2 yr for the *mobile-scavenger* stage, 1–2 yr for the *enrichment-opportunist stage,* and 5–50 yr for the *sulphophilic stage* at bathyal depths off California).

Smith et al. (1989) estimated that 500 gray whales sink to the sea floor each year within a northeast Pacific habitat area of $8 km^2 \times 10^5 km^2$. This estimate used a gray-whale population size of 18 000, and assumed that 50% of dying whales sink to, and remain at, the sea floor. A sinking rate of 90% is probably realistic because most whales suffering natural mortality are in poor nutritional condition and negatively buoyant (Ashley 1926, D. W. Rice, pers. comm.). The percentage of sunken whales that remain at the sea floor will depend, in part, on the water depth and resultant hydrostatic pressure, which limits the generation of buoyant decompositional gases (Allison et al. 1991). Below a depth of 1000 m, the amount of microbial tissue decay required to refloat a carcass (e.g. ~67% of carcass mass through fermentation) is prohibitive; the soft tissue will be scavenged and/or disintegrate long before sufficient buoyancy can be generated (Allison et al. 1991). At shallower depths, there is some probability that gas generation will refloat the carcass, although this will depend on the rate of soft tissue removal by scavengers versus microbial decomposition. A partially scavenged, but otherwise intact, gray-whale carcass has been found at 150 m depth in Alaskan waters (Thomas Shirley, pers. comm.), suggesting that 15 atm of hydrostatic pressure may, at least in cold water, be adequate to prevent decompositional buoyancy for large whales. Given these uncertainties, the assumption that 50% of dying whales sink to, and remain at, the sea floor seems to be a reasonable (and probably conservative) best guess.

Using the approach of Smith et al. (1989), we have estimated current abundances of sea floor whale-fall communities in the first three successional stages (Tables 4, 5). The calculations are in two parts, (a) whale falls resulting from gray whales in the northeast Pacific, and (b) those resulting from the mortality of the nine most common large whale species throughout the global ocean. Within the gray-whale range, rough estimates suggest that whale-fall communities have mean nearest-neighbour distances ranging from 5 km to 16 km, depending on successional stage. The nearest-neighbour distances for the *enrichment-opportunist* and *sulphophilic* stages (5–13 km) fall well within documented larval transport distances and scales of gene flow for animals living in other energy-rich, island-type habitats in the deep sea such as hydrothermal vents and cold seeps (Lutz et al. 1984, Black et al. 1994, 1998, Vrijenhoek 1997, Van Dover 2000, Marsh et al. 2001). It is thus entirely feasible that species attaining population sizes of $10^3–10^4$ on California whale falls (e.g. *I. washingtonia, Vigtorniella* n. sp., and a number of gastropod species) may routinely disperse between whale falls, potentially using them as their primary habitat, or as dispersal stepping stones between other types of habitat islands (Smith et al. 1989). Our global calculations for the nine large whale species also indicate moderate nearest-neighbour distances of 12–30 km for the *enrichment-opportunist* and *sulphophilic* stages, again suggesting that species might routinely disperse between whale falls. In reality, whale falls are likely to be more closely spaced than calculated for the global ocean because whale mortalities are non-randomly distributed; they are likely to be concentrated along whale migration routes and in feeding grounds, which often occur near ocean margins (Gaskin 1982, Katona & Whitehead 1988, Smith et al. 1989, Butman et al. 1995, Perry et al. 1999).

Table 4 Body size, recent estimates of worldwide population size, and estimates of natural mortality for 9 of the 10 largest species of Cetacea. Bryde's whale (*Balaenoptera edeni*) was not included because we could find no recent estimates of population size. *No estimate of natural mortality for this species was available so the mean of the rate estimates for blue, fin, gray, humpback, right, sei and sperm whales was used. **International Whaling Commission website (http://www.iwcoffice.org/estimate.htm), July 2002.

Common name	Species	Approximate adult size range (10³kg ww)	Recent population size estimate	Natural mortality rate (yr⁻¹)	Annual population mortality	References
Blue	*Balaenoptera musculus*	40–160	8500	0.04	300	Lockyer 1976, Perry et al. 1999
Bowhead	*Balaenoptera mysticetus*	30–100	9000	0.05*	500	Lockyer 1976, Sheldon & Rugh 1995
Fin	*Balaenoptera physalis*	25–80	128000	0.04	5100	Lockyer 1976, Perry et al. 1999
Gray	*Eschrichtius robustus*	12–40	26000	0.06	1600	Lockyer 1976, Rice et al. 1984
Humpback	*Megaptera novaeangliae*	15–60	36000	0.05	1800	Lockyer 1976, Perry et al. 1999
Minke	*Balaenoptera acutorostrata*	5–10	935000	0.05*	47000	Lockyer 1976, IWC**
Right	*Balaena glacialis*	30–80	8600	0.03	300	Lockyer 1976, Perry et al. 1999
Sei	*Balaenoptera borealis*	10–30	24000	0.08	1900	Lockyer 1976, Perry et al. 1999
Sperm	*Physeter macrocephalus*	13–70	220000	0.05	11000	Lockyer 1976, Perry et al. 1999
				Ave. = 0.05	$\Sigma = 69000$	

Table 5 Estimated average nearest neighbour distances for whale falls in the various successional stages for gray whales in the northeast Pacific and nine large species of whales (combined) in the global ocean. Note that the estimates of stage duration time are rough, and chosen to be conservative. Also, note that the estimates assume population sizes and mortality rates (Table 3) to be at steady state, and that 50% of carcasses sink to, and remain on, the sea floor. Mean nearest neighbour distance (Pielou 1969), assuming a random distribution, $= 0.5$ (mean area per carcass)$^{0.5}$.

Successional stage	Stage duration (yr) assumed (range)	Number of sea-floor carcasses in stage	Mean sea-floor area per carcass (km²)	Mean nearest neighbour distance (km)
Gray whales in the NE Pacific				
Mobile scavenger stage	1 (0.33–2)	800	1000	16
Enrichment opportunist stage	1.5 (1–2?)	1200	670	13
Sulphophilic stage	10 (5–>50)	8000	100	5
Nine large whale species in the global ocean				
Mobile scavenger stage	1 (0.33–2)	69 000	5200	36
Enrichment opportunist stage	1.5 (1–2?)	103 000	3500	30
Sulphophilic stage	10 (5–>50)	690 000	520	12

Nearest neighbour distances are somewhat larger for the *mobile scavenger* stage (i.e. 16 km and 36 km, for gray whales and the nine pooled species, respectively) and it is very unlikely that the dominant members of this successional stage are whale-fall specialists. Deep-sea scavengers typically disperse as large adults, not as low-cost larvae broadcasted in the hundreds to thousands by spawning individuals. These scavengers appear to respond to carrion falls over distances of 10–1000 m (e.g. Smith 1985, Priede et al. 1991, Collins et al. 1998, Klages et al. 2002, discussion above for hagfishes) making it very difficult to specialise on whale falls spaced tens of kilometres apart. Even for those species able to fast for many months (such as large lysianassids and hagfishes (Hargrave et al. 1994, Tamburri & Barry 1999)), the probability that a single drifting or swimming individual would find a whale carcass over a period of months must be very low. In fact, a simple calculation can illustrate this point. Collins et al. (1998) estimated that rat-tails, after feeding, move away from a deep-sea baitfall at radial velocities averaging 1.4 km d^{-1}. Thus, an average rat-tail would require of the order of 10 days to cover the nearest-neighbour distance of 16 km between gray-whale falls in the *mobile scavenger* stage. Assuming (a) that rat-tails move outward in random directions (Collins et al. 1998) and (b) that they can detect a whale fall from a range of 500 m, a rat-tail has roughly a 1/100 chance (i.e. two times the detection range divided by the 100 km circumference of a circle of radius 16 km) of finding a whale carcass 16 km away. To have, on average, a 50% chance of finding a whale carcass with this nearest-neighbour spacing, a rat-tail would have to make n randomly oriented steps of 16 km, where n can be calculated from the following equation:

$$0.5 = 1 - (99/100)^n$$

Solving this equation gives an n of approximately 70. Since each of the 70 steps of 16 km would require of order 10 days of rat-tail movement, on average, a rat-tail would have a 50% chance of finding a whale fall roughly every 700 days. With maximum fasting times of 30–660 days (Hargrave et al. 1994, Tamburri & Barry 1999), it thus appears unlikely that large scavengers could specialise on whale falls.

It should be noted that our estimates of whale-fall abundances are based on current whale population sizes that, excluding northeast Pacific gray whales, are typically thought to be 10% to 50% of population sizes prior to large-scale whaling operations, that is, prior to the year 1800 (Gaskin 1982, Braham 1984, Braham & Rice 1984, Gosho et al. 1984, Johnson & Wolman 1984, Mizroch et al. 1984a,b,c, Rice et al. 1984, Shelden & Rugh 1995). Before industrial whaling, whale falls at the sea floor must have been substantially more abundant (Butman et al. 1995); in fact, Jelmert & Oppen-Bernsten (1996) calculate that, prior to whaling, there were 3.9×10^5 carcasses sinking per year, making whale falls six times more abundant than at present. Thus, the evolution and survival of whale-fall specialists, and the use of whale skeletons as dispersal stepping stones by vent and seep species, would have occurred much more readily prior to the industrial revolution (Butman et al. 1995). In fact, it is quite feasible that the vast diminution in cetacean populations resulting from whaling reduced deep-sea biodiversity by removing organic-rich habitat islands and sulphide-rich dispersal stepping stones at the deep-sea floor (Butman et al. 1995, 1996; see Jelmert & Oppen-Bernsten 1996, for a contrasting view). Both whale-fall specialists and some more generalised components of reducing-habitat faunas may have been driven to extinction due to massive loss of whale-fall habitats over the past 200 yr (Butman et al. 1995).

Relationships of California whale falls to other modern communities

Scavenger assemblages   During the *mobile-scavenger* stage, whale carcasses off California are consumed by a suite of apparently generalised scavengers. The dominant whale-fall scavengers, in particular hagfishes (*Eptatretus deani* and *Mixine circifrons*), sleeper sharks (*Somniosus pacificus*), lysianassid amphipods, macrourids, and lithodid crabs, are known to scavenge fish falls of a broad range of sizes (Dayton & Hessler 1972, Isaacs & Schwartzlose 1975a, Smith 1985). As might be expected, the aggregation sizes for some of these scavengers, in particular hagfishes and amphipods, are at least an order of magnitude larger on whale falls of 5000–35 000 kg than on fish parcels ranging in size from 1 kg to 40 kg (Table 2 and Smith 1985).

It should be noted that the *mobile-scavenger* stage for bathyal California whales may not entirely overlap scavenger assemblages on fish falls. Sablefish (*Anoplopoma fimbria*) and the brittle star *Ophiophthalmus normani* feed actively on fish falls (Isaacs & Schwatzlose 1975b, Smith 1985) but have not been observed feeding on whale falls, even though these species occur in the San Diego Trough and, possibly, in the Santa Cruz Basin. The absence of these scavengers from the San Diego Trough whale fall may indicate an avoidance of cetacean flesh or, alternatively, of putrifying flesh. Additional experiments are required to determine whether some necrophagous species off California fail to feed on fresh whale carrion.

In other ocean basins, cetacean falls also appear to be consumed by generalised scavengers. For example, Jones et al. (1998) found that scavenger assemblages on small cetacean carcasses (53–100 kg ww) in the North Atlantic abyss included macrourids and lysianassid amphipods, and were similar to those on other types of baitfalls. In addition, the facultative scavenging shark, *Centroscyllium coelolepis*, is commonly taken at bathyal depths in the North Atlantic with whale tissue (including skinless blubber), in its stomach contents, which suggests feeding on whale falls (Nils-Roar Hareida, pers. comm.).

Communities on plant and other organic substrata   In addition to whale bones, other submerged organic debris, such as sunken wood, seagrass, and algal holdfasts, harbours a specialised fauna (e.g. Turner 1973, 1977, Wolff 1979). The molluscan fauna of these biogenic substrata are best documented, most likely because molluscs often remain attached to their substratum when recovered in trawls. Cocculiniform limpets are diverse on biogenic substrata (Wolff 1979, Haszprunar 1988) and bathymodiolin mussels (Bivalvia: Mytilidae) can be extremely abundant (Wolff 1979). Not surprisingly, these are also the two main groups that overlap with whale-fall habitats. Whale skeletons in the *sulphophilic* stage have seven species in common with sunken wood; the polychaete *Nereis anoculis* (Wolff 1979, Baco & Smith, unpubl. data), the limpet *Paracocculina cervae*, also found on algal holdfasts (Marshall 1994), and the mussels *Idas washingtonia*, *I. argenteus*, *I. ghisottii*, *I. (Adipicola) simpsoni*, and *Adipicola osseocola* (Tebble 1966, Dell 1987, 1995, Warén 1991, 1993, Baco & Smith, unpubl. data). *A. osseocola* is also found on fish bones (Dell 1996). Further sampling of both whale falls and sunken wood seems very likely to yield additional species overlap.

At higher taxonomic levels, the limpet suborder Cocculiniformia is found almost exclusively on biogenic substrata (e.g. Haszprunar 1988). To date there are eight cocculiniform species known from sulphophilic whale skeletons in the genera *Cocculina*, *Paracocculina*, *Pyropelta* and *Osteopelta*. *Xylodiscula* is another whale-fall gastropod genus that overlaps with sunken wood and seagrass (Marshall 1994). The bathymodiolin genera *Idas* and

Adipicola also seem to be associated primarily with deep-sea biogenic substrata (e.g. Dell 1987, 1996). Besides the bathymodiolin species mentioned above, several species in each genus are exclusive to either whale bones or sunken wood. Another, non-molluscan, taxon shared between whale falls and wood is the sipunculan genus *Phascolosoma*. Two deep-sea species are known in this genus, one from wood falls (*P. turnerae*), and the other from whale bones (*P. saprophagicum*) (Gibbs 1987). The substantial overlap at higher taxonomic levels between whale falls and other types of sunken organic debris suggests a close evolutionary history for some of their faunal components (see Evolutionary stepping stone section, p. 343).

Enrichment opportunists Whale-fall communities, particularly during the *enrichment-opportunist stage*, share genera and some species with communities associated with other types of organic enrichment in shallow-water and deep-sea settings. The prominence of dorvilleid polychaetes, particularly the genus *Ophryotrocha*, is a common feature at whale falls, in communities around sewer outfalls in shallow water, as well as in organically-enriched sediment trays and *Sargassum* falls in the deep North Atlantic and North Pacific (Pearson & Rosenberg 1978, Desbruyeres et al. 1980, Levin & Smith 1984, Grassle & Morse-Porteous 1987, Levin et al. 1994). In addition, the polynoid polychaete genus *Peinaleopolynoe* appears to respond both to whale falls off California and to organically enriched sediment trays at depths of 2000 m in the northeast Atlantic (Desbruyeres and Laubier 1988, Pettibone 1993). This genus bears branchiae and has life-history characteristics allowing it to exploit intense habitat islands of organic enrichment (Desbruyeres and Laubier 1988). Cumaceans in the genus *Cumella*, which were abundant around whale falls in the *organic-enrichment stage*, may occur also in high densities around fish falls and in enriched sediment trays in the deep sea (Smith 1986, Snelgrove et al. 1994). In addition, organically-enriched sediments underlying salmon pens in Norwegian fjords harbour chrysopetalids morphologically very similar to *Vigtorniella* n. sp. found in abundance on the California whale falls. Thus, bathyal whale falls off California do appear to foster species potentially belonging to a generalised enrichment fauna. This similarity contrasts with the faunal response to organically-enriched sediments beneath at least some oxygen minimum zones in the bathyal northeast Pacific, which apparently fail to attract generalised enrichment respondents (Levin et al. 1994).

Sulphophilic communities – modern vent and seep affinities Smith et al. (1989) hypothesised that whale skeletons might provide important dispersal stepping stones for vent and seep species dependent on sulphide availability at the deep-sea floor. This hypothesis has been somewhat controversial (Tunnicliffe & Juniper l990, Martill et al. 1991, Squires et al. 1991, Butman et al. 1995, 1996, Tunnicliffe & Fowler 1996, Jelmert & Oppen-Bernsten 1996) and could be rejected if no overlap were found between the faunas of whale falls, hydrothermal vents, and cold seeps. In fact, a number of species are shared among whale falls and vents or seeps, with some of these being abundant in both habitats.

Thus far, 11 macrofaunal/megafaunal species are known to be shared between whale-falls and hydrothermal vents, with the main vent overlap coming from soft-sedimented vent sites in Guaymas Basin, and Middle Valley on the Juan de Fuca Ridge (Table 6). In addition, 20 species are known to occur at both whale-falls and cold seeps (Table 6, Warén & Bouchet 2001). This is a small percentage (2–10%) of the species found in any of these habitats, indicating that, at the species level, the whale-fall, vent and seep biotas are largely distinct. It is,

Table 6 Species overlap among whale falls from southern California and hydrothermal vents at Guaymas Basin and on the Juan de Fuca Ridge, Northeast Pacific seeps at various locations, and Gulf of Mexico seeps. For details see: Bennet et al. 1994, Baco et al. 1999, Baco-Taylor 2002, Smith et al. 2002, Baco & Smith, unpubl. data, and Poehls et al., unpubl. data). One cross = species present in the habitat; two crosses = species abundant in the habitat. *In the North Atlantic, the limpet *Protolira thorvaldssoni* was described from whale bones and is common at vents (Warén & Bouchet 2001).

Major taxon	Species	Whale skeletons	Guaymas vents	Habitat Juan de Fuca vents	Northeast Pacific seeps	Gulf of Mexico seeps
Bivalves	*Vesicomya gigas*	++	++	++		
	Calyptogena kilmeri	+			++	
	Calyptogena elongata	+		+	++	
	Calyptogena pacifica?	++	++		++	
	Idas washingtonia	++	+	+	+	
Gastropods	*Pyropelta corymba*	++	+			
	Pyropelta musaica	++		+	++	
	Cocculina craigsmithi	++		+	+	
	Neoleptopsis sp?	+			+	
	Astyris permodesta	++			+	
	Provanna lomana	++			++	
	Eulimella lomana	++	+		++	
Isopods	*Ilyarachna profunda*	++			+	
	Janiridae sp.	+			++	
Polychaetes	*Bathykurila guaymasensis*	+	+			
	Syllid sp. A	+			++	
	Sabellid sp. C	+			+	
	Maldanid sp. C	+			+	
	Dorvilleid sp.	+			+	
	Harmothoe craigsmithi	++			+	
Vestimentiferans	*Escarpia spicata*	+	+		++	+
Entoprocts	Entoproct sp. B	+			+	
Cnidarians	Octocoral sp. A	+			++	
Totals			Vents 10*		Seeps 20	

however, important to note that many whale-fall species (most likely dozens) remain to be identified. In addition, only one seep in proximity to southern California whale falls, the San Clemente Basin seep, has been sampled for macrofauna (Poehls et al., in prep.), and this site alone shares 12 species with the California-slope whale falls. It can be expected that further sampling of whale skeletons in the proximity of vents and seeps, and increased identification of whale-fall species, will likely increase the known species overlap among these habitats. Nonetheless, only a subset of vent and seep species are likely ever to be found on whale falls and potentially use them as dispersal stepping stones.

In addition to the species-level overlap, these reducing habitats also share a number of genera. The limpet genus *Pyropelta* includes two whale-fall species, *P. corymba* and *P. musaica* which occur at vents but also *P. wakefieldi*, which has been found only on whale falls (McLean & Haozprunar 1987, McLean 1992). Two snail genera, *Bruciella* and *Xylodiscula*, which were described from vents, have representatives in whale-fall habitats (Marshall 1994). Also, several unidentified whale-fall species have been preliminarily placed into genera that are known from vents or seeps. For example, "Snail sp. J" from the Santa Cruz skeleton and sediments at 1.5 yr is likely to be a new species of *Hyalogyrina* (Hyalogyrinidae) (J. McLean, pers. comm.), a genus reported by Warén & Bouchet (1993, 2001) from seep habitats. At least two vescomyid genera, *Calyptogena* and *Vesicomya*, also appear to be shared among whale-fall, vent and seep habitats (Baco et al. 1999).

Sulphophilic whale-fall communities appear to differ from other reducing habitats in the apportionment of macrofaunal species among phyla. Based on worldwide species lists, Mollusca and Arthropoda are the most speciose phyla at vents (Tunnicliffe et al. 1998), and Mollusca the most species-rich at seeps (Sibuet & Olu 1998). In contrast, annelids account for 47–60% of macrofaunal species in all whale-fall successional stages at all five whale falls intensively studied to date (Baco-Taylor 2002, Baco & Smith, unpubl. data).

Deep-sea hard substratum biota Whale bones appear to share few species with non-reducing, deep-sea hard substrata. Of the 26 macrofaunal species collected on rocks near the San Nicolas skeleton, only two species, an unidentified amphipod and a scale worm, were also present on the San Nicolas skeleton (Baco-Taylor 2002). There is also very little overlap between sponge stalks collected off Southern California and the Southern California whale falls (Beaulieu 2001, Baco-Taylor 2002, Baco & Smith, unpubl. data). Many species remain to be identified from both sponges and whale falls, however, raising the possibility that more overlap will be found.

As discussed above, whale bones appear to harbour the highest diversity of any deep-sea hard substratum. Densities of macrofaunal individuals on whale skeletons in the sulphophilic stage can also be relatively high, with macrofaunal densities reaching $22\,000\,\text{ind.}\,\text{m}^2$ (Baco-Taylor 2002, Baco & Smith, unpubl. data). Other deep-sea hard substratum habitats such as manganese nodules and sponge stalks had densities of macrofauna and meiofauna combined of $\sim11\,000\,\text{ind.}\,\text{m}^2$ (Beaulieu 2001, Mullineaux 1987). Densities on the Santa Catalina Basin (SCB) skeleton in 1999 ($\sim22\,000\,\text{ind.}\,\text{m}^2$) were also much greater than in background SCB sediments ($<7000\,\text{ind.}\,\text{m}^2$, Smith et al. 1998).

Whale fall specialists There is substantial evidence that deep-sea whale falls harbour a specialised fauna (i.e. one that is specifically adapted to live on whale remains). At least 28 macrofaunal species were first collected on whale falls, and 21 of these have not been found in any other habitat (Table 7). A number of the species thus far unique to whale carcasses

Table 7 Species (n = 29) first found at whale falls. The 21 species marked as "known only at whale falls" have been found in no other habitat. Where available, estimated population sizes on whale falls are given. *In addition to *Palpiphitime* sp. nov., at least 45 unidentified species of dorvilleids, with population sizes ranging from 10's to 1000's of individuals per whale fall, have been collected from whale falls in the Santa Catalina Basin, San Diego Trough, San Clemente Basin and Santa Cruz Basin (Baco & Smith, unpubl. data). Many of these species are likely to be new to science.

Higher taxon	Species	Known only at whale falls	Estimated pop. size	Location	Reference
Mollusca					
Archaeogastropoda	*Pyropelta wakefieldi*	X	>100	California	McLean 1992
	Cocculina craigsmithi		300–1100	California	McLean 1992
	Paracocculina cervae			New Zealand	Marshall 1994
	Osteopelta praeceps	X	>200	New Zealand	Marshall 1994
	Osteopelta ceticola			Iceland	Warén 1989
	Osteopelta mirabilis	X		New Zealand	Marshall 1987
	Protolira thorvaldsoni			Iceland	Warén 1996
Gastropoda	*Bruciella laevigata*	X		New Zealand	Marshall 1994
	Bruciella pruinosa	X		New Zealand	Marshall 1994
	Xylodiscula osteophila	X		New Zealand	Marshall 1994
	Hyalogyrina n.sp.			California	McLean & Warén, pers. comm.
Bivalvia					
Bathymodiolinae	*Adipicola pelagica*	X		South Atlantic	Dell 1987
	Myrina (Adipicola) pacifica	X		Japan, Hawaii	Dell 1987
	Adipicola (Idas) arcuatilis			New Zealand	Dell 1996
	Adipicola osseocola			New Zealand	Dell 1996
	Idas pelagica	X		North Atlantic	Warén 1993
	Idas ghisottii			North Atlantic	Warén 1993
Vesicomyid	New species?	X		California	Baco et al. 1999
Thyasiridae	*Axinodon* sp. nov.	X		California	P. Scott, pers. comm.
Aplacophora	New genus	X		California	Scheltema, in prep.
Arthropoda					
Anomura	*Paralomis manningi*	X		California	Williams et al. 2000
Annelida					
Polychaeta					
Polynoidae	*Harmathoe craigsmithi*	X		California	Pettibone 1993
	Peinaleopolynoe santacatalina	X		California	Pettibone 1993
Chrysopetalidae	*Vigtorniella* n. sp.	X	1000–100 000	California	Smith et al. 2002, Dahlgren et al., in prep.
Ampharetidae	Ampharetid gen nov.	X	>10	California	B. Hilbig, pers. comm.
	Asabellides sp. nov.	X	>10	California	B. Hilbig, pers. comm.
	Anobothrus sp. nov.	X		California	B. Hilbig, pers. comm.
Dorvilleidae*	*Palpiphitime* sp. nov.	X	>10000	California	B. Hilbig, pers. comm.
Sipuncula	*Phascolosoma saprophagicum*	X	>20–>200	New Zealand	Gibbs 1987

Table 8 Species overwhelmingly more abundant on whale skeletons than in any of their other known habitats. Estimated population sizes on whale skeletons, and the total number of specimens collected in other habitats, are indicated for each species. Data from Bennett et al. (1994), Smith et al. (1998), Baco-Taylor (2002), Smith et al. (2002), Baco & Smith (unpubl. data), Poehls et al. (in prep.) and McLean (pers. comm.).

Species	Population size on whale skeletons	Number collected in other habitat(s)
Bivalvia		
Idas washingtonia	>10 000–>20 000	1–10 (wood, vents, seeps)
Gastropoda		
Cocculina craigsmithi	300–1100	1–10 (vents)
Pyropelta corymba	1000–1200	1–10 (vents)
Pyropelta musaica	>250	1–10 (vents)
Crustacea		
Ilyarachna profunda	500–1800	1–90 (sediments, seeps)

are very abundant, indicating that they are well adapted to whale falls and can attain large population sizes given suitable conditions. Their absence in samples from other related habitats (e.g. wood falls, algal falls, enriched sediment trays, hydrothermal vents and cold seeps) suggests that these species may indeed be endemic to whale falls.

In addition to the 21 potential whale-fall endemics, there are at least five species which attain very high densities on whale falls, and yet appear to occur only as isolated individuals in other habitats (Table 8). It is quite feasible that a large proportion of the total individuals within these species occur in the whale-fall habitat, essentially making them whale-fall specialists (e.g. with their evolution largely shaped by the selective milieu of whale falls). This brings the total number of potential whale-fall specialists to 26. It should be noted that this number will surely rise as the diverse dorvilleid (>45 species), amphipod, and copepod components of the whale-fall fauna are rigorously examined by taxonomists.

The taxonomic and functional diversity of the potential whale-fall specialists is noteworthy. These "specialists" come from five different phyla, and appear to include whale-bone feeders (the sipunculid and some limpets), bacterial grazers (some limpets, *Ilyarachna profunda*), species utilising chemoautotrophic endosymbionts (the bathymodiolins, thyasirid and vesicomyid), deposit feeders (the ampharetids), facultative suspensions feeders (the bathymodiolins), and predators (the polynoids and *Paralomis manningi*) (see discussion of food webs above). This diversity, in combination with the abundance patterns of macrofaunal species on whale skeletons (Bennett et al. 1994), suggest that a variety of taxa and trophic types may have become specifically adapted to whale-fall niches.

Ancient/evolutionary relationships

Ancient whales and reptiles

Large cetaceans have existed for >40 myr (million years) (Briggs & Crowther 1990). Because ancient oceans contained scavengers, decomposers, and molluscs with chemoautotrophic endosymbionts functionally similar to those in the modern ocean (Hogler 1994), it

seems very likely that whale-fall succession has generally followed the patterns we describe above for tens of millions of years (cf. Hogler 1994). Fossil chemoautotrophic communities have been found on fossil whale skeletons as old as 30 myr (Squires et al. 1991, Goedert et al. 1995). During the Mesozoic, before the existence of whales, it is likely that large marine reptiles, particularly ichthyosaurs and plesiosaurs, supported chemoautotrophy-based communities (Martill et al. 1991, Hogler 1994, Marshall 1994).

Squires et al. (1991) and Goedert et al. (1995) provide fossil evidence of chemosynthetic communities associated with a variety of deep-sea whale skeletons as early as the Oligocene (30 mya). Eight whale skeletons in the Makah and Pysht formations on the Olympic Penin-sula (Washington State) harboured a molluscan fauna characteristic of reducing habitats, including mytilid, thyasirid, and lucinid bivalves; modern representatives of these families are known to harbour chemoautotrophic endosymbionts. Based on these findings, Goedert et al. (1995) estimate that whale skeletons have been able to support chemoautotrophic communities for at least the past 30–35 myr.

Martill et al. (1991) suggest that other large marine vertebrates, such as tetrapods and marine reptiles, may have supported chemoautotrophic fauna as early as 200 mya. From ichthyosaur and plesiosaur remains, they found evidence of molluscs that are also associated with Eocene seeps. Marshall (1994) found a fossilised limpet, *Osteopelta* cf. *mirabilis*, in close association with bones of a fossil leatherback turtle from the Middle Eocene. Similar limpets are also known from modern whale falls in New Zealand and Iceland (Marshall 1987, Warén 1989). Kitazato & Shirayama's (1996) experiment with cow bones also showed that bones of other vertebrates are capable of supporting chemoautotrophic produc-tion.

Dispersal stepping stones in ecological and evolutionary time

Smith et al. (1989) hypothesised that whale skeletons might provide important dispersal stepping stones for species (e.g. some from hydrothermal vents and cold seeps) dependent on sulphide availability at the deep-sea floor. When initially posed, this hypothesis was con-troversial (e.g. Tunnicliffe & Juniper 1990, Goedert et al. 1995), although the data were clearly inadequate to provide a definitive test. It now appears reasonable that at least a few taxa may have used whale falls for dispersal among reducing habitats in ecological and evo-lutionary time.

One group of species which may have used whale falls as dispersal stepping stones are the vesicomyid clams. Using mitochondrial COI DNA sequences, three to four species of vesicomyid clams have been identified on whale falls (Baco et al. 1999). These clams were conspecific with (a) *Vesicomya gigas*, a species collected from northeast Pacific vent sites, (b) *Calyptogena kilmeri*, a species found at northeast Pacific cold seeps, and (c) *Calyptogena elongata*, a species found in anoxic California basins (Baco et al. 1999). Because the whale-fall clams are conspecific with vent and seep species, and because they occur in reproduc-tively viable population sizes at whale falls, these results offer support for the dispersal stepping-stone hypothesis.

Baco et al. (1999) also showed that whale falls may have played a role in the evolution of vesicomyid clams. Peek et al. (1997) suggested that most vesicomyid lineages are restricted to a single type of reducing habitat (i.e. vents, seeps or anoxic basins). However, whale-fall vesicomyids deviate from this pattern, containing vesicomyid lineages found also at

soft-sediment hydrothermal vents, cold seeps and anoxic basins. This suggests that whale falls may offer habitat conditions intermediate to, or broader than, those found in other reducing habitats. Whale falls may well represent an intermediate habitat type between soft-sediment vents and seeps, with the potential to provide evolutionary stepping-stones between divergent soft-sediment reducing habitats at the deep-sea floor (Baco et al. 1999). Based on very rough estimates, the diversification of vesicomyid clams was approximately synchronous with the diversification of large cetaceans, suggesting that the relationship between whale and vesicomyid evolution merits further scrutiny (Baco et al. 1999).

Whale falls may also have been important in the evolution of vent-seep mytilids. The evolutionary origins of hydrothermal-vent and cold-seep species have been the subject of speculation. Many vent species are thought to have evolved from seep ancestors, with evolution progressing from shallow water to the deep sea (Hecker 1985, McLean 1985, Craddock et al. 1995). Until very recently, little attention had been given to the potential importance of organic-remain habitats (i.e. whale falls, wood falls, algal falls) in the evolution of vent-seep faunas. By studying DNA sequences of the nuclear 18S gene in mytilids from a range of deep-sea reducing habitats including hydrothermal vents, cold seeps, whale falls and wood islands, Distel et al. (2000) showed that whale fall and wood mussels in the genera *Idas*, *Adipicola* and *Benthomodiolus* were closely related to vent and seep mussels in the genera *Tamu* and *Bathymodiolus* (Distel et al. 2000). Baco et al. (Baco-Taylor 2002, Baco et al., unpubl. data) then used Mitochondrial 16S and COI DNA gene sequences to demonstrate an evolutionary sequence from sunken wood to whale falls to seeps and finally to vents, suggesting organic-remains mytilids preceded vent and seep mytilids in evolutionary time (Baco-Taylor 2002, Baco et al., unpubl. data). All three genes revealed that the organic-remains, vent, and seep mytilids form a monophyletic subfamily that evolved <30 mya from a shallow water ancestor (Distel et al. 2000, Baco-Taylor 2002, Baco et al., unpubl. data), consistent with the estimated diversification times for vesicomyid clams and large whales (see above).

Baco et al. (unpubl. data) also used carbon isotopic data combined with the mitochondrial DNA phylogenies to yield insights into the evolutionary history of mytilid-endosymbiont associations (Baco-Taylor 2002, Baco et al., unpubl. data). Many vent and seep mytilids are known to harbour sulphur-oxidising and/or methanotrophic endosymbionts. Based on $\delta^{13}C$ values, Baco et al. provided evidence that species on organic remains exhibited an increasing dependence on sulphur-oxidising chemoautotrophy over evolutionary time (Baco-Taylor 2002, Baco et al., unpubl. data). Stable isotope data also suggest that the mytilid-endosymbiont relationship evolved in organic remains-habitats, rather than in vent and seep environments (Baco-Taylor 2002, Baco et al., unpubl. data). All of these results provide strong support for the hypothesis that organic remains, including whale falls, have provided evolutionary stepping-stones as mytilids have radiated from shallow water into deep-sea vent and seep habitats.

Biotechnological spinoffs

When a whale carcass arrives at the deep-sea floor, a diverse assemblage of microbes colonises and decomposes the lipids and proteins contained in the remains (e.g. Allison et al. 1991, Deming et al. 1997). Because deep-sea habitats generally are cold (2–4°C), the bacter-

ial decomposers on whale falls are typically psychrophilic (i.e. they have optimal growth temperatures below 20°C) or psychrotrophic (i.e. are facultative psychrophiles). The enzymes of psychrotrophic bacteria are of particular commercial interest because they sustain high activities at low temperatures and yet remain relatively stable at high temperatures (J. Stein, pers. comm.). Enzymes with these characteristics are desirable in the detergent, pharmaceutical and food-processing industries. This potential for discovering psychrotrophs has led to the exploration of lipid-rich whale-fall habitats for novel bacterial enzymes (e.g. lipases and proteases) for use in cold-water detergents and other industrial applications.

Through use of recombinant cloning techniques, the biotechnology company Diversa, Inc. identified a large number of bacterial clones from whale carcasses with cold-adapted lipase activity. This approach allows direct access to the genomic information of natural microbial assemblages, in which >99% of the diversity remains unculturable. Some of the whale-carcass lipases appear to have promise as detergent additives, potentially allowing stains to be removed more efficiently from laundry during cold-water washing. The successful application of such enzyme to detergents could yield significant energy savings and prove profitable; the USA demand for detergent enzymes currently supports a market estimated at roughly \$150 million yr^{-1} (J. Stein, pers. comm.).

Anthropogenic influences on whale-fall communities

The populations sizes of large cetaceans have suffered major depredations from human whaling activities over the last 200 yr. In particular, the abundance of all the great whale species were drastically reduced, and some species exterminated (e.g. the North Atlantic gray whale), between 1860 and 1986 (Butman et al. 1995). Clearly, whaling has dramatically altered the rates and geographic distribution of whale falls to the deep-sea floor (Butman et al. 1995, 1996). Because whale falls harbour a specialised fauna and may provide dispersal stepping stones for some deep-sea sulphophiles, this reduction in whale falls may have caused species extinctions, and reduced species diversity, in deep-sea ecosystems ranging from whale falls to hydrothermal vents (Butman et al. 1995, 1996). Those species most dependent on whale falls are the most likely to have been exterminated, raising the possibility that whale-carcass habitats now retain only the most generalised subset of their original biota. Unfortunately, the structure of whale-fall communities, and assemblages in other deep-reducing habitats such as vents and seeps, has been studied only very recently, with data collection initiated in 1977 (Van Dover 2000). Thus, it will be very difficult to evaluate the biodiversity losses in whale-fall communities, and other deep-sea habitats, caused by intensive whaling. Some insights into the effects of fluctuating whale-carcass supply may be gained by studying whale-fall ecology and biogeography as global whale populations rebound from their hunting-induced lows (Butman et al. 1995). However, even such studies will fail to elucidate the identity and characteristics of species driven to extinction as an indirect consequence of whaling. This sobering thought highlights the need to explore the remote, poorly known ecosystems of the deep ocean prior to the further anthropogenic alteration of marine ecosystems (e.g. due to pollution, overfishing, and most significantly, global climate change) if we wish to reveal (and preserve) the ecological and evolutionary wonders of the deep sea.

Future directions

The last 15 yr have witnessed dramatic advances in our understanding of the ecology of whale falls. Nonetheless large gaps in our knowledge remain. A few research areas that could yield dramatic progress are highlighted below.

Microbial community structure and dynamics

Deep-sea whale bones and surrounding organically-enriched sediments are extreme environments in terms of organic loading, electron-acceptor availability, low temperature, and high hydrostatic pressure. In addition, whale falls are ephemeral, eutrophic habitat islands embedded in a generally oligotrophic sea floor. Such conditions may select for novel microbial metabolic strategies, dynamics, consortia and symbioses within the lipid-rich bone matrix, on bone surfaces, within the tissues of Metazoa, and in surrounding impacted sediments. While limited bio-prospecting for novel microbial enzymes has occurred in the whale-fall habitat (see above), virtually nothing is known about microbial biodiversity or the dynamics of microbially mediated biogeochemical transformations in deep-sea whale falls. In addition, the nature of microbial symbioses in bathymodiolin mussels on whale falls, and in organic-remains habitats is poorly understood. Because whale- and wood-fall bathymodiolins show evidence of increasing reliance on chemoautotrophic production (Baco et al. unpubl. data), studies of the mussels may provide insights into the evolution of chemoautotrophic endosymbiosis.

Macrofaunal reproduction, dispersal and gene flow

Because of the fragmented, relatively ephemeral nature of whale-fall habitats, whale-fall specialists are likely to exhibit reproduction and dispersal strategies atypical for the general deep sea, but potentially similar to those from hydrothermal vents and cold seeps (Van Dover 2000). Reproductive and dispersal strategies for whale-fall biota remain largely unknown, as do rates of gene flow among whale falls, and between whale falls and other types of reducing habitats. Settling cues for whale-fall specialists may be particularly unusual by deep-sea standards, and might include compounds characteristic of putrefaction, such as the diamines putrescine and cadaverine (Hart & Schuetz 1972).

Succession

Many issues concerning the structure and dynamics of whale-succession remain unresolved. How long can the sulphophilic stage last? Is faunal succession functionally and taxonomically similar on sunken whale carcasses in regions beyond the California slope, on the carcasses of other large invertebrates (e.g. whale sharks), or on other large concentrations of labile organic matter at the deep-sea floor (e.g. packages of sewage sludge, boluses of trawl discard)? How far back in the fossil record can such patterns of succession be documented for large carcasses (e.g. ichthyosaurs and plesiosaurs; see Hogler 1994 for speculation)? The answers to such questions are essential to understanding the dynamics of whale-fall habitat

islands, the recycling of large parcels of organic matter, and the evolution of sulphophiles and opportunistic species at the deep-sea floor.

Relationships between whale-fall, kelp-fall and wood-fall communities

While the communities associated with plant debris have been documented in many parts of the deep sea (e.g. Wolff 1976), faunal assemblages associated with large kelp falls and wood falls remain largely unstudied in the deep northeast Pacific, even though kelp falls may be common (e.g. Smith 1983, Harrold et al. 1998). Because large plant falls may provide concentrated and persistent sources of organic enrichment and reduced inorganic species (e.g. sulphide and methane; Smith 1983, Vetter 1994, Distel et al. 2000), they may foster assemblages closely related to the whale fall biota. In fact, it is quite conceivable that some of the species now regarded as potential whale-fall specialists utilise large kelp or wood falls as their primary habitat.

Biogeography and evolution of whale-fall communities

The structure of whale-fall assemblages on the California slope is reasonably well known but the sampling of whale-fall communities in other oceanic regions is extremely fragmentary. Thus far, several whale-fall species are known to be widespread within ocean basins (e.g. *Vigtorniella* n. sp. on Californian and Hawaiian bones (Dahlgren et al., unpubl. data), *Adipicola pelagica* in the North and South Atlantic (Dell 1987)) but it is impossible to say whether pan-basin distributions are the rule or exception. We are even further from describing the biogeographic provinces of the whale-fall biota, and how their structure is related to the distribution of whale feeding grounds and migration corridors, and to the documented biogeographic patterns of hydrothermal vents and cold seeps (Van Dover et al. 2002). Knowledge of these biogeographic patterns is essential to rigorous evaluation of the evolutionary history of the whale-fall, vent and seep biotas. Rather than speculate on these patterns, we look forward to more widespread studies of the ecology and biogeography of whale falls and other reducing habitats within the framework of such programmes as the Census of Marine Life's Chemosynthetic Ecosystems Project (ChEss; Tyler et al., in press).

Acknowledgements

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