Bigger is Better: The Role of Whales as Detritus in Marine Ecosystems

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Abstract. Dead whales are the largest, most food-rich detrital particles in the ocean, typically containing $>10^6$ g of organic carbon in energy-rich lipids and proteins. Most whales suffering natural mortality appear to sink rapidly to the deep-sea floor, with little loss of tissue during transit. Although whale detritus constitutes a small proportion of total organic flux to the deep sea, whale falls provide energy-rich habitat islands that are frequent on regional scales (e.g., with a mean nearest neighbor distance of $<16$ km in the northeast Pacific). Experimental studies on the California slope demonstrate that deep-sea whale falls support a succession of diverse macrofaunal assemblages, characterized in sequence by (1) mobile scavengers, (2) enrichment opportunists, and (3) sulfophiles (including chemoautotrophs); the entire successional process lasts for decades on large carcasses. The enrichment-opportunist and mobile-scavenger stages harbor at least 32 species that appear to be whale-fall specialists. Whale detritus in pelagic, continental shelf, and intertidal ecosystems does not appear to be a significant source of energy or habitat for novel animals, although some mobile, intertidal scavengers (e.g., polar bears), may obtain significant energetic benefits from whale carrion. Commercial whaling drastically reduced the occurrence of detrital whales in all marine ecosystems, and is likely to have caused substantial species extinction in deep-sea whale-fall assemblages due to loss of 65-90% of the whale-fall habitat. The species extinctions were likely most severe in the North Atlantic where whales were decimated in the 1800’s, and may be ongoing in the Southern Ocean and northeast Pacific, where intense whaling occurred into the 1960’s and 1970’s. Whaling may also have caused a decline in highly mobile coastal scavengers, in particular the California condor, that depended on stranded-whale carrion. Experimental implantation of lipid-rich, whale-bone packages in a variety of ocean basins could help to determine whether whaling induced extinctions have modulated biodiversity levels of whale-fall communities.
INTRODUCTION

Organic detritus plays fundamental roles in the structure and dynamics of all marine ecosystems. The importance of a particular type of organic detritus (i.e., non-living organic matter) in an ecosystem depends on a number of key characteristics, including: (1) The size of the detrital particles; (2) The nature of organic materials contained within the particles (e.g., the presence of energy-rich lipids and proteins); (3) The flux of organic carbon, or limiting nutrient, entering the ecosystem in the form of the detritus (especially relative to fluxes in other forms); (4) The frequency of occurrence of the detrital particles (essentially flux divided by particle size). These characteristics constrain the use of a particular detrital type by detritivores, and ultimately control the ecological and evolutionary opportunities (and selective milieu) provided by the detritus.

Dead-whale detritus has remarkable characteristics, and thus may play unusual roles in marine ecosystems. Cetaceans are by far the largest parcels of organic matter formed in the ocean, with adult body masses of the nine largest species, or the “great whales,” ranging from 5 to >160 tonnes (e.g., Lockyer 1976). The enormous size of adult great whales provides a refuge from most predators with the consequence that much of the natural whale mortality may occur from nutritional or disease stresses sustained during migrations (e.g., Gaskin 1982, Corkeron and Conner 1999, Moore et al. 2003). Based on relative population production rates, even the successful whale predators, i.e., the killer whales (*Orcinus orca*), appear to utilize a small
proportion of adult great-whale production. When predation events do occur, the
disproportionate mass of a great whale, and the sinking of carcasses, often precludes predators
from consuming most of the carcass (e.g., Silber et. al. 1990, Guinet et al. 2000). Thus, in
contrast to most other marine animals, great whale biomass typically enters the marine food web
as fresh carrion parcels many tonnes in size (Britton and Morton, 1994).

A fresh detrital whale consists mostly of soft tissues (87-92% by weight, Robineau and
de Buffrénil, 1993), with a 40 t carcass containing $1.6 \times 10^6$ g C in labile organic compounds
such as lipids and proteins. As a consequence, dead whales are among the most nutrient rich of
all detritus on both a weight- and particle-specific basis. The cetacean skeleton is also laden with
organic material, with large bones often exceeding 60% lipid by weight (Deming et al. 1987,
Smith and Baco 2003, Schuller et al. 2004). Thus, the ossified skeleton of a 40-t whale may
harbor 2000-3000 kg of lipid (Smith and Baco 2003), potentially providing substantial
nutritional resources, as well as habitat, for a variety of organisms.

Due to large body size, whale populations have low production rates compared to most
other organisms in the ocean (Katona and Whitehead 1988); thus, when averaged over large
areas, the flux of carbon through whale detritus is small relative to total detrital flux, even in the
most organic-poor ecosystems such as the abyssal seafloor (Jelmert and Oppen-Bernsten 1996;
see calculations below). Nonetheless, end-member characteristics in particle size and quality
potentially allow whale detritus to play disproportionate roles in the structure and evolution of
marine ecosystems.
Below I discuss current ecosystem responses to the input of whale detritus. I then estimate the effects of industrial whaling on the production of dead whales, and speculate on the consequences of these changes for marine ecosystems. Finally, I propose an experimental approach to test some of these speculations.

CURRENT ECOSYSTEM RESPONSES TO WHALE DETRITUS

Production and initial fate of whale detritus

Great whales suffering natural mortality are typically in poor nutritional condition and negatively buoyant upon death; as a consequence, most whale carcasses initially sink towards the seafloor (Ashley, 1926, Schafer 1972, Gaskin 1982, Guinet et al. 2000, Smith and Baco 2003, D. W. Rice personal comm.). Because there appear to be few scavengers on whale sized particles in midwater (Britton and Morton 1994), and because whale carcasses will sink rapidly following lung deflation from hydrostatic pressure, it is extremely likely that relatively little tissue removal will occur during a dead whale’s descent to the seafloor. If a whale carcass sinks in deep enough water, hydrostatic pressure will limit the generation of buoyant decompositional gases through reduction of gas volume and increased gas solubility (Allison et al. 1991). At depths greater than 1000 m, the amount of microbial tissue decay required to generate carcass buoyancy (e.g., >67 % of carcass mass through fermentation) is prohibitive; the soft tissue of a carcass will be removed by scavengers or disintegrate from microbial decomposition long before positive buoyancy can be generated, and the carcass will remain on the seafloor (Allison et al. 1991). At shallower depths, there is some probability that gas generation could refloat a whale carcass, although this
will depend in part on the outcome of competition for soft tissue between scavengers and microbes. It is interesting to note that an essentially intact gray-whale carcass has been found at 150 m depth in Alaskan waters, suggesting that, in cold waters where whales often abound, even 15 atm of pressure may prevent decompositional flotation of a whale carcass (Smith and Baco, 2003).

Based on this reasoning, most great-whale “detritus” will be rapidly deposited onto the seafloor. Because 88% of the ocean is underlain by ocean bottom deeper than 1000 m, the vast bulk of great-whale detritus is very likely to begin recycling at the deep-sea floor. In contrast, while whale strandings receive prominent play in the mass media, a relatively small proportion of great-whale detritus appears to reach the intertidal zone. For example, out of ~1600 gray whales (Eschrichtius robustus) dying annually in the Northeast Pacific (Smith and Baco, 2003, and references therein), only ~50 per year become stranded along the shoreline in a typical year, and the record 273 strandings in 1999 represented less than 20% of average annual gray-whale mortality (Rugh et al., 1999). Because most whale detritus likely ends up at the deep-sea floor, the deep-sea ecosystem response to great-whale detritus is discussed first.

Deep-sea effects of whale detritus

When averaged over the entire deep-sea floor, the flux of particulate organic carbon (POC) in the form of great-whale carcasses is modest. The flux of small POC to the deep-sea floor ranges between ~0.3 and 10 g C$_{org}$ m$^{-2}$ y$^{-1}$ (e.g., Smith and Demopoulos, 2003). For comparison, Smith and Baco (2003) estimated that approximately 69,000 great whales die each
If we assume that whale biomass is 5% organic carbon, that the average weight of a dying great whale is 40 t, and that the ocean covers $3.6 \times 10^8$ km$^2$, the flux of organic carbon to seafloor from whale falls averages $3.8 \times 10^{-4}$ g C$_{org}$ y$^{-1}$ (see Jelmert and Oppen-Bernsten (1996) for similar calculations). This is only about 0.1% of the background POC flux to the deep-sea floor under the most oligotrophic central gyre waters. Even if whale mortality and flux is 10-fold greater along migration corridors or in whale feeding grounds, background POC flux will also be higher in these regions because they typically occur along ocean margins or oceanographic fronts. Thus, it is difficult to imagine that the flux of great-whale detritus would exceed 0.3% of seafloor POC flux anywhere in the deep sea.

However, whales do not sink as an even veneer of organic matter, but rather as giant organic-rich lumps (e.g., Butman et al. 1995). The ~50 m$^2$ of sediments immediately underlying a fresh whale fall sustains, in a single pulse, the equivalent of about 2000 yr of background POC flux at abyssal depths (Smith and Baco 2003). In addition, these massive enrichment events can be common on regional scales. For example, Smith and Baco (2003) estimated conservatively that within the North Pacific gray-whale range, whale falls occur annually with an average nearest neighbor distance of <16 km. If whale falls produced organic-rich “islands” at the food-poor deep-sea floor for extended time periods (e.g., Stockton and DeLaca, 1982), they could support archipelagos of specialized communities, much as do hydrothermal vents and cold seeps (Van Dover, 2000).

How do deep-sea ecosystems respond to the massive flux event of a whale fall? Although the deep-sea floor is remote and relatively poorly studied, there is now substantial evidence that
sunken whales create persistent, ecologically significant habitats. Most information concerning
the seafloor fate and impacts of whale detritus comes from the California slope, beneath the
migration corridor of the northeast Pacific gray whale. I will review the California-slope data
first, and then summarize knowledge from other deep-sea regions.

The first natural whale-fall community was discovered on the California slope in 1987
(Smith et al. 1989). Study of this assemblage led to the hypothesis that deep-sea whale falls pass
through four successional stages (Bennett et al. 1994):

1) A mobile scavenger stage, during which necrophagous fish and invertebrates rapidly
   remove whale soft tissue,

2) An enrichment-opportunist stage, during which dense assemblages of heterotrophic
   bacteria and invertebrates colonize the lipid-laden skeleton and surrounding
   sediments enriched by whale-tissue “fallout,”

3) A sulfophilic stage, during which chemoautotrophic assemblages colonize the
   skeleton as it emits sulfide from anaerobic decomposition of internal lipids, and

4) A reef stage, during which the hard, elevated skeletal remains are colonized by
   suspension feeders exploiting flow enhancement.
Experimental, time-series studies of whale falls at depths between 1000 and 2000 m on the California slope provide strong evidence for the first three successional stages; these data are reviewed below.

The mobile-scavenger stage. Whale carcasses (n= 2, wet weights of 5 and 35 t) studied at 0.25 and 1.5 months after arrival at the seafloor exhibited community patterns consistent with a mobile scavenger stage (Fig. 1). Within this time frame, carcasses were largely intact, with the predominant scavengers including hundreds of hagfish (mostly *Eptatretus deani*), and several sleeper sharks (*Somniosus pacificus*) 1.5-3.5 m in length (Smith *et al.*, 2002). Other important scavengers included many thousands of small (~0.5 cm long) lysianassid amphipods on one carcass, and large lithodid crabs, possibly *Paralomis multispina*, on the other (Smith and Baco, 2003). During this stage, hagfish were drawn from minimum distances of 0.6 – 0.8 km (Smith and Baco, 2003) and the stage lasted approximately 0.3 – 1.5 yr, depending on carcass size (5 or 35 t). Time-lapse photography and *in situ* sampling suggested that most of the soft tissue was directly removed by necrophages, especially *S. pacificus*, even though putrefaction was occurring within the whale flesh. The resultant tissue removal rates estimated for the scavenger assemblages (40 – 60 kg d\(^{-1}\)) imply that a 160 t blue whale (*Balaenoptera musculus*) carcass might support a mobile scavenger stage for as long as 7-11 yr. A total of 38 species of megafauna and macrofauna have been identified from whale falls in the mobile scavenger stage (Baco-Taylor, 2002, Smith and Baco, 2003), with most species apparently being generalized scavengers. Calculations combining whale-fall spacing (for *Eschrichtius robustus* in the northeast Pacific) with scavenger foraging rates and fasting times indicate that large mobile scavengers such as rattails, hagfish and lysianassids are unable to specialize on whale falls, given
current stock sizes of great whales in the northeast Pacific (Smith and Baco, 2003). Nonetheless, the scavenger assemblages on the California slope are well adapted to recycle the soft tissue of whale carcasses over surprisingly short time scales (i.e., months to years).

*The enrichment-opportunist stage.* Communities consistent with an enrichment-opportunist stage were documented on carcasses (n=3) ranging in size from 5 – 35 t at the seafloor for 0.3 – 4.5 yr. During this stage, sediments within 1-3 m of the skeleton were heavily enriched in organic matter (in some cases exceeding 10% organic carbon by weight) by tissue particles dispersed by scavengers. Organic-rich bones and sediments during this time were colonized by extremely high densities of heterotrophic macrobenthic polychaetes, mollusks and crustaceans (Fig. 1)(Smith et al. 2002, Smith and Baco 2003). In some areas, bacterial mats also covered sediments nearby the skeleton. Macrofaunal densities in the sediments within 1-3 m of the carcass attained 20,000 – 45,000 individuals m$^{-2}$ in as little as 4 months (Fig. 2); these densities exceeded background levels by an order of magnitude, and are the highest ever reported for macrofauna below 1000 m depths (Smith and Baco 2003). A number of the most abundant species in organic-rich sediments and on whale bones are new to science (e.g., two dorvilleid polychaetes, a chrysopetalloid polychaete, and a gastropod) and could be whale-fall specialists; other species abundant on the whale falls during this stage have been collected at other types of organic enrichment (e.g., fish falls, Smith 1986) and are likely to be generalized opportunists. Despite high macrofaunal densities near the whale carcasses, species diversity adjacent to the skeletons was low (e.g., only 18 macrofaunal species)(Fig. 2). This rapid colonization by a high-density, low-diversity assemblage is strongly reminiscent of shallow-water opportunistic communities around sewage outfalls and beneath salmon pens (e.g. Pearson and Rosenberg
1978, Weston 1990, Zmarzly et al. 1994), and indicates that intense pulses of organic enrichment (e.g., whale falls, large kelp falls, etc.) are common enough at slope depths off California to have allowed the evolution of enrichment opportunists (Smith and Baco 2003). The duration of the *enrichment-opportunist stage* is likely to vary substantially with whale-carcass size, and ranges from <2 yr for a 5-10 t carcass, to at least 4.5 yr for a 35 t carcass.

**The sulfophilic stage.** Following scavenger removal of soft tissue from great-whale carcasses on the California slope, the recycling of lipids trapped within the skeleton (5-8% of total body mass) appears to be dominated by anaerobic microbial decomposition (Smith 1992, Deming et al. 1997, Smith and Baco 2003). Sulfate reduction is particularly important, providing a sustained efflux of sulfides that can support sulfide-based chemosynthetic bacteria, both free-living and endosymbiotic within the tissues of mussels, clams, and vestimentiferan polychaetes. Such a sulfophilic stage, composed of chemosynthetic microbes and other sulfide-tolerant species, has been documented on four California-slope whale skeletons at the seafloor for > 2 yr (Bennett et al. 1994, Smith and Baco 2003). This stage is characterized by several key components including (Smith and Baco 2003):

1) Mats of heterotrophic and chemosynthetic bacteria growing on bone surfaces, and within bone sutures and trabaculae,

2) Large populations (>10,000 individuals per skeleton) of the mussel *Idas washingtonia*, which harbors chemosynthetic endosymbionts,

3) Rich macrofaunal communities (>30,000 individuals) composed of bivalves, isopods, amphipods, polychaetes, limpets, and snails constituting at least three trophic levels.
Whale-fall communities in the sulfophilic stage are remarkably species rich, with an average of 185 species per skeleton; they appear to have the highest local species richness of any known deep-sea, hard-substrate community (Baco and Smith 2003). Many of the species from the sulfophilic stage are extremely abundant on whale skeletons, but have rarely, if ever, been collected in surrounding habitats; they thus may be specialists that have evolved in sulfide-rich, whale-skeleton habitats (see discussion below). The sulfophilic stage also exhibits faunal overlap with other deep-sea, chemosynthetic communities, sharing 11 species (including vesicomyid clams, bathymodiolin mussels, and a vestimentiferan polychaete) with hydothermal vents, and 20 species with cold seeps (Baco et al., 1999, Smith and Baco 2003).

Large whale skeletons on the California slope sustain rich sulfophilic communities for extended time periods. Schuler et al. (2004) used $^{210}$Pb/$^{226}$Ra disequilibrium and lipid degradation rates in whale bones to show that large whale skeletons may support sulfophilic communities for 40 – 80 yrs. The skeletons of juvenile gray whales appear to support the sulfophilic stage for much shorter periods of time (e.g., several years) because the poorly calcified bones disintegrate much more rapidly, releasing the lipid reservoir (Baco-Taylor 2002, Smith and Baco 2003).

**Whale-fall succession in other regions.** Considerably less is known about deep-sea community response to whale falls beyond the California slope, but there is evidence that a succession of scavengers, enrichment opportunists and sulfophiles will also colonize carcasses in other regions. For example, numerous studies suggest that mobile scavengers will feed voraciously on fresh
whale falls throughout the well-oxygenated deep sea (Isaacs and Schwartzlose 1975, Hessler et al. 1978, Jones et al. 1998, Smith and Baco 2003). Furthermore, organic-rich sediments with an abundant microbial assemblage are documented beneath a whale fall in the western Pacific (Naganuma et al., 2001), and enrichment opportunists are known from sites of organic loading in a range of deep-sea settings (e.g., Turner 1977, Grassle and Morse-Porteus 1987, Desbruyeres and Laubier 1988, Levin et al. 1994, Snelgrove et al. 1994, Kitazato and Shirayama 1996, Snelgrove and Smith 2002). Finally, sulfophilic assemblages appear to be widespread on whale carcasses in the deep sea because bathymodiolin mussels with chemoautotrophic endosymbionts have been recovered from whale bones in the North and South Atlantic, and in the northwestern and southwestern Pacific, at depths ranging from 220 to 4037 m (Wada et al. 1994, Naganuma et al. 1996, 2001, Baco-Taylor 2002, Smith and Baco 2003). Sulfophilic assemblages have also been found on fossil deep-sea whale skeletons as old as 30 myr (Squires et al. 1991, Goedert et al. 1995), indicating that whale skeletons have supported chemoautotrophic communities over evolutionary time (Distel et al. 2000). Thus, succession on whale falls in the deep-sea in general is likely to be functionally similar to that on the California slope, and this successional process, including colonization by sulfophiles, is likely to have occurred for at least 30 myr. Nonetheless, species structure and rates of successional change may differ dramatically in other parts of the deep sea, and patterns of succession are likely to have varied following the radiation of large whales since the Miocene (Gaskin 1982, Distel 2000). In particular, in the modern ocean in regions such as the North Pacific central gyre, where whale falls should be much less common and seafloor communities are much more depauperate (e.g., Smith and Demopoulos 2003), whale-fall succession is expected to be extremely protracted (potentially lasting > 100 yr) and species-poor compared to the California slope.
**Biodiversity and whale-fall specialists.** Deep-sea whale-fall communities, in particular those in the sulfophilic stage, may harbor remarkable levels of both local and global species richness. Whale falls are perhaps the least-studied chemosynthetic habitats in the deep sea, having been intensively sampled only along the California slope. Nonetheless, 407 animal species are known from whale falls, with 91% coming from California-slope whale falls alone (Baco and Smith 2003). This rivals the global species richness (469) known for far more intensively studied hydrothermal vents (Tunnicliffe et al. 1998), and substantially exceeds the number (~230) known from cold seeps (Sibuet and Olu 1998, Baco and Smith 2003). The relatively high species richness on lipid-rich whale skeletons likely results from the broad array of nutritional modes sustained by whale falls; a whale skeleton supports sulfophiles (e.g., species with chemoautotrophic endosymbionts), bone-matrix feeders, saprophages, generalized organic-enrichment respondents, and typical deep-sea deposit feeders and suspension feeders, all in close proximity (Baco and Smith 2003). Clearly, whale falls are heavily exploited habitat islands at the deep-sea floor.

There is increasing evidence that whale falls provide habitat for a specialized fauna, i.e., a suite of species that is specifically adapted to live on whale remains. Bennett et al. (1994) first noted a bimodal pattern in the frequency distribution of species abundances on whale skeletons suggesting the presence of core species particularly adapted to whale-bone niches (qualitatively similar patterns are observed in dung and carrion assemblages in terrestrial environments). To date, 36 macrofaunal species were first collected on whale falls, and 28 of these have not been
found in any other habitat (Table 1). A number of the species thus far unique to whale carcasses are extremely abundant, indicating that they are well adapted to whale falls and can attain substantial population sizes given suitable conditions. The absence of these species in samples from other related habitats (e.g., wood falls, algal falls, enriched sediment trays, hydrothermal vents, and cold seeps), suggests that they may indeed be endemic to whale falls.

In addition to the 28 potential whale-fall endemics, there are at least five other species that may be dependent on whale falls (Table 2). These are species that attain extraordinary abundance on whale carcasses, but occur only as isolated individuals in other habitats. It is likely that a large proportion of the total individuals within these species live on whale falls, essentially making them whale-fall specialists (i.e., their evolution has been largely shaped by selective pressures at whale falls)(Bennett et al., 1994). This brings the total number of potential whale-fall specialists to 33. This number of potential whale-fall specialists is likely to rise substantially as the diverse dorvilleid (estimated to be 40 species), amphipod, and copepod components of the California-slope whale-fall fauna are rigorously examined by taxonomists, and as whale-fall communities are more intensively sampled throughout the world ocean.

It should be noted that potential whale-fall specialists span a broad range of taxonomic and functional groups. These “specialists” come from five different phyla, and appear to include whale-bone feeders (*Oseax*, a sipunculid and some limpets), bacterial grazers (some limpets, *Ilyaracha profunda*), species utilizing chemoautotrophic endosymbionts (the bathymodiolins, thyasirid, vesicomyid, and siboglinid), deposit feeders (the ampharetids), facultative suspensions feeders (the bathymodiolins), and predators (the polynoids, *Paralomis manningi*)(see discussion
of food webs above). This diversity suggests that a variety of taxa and trophic types have
become specifically adapted to whale-fall niches, and depend (in aggregate) on a variety of
resources provided by the whale-fall habitat.

*Whale detritus at shelf depths*

Remarkably little is known about the ecosystem response to whale falls at shelf depths.
Because seafloor POC flux rates are typically much higher on the shelf than in the deep sea, the
flux of organic carbon to the shelf floor in the form of whale detritus likely makes an
insignificant contribution to the nutrient budgets of the continental shelf (e.g., Katona and
Whitehead 1988). Exceptions to this generalization might occur in calving lagoons, such as Ojo
de Liebre and San Ignacio Lagoons in Mexico, where gray-whale strandings, and mortality in
general, are likely to be concentrated in unusually small areas (e.g., Rugh et al. 1999).

Whale falls are certain to attract scavenger aggregations and undergo community
succession on the continental shelf floor, but only very limited, anecdotal information concerning
such shelf processes is available. At 150 m depths off Alaska, a gray-whale carcass with
substantial remaining soft tissue had attracted dense clouds of scavenging lysianassid amphipods
(T. Shirley, personal communication). At 90-m depths in the Strait of Juan de Fuca near San
Juan Island, a 30 t fin whale (*Balaenoptera physalus*) placed at the seafloor for three months
attracted a moderate diversity of facultative fish and shrimp scavengers, although little tissue
removal had occurred (A. Shepard, D. Duggins and C. Smith, unpublished data). In this
relatively high-flow setting, no bacteria mats were visible on the carcass, possibly due to
disruption by currents. After 28 months at the seafloor, the fin-whale carcass had been stripped of soft tissue (D. Duggins, personal communication).

There are very few data to indicate whether lipid-rich whale bones support a specialized fauna at shelf depths. The mussel *Myrina pacifica*, which is thus far known only from whale bones, has been collected at 220 m on the Japanese slope (Baco-Taylor 2002, Smith and Baco 2003), but this may reflect the upper end of a bathyal (i.e., deep-sea) depth distribution. In addition, a new species of Polyplacophora (*Callistochiton* sp.) has been collected on whale bones from 240 m off Concepcion, Chile (J. Sellanes, personal communication), but once again it is unclear whether this is predominantly a shelf or bathyal species. It is conceivable that whale falls, like hydrothermal vents (Van Dover 2000), only support an endemic fauna in the deep sea, below depths of a few hundred meters. If true, this contrasts with other organic-rich substrates, in particular wood falls, which support highly specialized (albeit, non-overlapping) species in both the deep sea and shallow water (e.g., Turner 1973, 1977, Coan et al. 2000). Clearly, the dynamics and biogeography of whale falls at shelf depths merit substantial further study.

*Whale detritus in the intertidal*

Only a small percentage of great-whale mortalities result in strandings in the intertidal, even for essentially coastal species such as the gray whale, *E. robustus* (Jones et al. 1984). For example, roughly 50 gray whales in the northeast Pacific, comprising < 5% of annual mortality, come ashore in a typical year (Rugh et al. 1999, Moore 1999, Smith and Baco 2003). This represents approximately one gray-whale stranding per year per ~200 km of coastline along the...
~10,000-km gray-whale migration route, or a flux of organic carbon from whale detritus of \( \sim 10 \text{ g C}_{\text{org}} \text{ m}^{-1} \text{y}^{-1} \) (assuming each whale carcass weighs 30 t and is 5% organic carbon). The flux of drift carrion from other sources (e.g., jellyfishes, fishes, turtles, seabirds, and other marine mammals) to beaches in the northeast Pacific, based on very limited measurements, appears to be roughly an order of magnitude higher (Columbini and Chelazzi 2003). Thus, whale detritus (if left undisturbed on the beach) appears to be a relatively minor source of carrion for intertidal scavengers (e.g., Rose and Polis 1998). However, it has been suggested that cetacean carcasses are important in the diet of some highly mobile terrestrial scavengers such as polar bears (\textit{Ursus maritima}) and Arctic fox (\textit{Alopex lagopus}), and that whale carrion may have helped coastal populations of California condors (\textit{Gymnogyps californianus}) to survive following the extinction of the Pleistocene terrestrial megafauna (Katona and Whitehead 1988). Reliance on whale carrion by local populations of terrestrial scavengers seems especially likely around calving lagoons, such as Ojo de Liebre and San Ignacio in Mexico, where whale strandings are especially frequent (Rugh et al. 1999).

Very few data appear to be available on the natural recycling of stranded whale carcasses, but some generalizations appear possible. Although scavengers, such as seabirds, shorebirds, polar bears, foxes and vultures, may remove some of the soft tissue from whale carcasses (e.g., Schafer 1972, Katona and Whitehead 1988, Colombini and Chelazzi 2003), stranded cetaceans appear to be recycled primarily by microbes and terrestrial arthropods (e.g., flies, ants, and trogid, dermestid, and silphid beetles) (Columbini and Chelazzi 2003). Carcass reduction may take many months or even many years if mummification occurs (Schafer, 1972), and involves a variety of decompositional stages (e.g., bloat, internal-liquification, and dry-tissue stages) with...
successional patterns resembling those for large carcasses in fully terrestrial habitats (Schafer, 1972, Cornaby 1974, Colombini and Chelazzi 2003). Thus, whale detritus stranded on beaches appears to be largely removed from marine food webs, with very little direct impact on marine ecosystems. In essence, whale strandings constitute a small, natural detrital flux from the ocean to land.

*Whale detritus in the pelagic realm*

Whales that die in shallow water become inflated with decomposition gases within days, becoming buoyant detrital particles that may drift at the sea surface for weeks. The total flux of organic material in the form of whale detritus clearly is very small compared to other pelagic detrital sources (whale detrital carbon flux is < 0.0005% of primary production rates even in oligotrophic regions), suggesting the energy input from whale detritus is not significant. Very limited observations indicate that during the early stages of decomposition, floating whale carcasses may be scavenged by sharks (e.g., blue sharks, *Prionace glauca*, and tiger sharks, *Galeocerdo cuvier*) and seabirds, although massive tissue removal is not usually observed (C. Smith, personal observations). Over periods of weeks, microbial decay weakens the cetacean connective tissues, and large skeletal components with tissue attached (e.g., the jaw, skull, sections of vertebrae) break off the carcass and sink to the seafloor (Schafer 1972). Thus, even for whales that die and initially float at the sea surface, much of the organic matter contained in the carcass ultimately becomes recycled at the seafloor. The small flux and short residence time of whale detritus at the sea surface suggests that there is little opportunity for whale carcasses to support a specialized community in pelagic ecosystems.
IMPACTS OF WHALING ON THE ROLES OF WHALE DETRITUS

Hunting by humans caused massive reductions of great whale populations throughout the world oceans. The patterns of whale population depletion, carcass utilization and, in some cases, whale population recovery, differed substantially over time, among cetacean species, and among ocean basins, with the consequence that whaling has had complex effects on the availability of great-whale detritus to marine ecosystems. Below, I attempt to reconstruct patterns of whale-detritus depletion resulting from commercial whaling and speculate on some of the consequences, particularly for deep-sea whale-fall communities.

Effects of whaling on the production of whale detritus

To evaluate the impacts of whaling on the production of whale detritus, it would be extremely useful to reconstruct the population trajectories of exploited cetaceans in each ocean. Despite the efforts of the International Whaling Commission (IWC) and numerous scientists, such reconstructions are generally not possible, and estimates of pre-whaling cetacean population levels remained controversial and politically charged (e.g., Roman and Palumbi 2003). It does seem clear that great whales, especially coastal species such as the Atlantic gray whale, began to be intensively exploited in the North Atlantic in the early 1800’s (Tonnenssen and Johnson 1982, Whitehead 2002). Whaling efforts then intensified in the tropical and temperate Pacific in the mid 1800’s, in Antarctic waters after 1910, and in higher latitudes of the North Pacific and in the
Bering Sea as late as the 1950’s (IWC 1993, Whitehead, 2002, Springer et al. 2003, E. Danner, personal communication based on IWC catch statistics, Fig, 3). However, for many large species (e.g., fin, sperm, sei, blue, humpback, and minke whales), the bulk of the worldwide take occurred between approximately 1920 and 1980 (i.e., during 1-2 generations of a great whale), with the IWC estimating that roughly 2 million great whales were harvested from the oceans over this period (Fig. 3)(E. Danner, personal communication). For all but the sperm whale, it appears safe to say that great-whale population sizes were reduced an order of magnitude or more by whaling (e.g., IWC 1993, Best 1994, Roman and Palumbi 2003); for sperm whales, a reduction to ~30% of pre-whaling values appears to be the best estimate (Whitehead 2002). Thus, as a rule of thumb for estimating whaling effects on the production of whale detritus, I will assume a 10-fold reduction in great-whale standing stock. In many cases, especially in the North Atlantic, boreal North Pacific and Southern Oceans, great-whale populations remain at only 10-20% of pre-whaling levels (e.g., Best 1993, Springer et al. 2003, Roman and Palumbi 2003), with a few notable exceptions (e.g., the northeast Pacific gray whale, Rugh et al. 1999).

Pelagic/shelf/intertidal effects of whaling. During both the open-boat and modern era of whaling (i.e., pre- and post-1900, respectively, Whitehead 2002), the net effect of whaling must have been a straightforward reduction of whale detrital inputs to pelagic, shelf and intertidal ecosystems. This is because during the open-boat era, whale carcasses taken in the high seas typically were stripped of blubber and released to sink to the deep-sea floor (Tonnenssen and Johnson 1982); whales caught near shore (e.g., over the continental shelf) were likely to have been towed ashore for processing. Modern whaling leaves little detritus for the marine ecosystem because entire carcasses are processed on factory ships, or on shore (e.g., Tonnenssen and
Johnson 1982). Thus, with very localized exceptions (e.g., the inter- and subtidal in the immediate vicinity of whaling stations), harvested carcasses were essentially removed from pelagic, shelf and intertidal ecosystems.

By reducing great-whale populations by an order of magnitude, whaling must have forced a roughly 10-fold decline in the flux and availability of great-whale detritus in pelagic, shelf and intertidal ecosystems. For coastal populations of the California condor (*Gymnogyps californianus*), the loss of whale carrion may have been significant, and could have caused dramatic population declines. It also is conceivable that coastal populations of other wide-ranging scavengers that fed on stranded whales (e.g., polar bears, arctic foxes, and grizzly bears (*Ursus arctos horribilis*)) declined as a consequence of commercial whaling. It is interesting to note that while gray-whale populations have rebounded in the northeast Pacific, most stranded whale carcasses are still removed from beaches (C. Smith, personal observations), yielding on ongoing depletion of whale carrion. From a community-level perspective, the current energetic contribution of great-whale detritus to pelagic and shelf ecosystems appears to be so small that even if great-whale detrital fluxes were restored to pre-whaling levels, the ecosystem consequences would be modest. However, in some intertidal areas, a 10-fold increase in the frequency of whale strandings could yield a carbon flux approaching that from other sources of marine carrion (see discussion above), suggesting that, prior to commercial whaling, stranded whales could have been a significant source of carrion to mobile scavenger assemblages along coastlines. This conclusion must remain tentative until the intertidal flux of carrion from all sources is more intensively studied in various ocean regions.
As for shallow marine systems, whaling must ultimately have led to a dramatic decline in whale-fall habitats at the deep-sea floor, potentially yielding extinction of whale-fall specialists, and limiting the dispersal of species dependent on sulfide-rich whale skeletons as habitat stepping stones (Butman et al. 1995, 1996, Committee on Biological Diversity in Marine Systems 1995, Smith and Baco 2003). However, the effects of whaling on whale-fall abundance in the deep sea were not necessarily monotonic because of two opposing factors.

(1) Prior to ~1900, the initiation of whaling in a region increased flux of whale carcasses to the seafloor because whale carcasses were discarded to sink after removal of blubber, baleen, spermaceti and minor components (Tonnenssen and Johnsen 1982, Butman et al. 1995). The flux of carcasses to the deep-sea floor must also have been redistributed by carcass discards relative to natural whale mortality because early whaling was initiated near home ports, and then moved further afield as local populations became depleted (e.g., Butman et al. 1995, Springer et al. 2003). In contrast, natural whale mortality is likely to have been distributed along migration routes, in calving grounds, or in regions where whales spend substantial portions of their life cycles (Butman et al. 1995, Rugh et al. 1999, Smith and Baco 2003).

(2) Ultimately (and immediately in the modern era), whaling decreased the flux of carcasses to the deep-sea floor because whale populations were driven downward, leaving far fewer whales to suffer natural mortality and sink to the seafloor.
The initial increase and subsequent decrease in carcass production resulting from whaling, combined with spatial and temporal variations in the activities of whalers, have caused historical patterns of dead-whale flux to vary among ocean basins. In addition, whale-fall communities pass through successional stages with different persistence times (ranging from months to decades), yielding time lags between a reduction in whale-carcass flux and the decline of particular community types at the seafloor. Without accurate population trajectories for all great whales in all basins, a detailed reconstruction of whale-fall habitat loss and likely patterns of species extinctions is not possible. However, the limited data available on whale-population trajectories do provide some insights into the historical biogeography of whale-fall habitat loss.

The most comprehensive population trajectory available in the refereed literature for any great-whale species was developed by Whitehead (2002) for the sperm whale (*Physeter macrocephalus*), with reconstruction of the global population size since 1800. Using a few reasonable assumptions, the abundance over time of sperm-whale carcasses supporting mobile-scavenger, enrichment-opportunist, and sulfophilic communities in the deep sea can be estimated using the sperm-whale population trajectory (Fig. 4). The largest number of potential whale-fall specialists are found in sulfophilic communities (Tables 1 and 2) (Smith and Baco 2003), so the dynamics of this community type are perhaps most relevant to species extinction. Several points emerge from modeling the abundance of sperm-whale falls at the deep-sea floor over time since 1800. (1) The discard of whale carcasses only modestly enhanced the number of whale-fall communities, e.g., increasing the number of sulfophilic communities by ~ 20% over natural processes in 1850 (Fig 4). (2) Because of short residence times, the abundances of mobile-
scavenger and enrichment-opportunist communities respond rapidly to changes in whale-fall abundance, while sulfophilic communities respond with a 40-yr time lag to whale depletion. Thus, the number of sulfophilic communities on sperm-whale skeletons is estimated to be declining now, even though sperm-whale abundance passed a minimum in 1981, and is currently about 40% of pre-exploitation levels (Fig. 4). Based on the global sperm-whale trajectory, whale-fall specialists may be only now approaching their greatest habitat loss, potentially causing species extinctions to be occurring at their highest historical rates. Species-area relationships suggest that loss of 60% of the area of a habitat, such as has occurred for sperm-whale falls, should yield extinction of 20% or more of its endemic fauna (e.g., Pimm and Askins 1995, Ney-Nilfe and Mangel 2000).

Regional asynchrony in the extermination of great whales suggests that ocean basins may be in different phases of whale-fall habitat loss and species extinction. Whale populations were first reduced in the North Atlantic in the 1800’s, and even now may remain at < 25% of pre-whaling levels (Roman and Palumbi 2003). Because whale abundance has remained low in the North Atlantic for approximately 150 yr (i.e., much longer than the lag time resulting from sulfophilic community persistence), the number of whale-fall habitats have long since adjusted to low whale abundance, and species extinction driven by habitat loss is likely to be well advanced (e.g., Brooks et al. 1999). The loss of species may be substantial in the North Atlantic because whale-fall habitat abundance has been held at 10-25% of pre-exploitation levels for an extended time; species-area relationships (e.g., Pimm and Askins 1995, Ney-Nifile and Mangel 2000) suggest that such habitat reduction will extinguish 30-50% of the specialized whale-fall fauna. In contrast, southern-hemisphere great whales were heavily exploited much later, i.e., between
1920 and 1965 (Fig. 3), with their populations remaining low to the present (e.g., Best 1993, Young 2000). As consequence, sulfophilic communities in the Southern Ocean are likely only now to be approaching their historic lows, with extinction of whale-fall specialists in the acceleration stage. Species extinctions are probably least advanced in the northeast Pacific, where the greatest depletion of most large whales did not occur until the 1970’s (Fig. 3, Springer et al. 2003). In addition, some species, such the gray whale, had substantially recovered by 1970 from depredation suffered in the 1800’s (Fig. 4), with the consequence that whale-fall habitats in the northeast Pacific may never have reached the relative lows experienced in the North Atlantic. Thus, one can predict that species extinctions and diversity loss in whale-fall communities have been greatest in the North Atlantic, have been substantial and are likely accelerating in the Southern Ocean, and have been least intense in the northeast Pacific. If species extinction due to whaling has dramatically altered the biodiversity of whale-fall communities, one would predict that current biodiversity levels are lowest in the North Atlantic and highest in the northeast Pacific.

Can we rigorously test this prediction to determine whether patterns of whale-fall biodiversity are consistent with whaling induced species extinctions? A reasonable experimental approach would be to emplace uniform packages of lipid-rich whale bones at similar depths in the North Atlantic, Southern Ocean and northeast Pacific, and then, after a sufficient time period (i.e., 2-3 yr), compare biodiversity levels of bone-colonizing assemblages across basins. This experimental approach is quite feasible because bone implantations have fostered sulfophilic community development on the California slope, and similar experimental approaches (i.e.,
using standardized colonization substrates) have been used to assess regional variations in the biodiversity of fouling assemblages in shallow-water communities (e.g., Ruiz et al. 2000).

**Conclusions**

Whale carcasses are end members in the spectrum of marine detritus, constituting the largest, most energy-rich organic particles in the ocean. Most great-whale carcasses sink essentially intact to the deep-sea floor, where they are recycled by a succession of scavenger, enrichment-opportunist, and sulfophilic assemblages. Although the flux of organic carbon in whale falls is small compared to total detrital flux, the massive energy concentrated in a whale fall can support a diverse deep-sea community (~370 species in the northeast Pacific) for decades, including a significant number of potential whale-fall specialists (> 32 species). The ecosystem impacts of detrital whales in epipelagic, shelf, and intertidal ecosystems is poorly known but appears to be small, although some highly mobile intertidal scavengers (e.g., polar bears) could obtain important nutritional inputs from whale carrion.

Commercial whaling has drastically reduced the flux of whale detritus to all marine ecosystems. In intertidal habitats, this may have caused population declines in some scavenging species (e.g., the California condor) dependent on whale carrion. At the deep-sea floor, whaling led to substantial habitat loss to whale-fall communities and likely caused the first anthropogenic extinctions of marine invertebrates in the 1800’s in the North Atlantic. Extinctions of whale-fall specialists are probably ongoing, and to date are likely to have been most severe in North
Atlantic, intermediate in Southern Ocean, and least intense in northeast Pacific whale-fall communities.

ACKNOWLEDGEMENTS

I especially thank Jim Estes for conceiving and organizing the fascinating and important symposium on Whales, Whaling and Marine Ecosystems. I also warmly thank the many people who have assisted at sea and on land during our whale-fall studies. The whale-fall work has been generously supported by the National Undersea Research Center Alaska (now the West Coast & Polar Regions Undersea Research Center), the U.S. National Science Foundation, the National Geographic Society, the British Broadcasting Corporation, and the University of Hawaii Research Council. This is contribution no. XXXX from the School of Ocean and Earth Science and Technology, University of Hawaii at Manoa.
LITERATURE CITED


Isaacs, J. D., and R. A. Schwartzlose. 1975. Active animals of the deep-sea floor. Scientific


FIGURE LEGENDS

Figure 1. Photographs of whale falls at the seafloor on the California slope illustrating three successional stages. (A) A ~35 t gray-whale carcass on the seafloor for 1.5 months at 1675 m in the Santa Cruz Basin in the *mobile-scavenger stage*. Dozens of hagfish (*Eptatretus deani*), each ~30-cm long, are feeding on the white carcass. Large bite marks formed by sleeper sharks (*Somniosus pacificus*) are also visible. (B-D) The Santa Cruz carcass after 18 m on the seafloor, now in the *enrichment-opportunist stage*. The whale soft tissue has been almost completely removed by scavengers, exposing vertebrae and ribs. The sediments around the skeleton (B) are colonized by a dense assemblage of gastropods, juvenile bivalves, cumacean crustaceans, and dorvilleid polychaetes (visible as white dots). The organic-rich bones (including the scapula (C) and ribs (D)) harbor high densities of polychaetes, including a new species of chrysopetalid (*Vigntorniella* n. sp.) that forms grass-like patches (C) and hanging curtains (D) on some areas of the skeleton. For scale, the polychaetes are 1-2 cm long. (E-F) The 21-m long skeleton of a balaenopterid at 1240 m in the Santa Catalina Basin illustrating the *sulfophilic stage*. This skeleton has been at the seafloor for several decades. Visible on the bones *in situ* are (E) white bacterial mats covering the ends of vertebrae, and the shells of vesicomyid clams (~10 cm long). (F) A bone recovered from the carcass harboring large numbers of the mussel *Idas washingtonia* nestled into bone crevices to exploit effluxing hydrogen sulfide (for scale, mussels are 0.5-0.8 cm long).
**Figure 2.** Macrofaunal community patterns around implanted whale falls in the San Diego Trough (t = 4 mo) and the Santa Cruz Basin (t = 18 mo) during the *enrichment-opportunist* stage. **Top:** Sediment macrofaunal densities around experimentally implanted whale falls in the San Diego Trough at 4 months, and in the Santa Cruz Basin at 18 months. Means ± one standard error are given. **Bottom:** Macrofaunal species diversity versus distance for the Santa Cruz Basin carcass.

**Figure 3.** Annual catches of great whales in the southern hemisphere and in the northern North Pacific by whalers, between 1910 and 1985. Data are from the International Whaling Commission, compiled by Eric Danner in 2003.

**Figure 4.** **Top:** “Population” trajectories for living sperm whales (*Physeter macrocephalus*), and the number of sperm-whale falls in various successional stages (mobile scavenger stage, enrichment opportunist stage, and sulfophilic stage) at the deep-sea floor since 1800. Living sperm whale trajectory is from Whitehead (2002). The estimates of the number of whale-fall communities in the various successional stages depend on the following assumptions: (1) A natural sperm-whale mortality rate of 0.05 y⁻¹; (2) 90% of discarded carcasses and 50% of carcasses resulting from natural mortality sink to the deep-sea floor; (3) persistence times of 1 yr, 4 yr and 40 yr for the mobile-scavenger stage, enrichment-opportunist stage, and sulfophilic stage, respectively (Smith and Baco, 2003; Schuler et al., in press). **Bottom:** Similar trajectories, based on the similar assumptions, for gray whales (*Eschrichtius robustus*) in the northeast Pacific. The trajectory for living gray whales is a combination of data from IWC (1993) and Rugh et al, in preparation (as communicated by J. Breiwick, 2003).
Figure 2
Figure 3
Figure 4
Table 1. Species (n = 32) first recorded at large whale falls. The 28 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. Note that more than half of these species have been collected from southern California whale falls, suggesting that whale-fall habitats in other regions may be grossly undersampled. (Modified from Smith and Baco, 2003).

<table>
<thead>
<tr>
<th>Higher Taxon</th>
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<th>Estimated pop. Size</th>
<th>Location</th>
<th>Reference</th>
</tr>
</thead>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
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<td>Archaeastropoda</td>
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<td>X</td>
<td>&gt;100</td>
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<td>McLean 1992</td>
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<tr>
<td></td>
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<td></td>
<td>300-1100</td>
<td>California</td>
<td>McLean 1992</td>
</tr>
<tr>
<td></td>
<td>Paracocculina cervae</td>
<td></td>
<td></td>
<td>New Zealand</td>
<td>Marshall 1994</td>
</tr>
<tr>
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<td>X</td>
<td>&gt;200</td>
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<td>Marshall 1994</td>
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<td>Osteopelta ceticola</td>
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<td></td>
<td>Iceland</td>
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<tr>
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<td></td>
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<td></td>
<td></td>
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<td>Adipicola pelagica</td>
<td>X</td>
<td></td>
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<td>Dell 1987</td>
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<tr>
<td>Bathymodiolinae</td>
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<td>X</td>
<td></td>
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<td></td>
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<td><em>Axinodon</em> sp. nov.</td>
<td>X</td>
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<td>P. Scott pers. comm.</td>
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<td>X 1000 – 100,000</td>
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<td>Smith et al. 2002, Dahlgren et al., 2004</td>
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<td><em>Asabellides</em> sp. nov.</td>
<td>X &gt;10</td>
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<td><strong>Sipuncula</strong></td>
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<td><em>Phascolosoma saprophagicum</em></td>
<td>X 20 - &gt;200</td>
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</table>

* In addition to *Palpiphitime* sp. nov. and *Dorvilleid* sp. nov., an estimated 38 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 and Smith 2003, and unpublished data). Many of these species are likely to be new to science.
Table 2. Macrofaunal species that appear to be overwhelming more abundant on whale skeletons than in any other known habitat. 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), Smith and Baco (2003), Baco and Smith (2003), Poehls et al. (in preparation), and McLean (personal communication). Table modified from Smith and Baco (2003).

<table>
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<th>Species</th>
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<th>Number Collected in Other Habitat(s)</th>
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<td><strong>Bivalvia</strong></td>
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<td>&gt;10,000 - &gt;20,000</td>
<td>1 – 10 (wood, vents, seeps)</td>
</tr>
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<td><strong>Gastropoda</strong></td>
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<td></td>
</tr>
<tr>
<td><em>Cocculina craigsmithi</em></td>
<td>300 - 1100</td>
<td>1 – 10 (vents)</td>
</tr>
<tr>
<td><em>Pyropelta corymba</em></td>
<td>&gt;1000</td>
<td>1 – 10 (vents)</td>
</tr>
<tr>
<td><em>Pyropelta musaica</em></td>
<td>&gt;250</td>
<td>1 – 10 (vents)</td>
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<td><em>Ilyarachna profunda</em></td>
<td>500 - 1800</td>
<td>1 – 90 (sediments, seeps)</td>
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