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

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

47 *Key words: whale falls; great whales; whaling; detritus; succession; extinctions; biodiversity;*
48 *carrion; scavengers; opportunists; chemoautotrophs; chemosynthesis*
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50 INTRODUCTION

51

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

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63 Dead-whale detritus has remarkable characteristics, and thus may play unusual roles in
64 marine ecosystems. Cetaceans are by far the largest parcels of organic matter formed in the
65 ocean, with adult body masses of the nine largest species, or the “great whales,” ranging from 5
66 to >160 tonnes (e.g., Lockyer 1976). The enormous size of adult great whales provides a refuge
67 from most predators with the consequence that much of the natural whale mortality may occur
68 from nutritional or disease stresses sustained during migrations (e.g., Gaskin 1982, Corkeron and
69 Conner 1999, Moore et al. 2003). Based on relative population production rates, even the
70 successful whale predators, i.e., the killer whales (*Orcinus orca*), appear to utilize a small

71 proportion of adult great-whale production. When predation events do occur, the
72 disproportionate mass of a great whale, and the sinking of carcasses, often precludes predators
73 from consuming most of the carcass (e.g., Silber et al. 1990, Guinet et al. 2000). Thus, in
74 contrast to most other marine animals, great whale biomass typically enters the marine food web
75 as fresh carrion parcels many tonnes in size (Britton and Morton, 1994).

76

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

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86 Due to large body size, whale populations have low production rates compared to most
87 other organisms in the ocean (Katona and Whitehead 1988); thus, when averaged over large
88 areas, the flux of carbon through whale detritus is small relative to total detrital flux, even in the
89 most organic-poor ecosystems such as the abyssal seafloor (Jelmert and Oppen-Bernsten 1996;
90 see calculations below). Nonetheless, end-member characteristics in particle size and quality
91 potentially allow whale detritus to play disproportionate roles in the structure and evolution of
92 marine ecosystems.

93

94 Below I discuss current ecosystem responses to the input of whale detritus. I then
95 estimate the effects of industrial whaling on the production of dead whales, and speculate on the
96 consequences of these changes for marine ecosystems. Finally, I propose an experimental
97 approach to test some of these speculations.

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99 CURRENT ECOSYSTEM RESPONSES TO WHALE DETRITUS

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101 *Production and initial fate of whale detritus*

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103 Great whales suffering natural mortality are typically in poor nutritional condition and
104 negatively buoyant upon death; as a consequence, most whale carcasses initially sink towards the
105 seafloor (Ashley, 1926, Schafer 1972, Gaskin 1982, Guinet et al. 2000, Smith and Baco 2003, D.
106 W. Rice personal comm.). Because there appear to be few scavengers on whale sized particles in
107 midwater (Britton and Morton 1994), and because whale carcasses will sink rapidly following
108 lung deflation from hydrostatic pressure, it is extremely likely that relatively little tissue removal
109 will occur during a dead whale's descent to the seafloor. If a whale carcass sinks in deep enough
110 water, hydrostatic pressure will limit the generation of buoyant decompositional gases through
111 reduction of gas volume and increased gas solubility (Allison et al. 1991). At depths greater than
112 1000 m, the amount of microbial tissue decay required to generate carcass buoyancy (e.g., >67 %
113 of carcass mass through fermentation) is prohibitive; the soft tissue of a carcass will be removed
114 by scavengers or disintegrate from microbial decomposition long before positive buoyancy can
115 be generated, and the carcass will remain on the seafloor (Allison et al. 1991). At shallower
116 depths, there is some probability that gas generation could refloat a whale carcass, although this

140 year. If we assume that whale biomass is 5% organic carbon, that the average weight of a dying
141 great whale is 40 t, and that the ocean covers $3.6 \times 10^8 \text{ km}^2$, the flux of organic carbon to seafloor
142 from whale falls averages $3.8 \times 10^{-4} \text{ g C}_{\text{org}} \text{ y}^{-1}$ (see Jelmert and Oppen-Bernsten (1996) for similar
143 calculations). This is only about 0.1% of the background POC flux to the deep-sea floor under
144 the most oligotrophic central gyre waters. Even if whale mortality and flux is 10-fold greater
145 along migration corridors or in whale feeding grounds, background POC flux will also be higher
146 in these regions because they typically occur along ocean margins or oceanographic fronts.
147 Thus, it is difficult to imagine that the flux of great-whale detritus would exceed 0.3% of seafloor
148 POC flux anywhere in the deep sea.

149

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

160

161 How do deep-sea ecosystems respond to the massive flux event of a whale fall? Although
162 the deep-sea floor is remote and relatively poorly studied, there is now substantial evidence that

163 sunken whales create persistent, ecologically significant habitats. Most information concerning
164 the seafloor fate and impacts of whale detritus comes from the California slope, beneath the
165 migration corridor of the northeast Pacific gray whale. I will review the California-slope data
166 first, and then summarize knowledge from other deep-sea regions.

167

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

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

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

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

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182 4) *A reef stage*, during which the hard, elevated skeletal remains are colonized by
183 suspension feeders exploiting flow enhancement.

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186 Experimental, time-series studies of whale falls at depths between 1000 and 2000 m on the
187 California slope provide strong evidence for the first three successional stages; these data are
188 reviewed below.

189

190 **The mobile-scavenger stage.** Whale carcasses (n= 2, wet weights of 5 and 35 t) studied at 0.25
191 and 1.5 months after arrival at the seafloor exhibited community patterns consistent with a
192 mobile scavenger stage (Fig. 1). Within this time frame, carcasses were largely intact, with the
193 predominant scavengers including hundreds of hagfish (mostly *Eptatretus deani*), and several
194 sleeper sharks (*Somniosus pacificus*) 1.5-3.5 m in length (Smith *at al.*, 2002). Other important
195 scavengers included many thousands of small (~0.5 cm long) lysianassid amphipods on one
196 carcass, and large lithodid crabs, possibly *Paralomis multispina*, on the other (Smith and Baco,
197 2003). During this stage, hagfish were drawn from minimum distances of 0.6 – 0.8 km (Smith
198 and Baco, 2003) and the stage lasted approximately 0.3 – 1.5 yr, depending on carcass size (5 or
199 35 t). Time-lapse photography and *in situ* sampling suggested that most of the soft tissue was
200 directly removed by necrophages, especially *S. pacificus*, even though putrefaction was
201 occurring within the whale flesh. The resultant tissue removal rates estimated for the scavenger
202 assemblages (40 – 60 kg d⁻¹) imply that a 160 t blue whale (*Balaenoptera musculus*) carcass
203 might support a mobile scavenger stage for as long as 7-11 yr. A total of 38 species of
204 megafauna and macrofauna have been identified from whale falls in the mobile scavenger stage
205 (Baco-Taylor, 2002, Smith and Baco, 2003), with most species apparently being generalized
206 scavengers. Calculations combining whale-fall spacing (for *Eschrichtius robustus* in the
207 northeast Pacific) with scavenger foraging rates and fasting times indicate that large mobile
208 scavengers such as rattails, hagfish and lysianassids are unable to specialize on whale falls, given

209 current stock sizes of great whales in the northeast Pacific (Smith and Baco, 2003). Nonetheless,
210 the scavenger assemblages on the California slope are well adapted to recycle the soft tissue of
211 whale carcasses over surprisingly short time scales (i.e., months to years).

212

213 **The enrichment-opportunist stage.** Communities consistent with an enrichment-opportunist
214 stage were documented on carcasses (n=3) ranging in size from 5 – 35 t at the seafloor for 0.3 –
215 4.5 yr. During this stage, sediments within 1-3 m of the skeleton were heavily enriched in
216 organic matter (in some cases exceeding 10% organic carbon by weight) by tissue particles
217 dispersed by scavengers. Organic-rich bones and sediments during this time were colonized by
218 extremely high densities of heterotrophic macrobenthic polychaetes, mollusks and crustaceans
219 (Fig. 1)(Smith et al. 2002, Smith and Baco 2003). In some areas, bacterial mats also covered
220 sediments nearby the skeleton. Macrofaunal densities in the sediments within 1-3 m of the
221 carcass attained 20,000 – 45,000 individuals m⁻² in as little as 4 months (Fig. 2); these densities
222 exceeded background levels by an order of magnitude, and are the highest ever reported for
223 macrofauna below 1000 m depths (Smith and Baco 2003). A number of the most abundant
224 species in organic-rich sediments and on whale bones are new to science (e.g., two dorvilleid
225 polychaetes, a chrysopetallid polychaete, and a gastropod) and could be whale-fall specialists;
226 other species abundant on the whale falls during this stage have been collected at other types of
227 organic enrichment (e.g., fish falls, Smith 1986) and are likely to be generalized opportunists.
228 Despite high macrofaunal densities near the whale carcasses, species diversity adjacent to the
229 skeletons was low (e.g., only 18 macrofaunal species)(Fig. 2). This rapid colonization by a high-
230 density, low-diversity assemblage is strongly reminiscent of shallow-water opportunistic
231 communities around sewage outfalls and beneath salmon pens (e.g. Pearson and Rosenberg

232 1978, Weston 1990, Zmarzly et al. 1994), and indicates that intense pulses of organic enrichment
233 (e.g., whale falls, large kelp falls, etc.) are common enough at slope depths off California to have
234 allowed the evolution of enrichment opportunists (Smith and Baco 2003). The duration of the
235 *enrichment-opportunist stage* is likely to vary substantially with whale-carcass size, and ranges
236 from <2 yr for a 5-10 t carcass, to at least 4.5 yr for a 35 t carcass.

237

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

248

- 249 1) Mats of heterotrophic and chemoautotrophic bacteria growing on bone surfaces, and
250 within bone sutures and trabaculae,
- 251 2) Large populations (>10,000 individuals per skeleton) of the mussel *Idas washingtonia*,
252 which harbors chemoautotrophic endosymbionts,
- 253 3) Rich macrofaunal communities (>30,000 individuals) composed of bivalves, isopods,
254 amphipods, polychaetes, limpets, and snails constituting at least three trophic levels.

255

256 Whale-fall communities in the sulfophilic stage are remarkably species rich, with an average of
257 185 species per skeleton; they appear to have the highest local species richness of any known
258 deep-sea, hard-substrate community (Baco and Smith 2003). Many of the species from the
259 sulfophilic stage are extremely abundant on whale skeletons, but have rarely, if ever, been
260 collected in surrounding habitats; they thus may be specialists that have evolved in sulfide-rich,
261 whale-skeleton habitats (see discussion below). The sulfophilic stage also exhibits faunal overlap
262 with other deep-sea, chemosynthetic communities, sharing 11 species (including vesicomid
263 clams, bathymodiolin mussels, and a vestimentiferan polychaete) with hydrothermal vents, and 20
264 species with cold seeps (Baco et al., 1999, Smith and Baco 2003).

265

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

273

274 **Whale-fall succession in other regions.** Considerably less is known about deep-sea community
275 response to whale falls beyond the California slope, but there is evidence that a succession of
276 scavengers, enrichment opportunists and sulfophiles will also colonize carcasses in other regions.
277 For example, numerous studies suggest that mobile scavengers will feed voraciously on fresh

278 whale falls throughout the well-oxygenated deep sea (Isaacs and Schwartzlose 1975, Hessler et
279 al. 1978, Jones et al. 1998, Smith and Baco 2003). Furthermore, organic-rich sediments with an
280 abundant microbial assemblage are documented beneath a whale fall in the western Pacific
281 (Naganuma et al., 2001), and enrichment opportunists are known from sites of organic loading in
282 a range of deep-sea settings (e.g., Turner 1977, Grassle and Morse-Porteus 1987, Desbruyeres
283 and Laubier 1988, Levin et al. 1994, Snelgrove et al. 1994, Kitazato and Shirayama 1996,
284 Snelgrove and Smith 2002). Finally, sulfophilic assemblages appear to be widespread on whale
285 carcasses in the deep sea because bathymodiolin mussels with chemoautotrophic endosymbionts
286 have been recovered from whale bones in the North and South Atlantic, and in the northwestern
287 and southwestern Pacific, at depths ranging from 220 to 4037 m (Wada et al. 1994, Naganuma et
288 al. 1996, 2001, Baco-Taylor 2002, Smith and Baco 2003). Sulfophilic assemblages have also
289 been found on fossil deep-sea whale skeletons as old as 30 myr (Squires et al. 1991, Goedert et
290 al. 1995), indicating that whale skeletons have supported chemoautotrophic communities over
291 evolutionary time (Distel et al. 2000). Thus, succession on whale falls in the deep-sea in general
292 is likely to be functionally similar to that on the California slope, and this successional process,
293 including colonization by sulfophiles, is likely to have occurred for at least 30 myr.

294 Nonetheless, species structure and rates of successional change may differ dramatically in other
295 parts of the deep sea, and patterns of succession are likely to have varied following the radiation
296 of large whales since the Miocene (Gaskin 1982, Distel 2000). In particular, in the modern
297 ocean in regions such as the North Pacific central gyre, where whale falls should be much less
298 common and seafloor communities are much more depauperate (e.g., Smith and Demopoulos
299 2003), whale-fall succession is expected to be extremely protracted (potentially lasting > 100 yr)
300 and species-poor compared to the California slope.

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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.

318 There is increasing evidence that whale falls provide habitat for a specialized fauna, i.e., a
319 suite of species that is specifically adapted to live on whale remains. Bennett et al. (1994) first
320 noted a bimodal pattern in the frequency distribution of species abundances on whale skeletons
321 suggesting the presence of core species particularly adapted to whale-bone niches (qualitatively
322 similar patterns are observed in dung and carrion assemblages in terrestrial environments). To
323 date, 36 macrofaunal species were first collected on whale falls, and 28 of these have not been

324 found in any other habitat (Table 1). A number of the species thus far unique to whale carcasses
325 are extremely abundant, indicating that they are well adapted to whale falls and can attain
326 substantial population sizes given suitable conditions. The absence of these species in samples
327 from other related habitats (e.g., wood falls, algal falls, enriched sediment trays, hydrothermal
328 vents, and cold seeps), suggests that they may indeed be endemic to whale falls.

329
330 In addition to the 28 potential whale-fall endemics, there are at least five other species
331 that may be dependent on whale falls (Table 2). These are species that attain extraordinary
332 abundance on whale carcasses, but occur only as isolated individuals in other habitats. It is
333 likely that a large proportion of the total individuals within these species live on whale falls,
334 essentially making them whale-fall specialists (i.e., their evolution has been largely shaped by
335 selective pressures at whale falls)(Bennett et al., 1994). This brings the total number of potential
336 whale-fall specialists to 33. This number of potential whale-fall specialists is likely to rise
337 substantially as the diverse dorvilleid (estimated to be 40 species), amphipod, and copepod
338 components of the California-slope whale-fall fauna are rigorously examined by taxonomists,
339 and as whale-fall communities are more intensively sampled throughout the world ocean.

340
341 It should be noted that potential whale-fall specialists span a broad range of taxonomic
342 and functional groups. These “specialists” come from five different phyla, and appear to include
343 whale-bone feeders (*Osedax*, a sipunculid and some limpets), bacterial grazers (some limpets,
344 *Ilyaracha profunda*), species utilizing chemoautotrophic endosymbionts (the bathymodiolins,
345 thyasirid, vesicomid, and siboglinid), deposit feeders (the ampharetids), facultative suspensions
346 feeders (the bathymodiolins), and predators (the polynoids, *Paralomis manningi*)(see discussion

347 of food webs above). This diversity suggests that a variety of taxa and trophic types have
348 become specifically adapted to whale-fall niches, and depend (in aggregate) on a variety of
349 resources provided by the whale-fall habitat.

350

351 *Whale detritus at shelf depths*

352

353 Remarkably little is know about the ecosystem response to whale falls at shelf depths.

354 Because seafloor POC flux rates are typically much higher on the shelf than in the deep sea, the

355 flux of organic carbon to the shelf floor in the form of whale detritus likely makes an

356 insignificant contribution to the nutrient budgets of the continental shelf (e.g., Katona and

357 Whitehead 1988). Exceptions to this generalization might occur in calving lagoons, such as Ojo

358 de Liebre and San Ignacio Lagoons in Mexico, where gray-whale strandings, and mortality in

359 general, are likely to be concentrated in unusually small areas (e.g., Rugh et al. 1999).

360

361 Whale falls are certain to attract scavenger aggregations and undergo community

362 succession on the continental shelf floor, but only very limited, anecdotal information concerning

363 such shelf processes is available. At 150 m depths off Alaska, a gray-whale carcass with

364 substantial remaining soft tissue had attracted dense clouds of scavenging lysianassid amphipods

365 (T. Shirley, personnal communication). At 90-m depths in the Strait of Juan de Fuca near San

366 Juan Island, a 30 t fin whale (*Baleanoptera physalus*) placed at the seafloor for three months

367 attracted a moderate diversity of facultative fish and shrimp scavengers, although little tissue

368 removal had occurred (A. Shepard, D. Duggins and C. Smith, unpublished data). In this

369 relatively high-flow setting, no bacteria mats were visible on the carcass, possibly due to

370 disruption by currents. After 28 months at the seafloor, the fin-whale carcass had been stripped
371 of soft tissue (D. Duggins, personal communication).

372

373 There are very few data to indicate whether lipid-rich whale bones support a specialized
374 fauna at shelf depths. The mussel *Myrina pacifica*, which is thus far known only from whale
375 bones, has been collected at 220 m on the Japanese slope (Baco-Taylor 2002, Smith and Baco
376 2003), but this may reflect the upper end of a bathyal (i.e., deep-sea) depth distribution. In
377 addition, a new species of Polyplacophora (*Callistochiton* sp.) has been collected on whale bones
378 from 240 m off Concepcion, Chile (J. Sellanes, personal communication), but once again it is
379 unclear whether this is predominantly a shelf or bathyal species. It is conceivable that whale
380 falls, like hydrothermal vents (Van Dover 2000), only support an endemic fauna in the deep sea,
381 below depths of a few hundred meters. If true, this contrasts with other organic-rich substrates,
382 in particular wood falls, which support highly specialized (albeit, non-overlapping) species in
383 both the deep sea and shallow water (e.g., Turner 1973, 1977, Coan et al. 2000). Clearly, the
384 dynamics and biogeography of whale falls at shelf depths merit substantial further study.

385

386 *Whale detritus in the intertidal*

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388 Only a small percentage of great-whale mortalities result in strandings in the intertidal,
389 even for essentially coastal species such as the gray whale, *E. robustus* (Jones et al. 1984). For
390 example, roughly 50 gray whales in the northeast Pacific, comprising < 5% of annual mortality,
391 come ashore in a typical year (Rugh et al. 1999, Moore 1999, Smith and Baco 2003). This
392 represents approximately one gray-whale stranding per year per ~200 km of coastline along the

393 ~10,000-km gray-whale migration route, or a flux of organic carbon from whale detritus of ~10 g
394 $C_{\text{org}} \text{ m}^{-1} \text{ y}^{-1}$ (assuming each whale carcass weighs 30 t and is 5% organic carbon). The flux of
395 drift carrion from other sources (e.g., jellyfishes, fishes, turtles, seabirds, and other marine
396 mammals) to beaches in the northeast Pacific, based on very limited measurements, appears to be
397 roughly an order of magnitude higher (Columbini and Chelazzi 2003). Thus, whale detritus (if
398 left undisturbed on the beach) appears to be a relatively minor source of carrion for intertidal
399 scavengers (e.g., Rose and Polis 1998). However, it has been suggested that cetacean carcasses
400 are important in the diet of some highly mobile terrestrial scavengers such as polar bears (*Ursus*
401 *maritima*) and Arctic fox (*Alopex lagopus*), and that whale carrion may have helped coastal
402 populations of California condors (*Gymnogyps californianus*) to survive following the extinction
403 of the Pleistocene terrestrial megafauna (Katona and Whitehead 1988). Reliance on whale
404 carrion by local populations of terrestrial scavengers seems especially likely around calving
405 lagoons, such as Ojo de Liebre and San Ignacio in Mexico, where whale strandings are
406 especially frequent (Rugh et al. 1999).

407

408 Very few data appear to be available on the natural recycling of stranded whale carcasses,
409 but some generalizations appear possible. Although scavengers, such as seabirds, shorebirds,
410 polar bears, foxes and vultures, may remove some of the soft tissue from whale carcasses (e.g.,
411 Schafer 1972, Katona and Whitehead 1988, Columbini and Chelazzi 2003), stranded cetaceans
412 appear to be recycled primarily by microbes and terrestrial arthropods (e.g., flies, ants, and
413 trogid, dermestid, and silphid beetles) (Columbini and Chelazzi 2003). Carcass reduction may
414 take many months or even many years if mummification occurs (Schafer, 1972), and involves a
415 variety of decompositional stages (e.g., bloat, internal-liquification, and dry-tissue stages) with

416 successional patterns resembling those for large carcasses in fully terrestrial habitats (Schafer,
417 1972, Cornaby 1974, Columbini and Chelazzi 2003). Thus, whale detritus stranded on beaches
418 appears to be largely removed from marine food webs, with very little direct impact on marine
419 ecosystems. In essence, whale strandings constitute a small, natural detrital flux from the ocean
420 to land.

421

422 *Whale detritus in the pelagic realm*

423

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

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IMPACTS OF WHALING ON THE ROLES OF WHALE DETRITUS

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443 Hunting by humans caused massive reductions of great whale populations throughout the

444 world oceans. The patterns of whale population depletion, carcass utilization and, in some cases,

445 whale population recovery, differed substantially over time, among cetacean species, and among

446 ocean basins, with the consequence that whaling has had complex effects on the availability of

447 great-whale detritus to marine ecosystems. Below, I attempt to reconstruct patterns of whale-

448 detritus depletion resulting from commercial whaling and speculate on some of the

449 consequences, particularly for deep-sea whale-fall communities.

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Effects of whaling on the production of whale detritus

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453 To evaluate the impacts of whaling on the production of whale detritus, it would be

454 extremely useful to reconstruct the population trajectories of exploited cetaceans in each ocean.

455 Despite the efforts of the International Whaling Commission (IWC) and numerous scientists,

456 such reconstructions are generally not possible, and estimates of pre-whaling cetacean population

457 levels remained controversial and politically charged (e.g., Roman and Palumbi 2003). It does

458 seem clear that great whales, especially coastal species such as the Atlantic gray whale, began to

459 be intensively exploited in the North Atlantic in the early 1800's (Tonnenssen and Johnson 1982,

460 Whitehead 2002). Whaling efforts then intensified in the tropical and temperate Pacific in the

461 mid 1800's, in Antarctic waters after 1910, and in higher latitudes of the North Pacific and in the

462 Bering Sea as late as the 1950's (IWC 1993, Whitehead, 2002, Springer et al. 2003, E. Danner,
463 personal communication based on IWC catch statistics, Fig. 3). However, for many large species
464 (e.g., fin, sperm, sei, blue, humpback, and minke whales), the bulk of the worldwide take
465 occurred between approximately 1920 and 1980 (i.e., during 1-2 generations of a great whale),
466 with the IWC estimating that roughly 2 million great whales were harvested from the oceans
467 over this period (Fig. 3)(E. Danner, personal communication). For all but the sperm whale, it
468 appears safe to say that great-whale population sizes were reduced an order of magnitude or
469 more by whaling (e.g., IWC 1993, Best 1994, Roman and Palumbi 2003); for sperm whales, a
470 reduction to ~30% of pre-whaling values appears to be the best estimate (Whitehead 2002).
471 Thus, as a rule of thumb for estimating whaling effects on the production of whale detritus, I will
472 assume a 10-fold reduction in great-whale standing stock. In many cases, especially in the North
473 Atlantic, boreal North Pacific and Southern Oceans, great-whale populations remain at only 10-
474 20% of pre-whaling levels (e.g., Best 1993, Springer et al. 2003, Roman and Palumbi 2003),
475 with a few notable exceptions (e.g., the northeast Pacific gray whale, Rugh et al. 1999).

476

477 **Pelagic/shelf/intertidal effects of whaling.** During both the open-boat and modern era of
478 whaling (i.e., pre- and post-1900, respectively, Whitehead 2002), the net effect of whaling must
479 have been a straightforward reduction of whale detrital inputs to pelagic, shelf and intertidal
480 ecosystems. This is because during the open-boat era, whale carcasses taken in the high seas
481 typically were stripped of blubber and released to sink to the *deep-sea* floor (Tonnenssen and
482 Johnson 1982); whales caught near shore (e.g., over the continental shelf) were likely to have
483 been towed ashore for processing. Modern whaling leaves little detritus for the marine ecosystem
484 because entire carcasses are processed on factory ships, or on shore (e.g., Tonnenssen and

485 Johnson 1982). Thus, with very localized exceptions (e.g., the inter- and subtidal in the
486 immediate vicinity of whaling stations), harvested carcasses were essentially removed from
487 pelagic, shelf and intertidal ecosystems.

488

489 By reducing great-whale populations by an order of magnitude, whaling must have
490 forced a roughly 10-fold decline in the flux and availability of great-whale detritus in pelagic,
491 shelf and intertidal ecosystems. For coastal populations of the California condor (*Gymnogyps*
492 *californianus*), the loss of whale carrion may have been significant, and could have caused
493 dramatic population declines. It also is conceivable that coastal populations of other wide-
494 ranging scavengers that fed on stranded whales (e.g., polar bears, arctic foxes, and grizzly bears
495 (*Ursus arctos horribilis*)) declined as a consequence of commercial whaling. It is interesting to
496 note that while gray-whale populations have rebounded in the northeast Pacific, most stranded
497 whale carcasses are still removed from beaches (C. Smith, personal observations), yielding on
498 ongoing depletion of whale carrion. From a community-level perspective, the current energetic
499 contribution of great-whale detritus to pelagic and shelf ecosystems appears to be so small that
500 even if great-whale detrital fluxes were restored to pre-whaling levels, the ecosystem
501 consequences would be modest. However, in some intertidal areas, a 10-fold increase in the
502 frequency of whale strandings could yield a carbon flux approaching that from other sources of
503 marine carrion (see discussion above), suggesting that, prior to commercial whaling, stranded
504 whales could have been a significant source of carrion to mobile scavenger assemblages along
505 coastlines. This conclusion must remain tentative until the intertidal flux of carrion from all
506 sources is more intensively studied in various ocean regions.

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The impacts of whaling on deep-sea ecosystems

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.

531

532 The initial increase and subsequent decrease in carcass production resulting from
533 whaling, combined with spatial and temporal variations in the activities of whalers, have caused
534 historical patterns of dead-whale flux to vary among ocean basins. In addition, whale-fall
535 communities pass through successional stages with different persistence times (ranging from
536 months to decades), yielding time lags between a reduction in whale-carcass flux and the decline
537 of particular community types at the seafloor. Without accurate population trajectories for all
538 great whales in all basins, a detailed reconstruction of whale-fall habitat loss and likely patterns
539 of species extinctions is not possible. However, the limited data available on whale-population
540 trajectories do provide some insights into the historical biogeography of whale-fall habitat loss.

541

542 The most comprehensive population trajectory available in the refereed literature for any
543 great-whale species was developed by Whitehead (2002) for the sperm whale (*Physeter*
544 *macrocephalus*), with reconstruction of the global population size since 1800. Using a few
545 reasonable assumptions, the abundance over time of sperm-whale carcasses supporting mobile-
546 scavenger, enrichment-opportunist, and sulfophilic communities in the deep sea can be estimated
547 using the sperm-whale population trajectory (Fig. 4). The largest number of potential whale-fall
548 specialists are found in sulfophilic communities (Tables 1 and 2) (Smith and Baco 2003), so the
549 dynamics of this community type are perhaps most relevant to species extinction. Several points
550 emerge from modeling the abundance of sperm-whale falls at the deep-sea floor over time since
551 1800. (1) The discard of whale carcasses only modestly enhanced the number of whale-fall
552 communities, e.g., increasing the number of sulfophilic communities by ~ 20% over natural
553 processes in 1850 (Fig 4). (2) Because of short residence times, the abundances of mobile-

554 scavenger and enrichment-opportunist communities respond rapidly to changes in whale-fall
555 abundance, while sulfophilic communities respond with a 40-yr time lag to whale depletion.
556 Thus, the number of sulfophilic communities on sperm-whale skeletons is estimated to be
557 declining now, even though sperm-whale abundance passed a minimum in 1981, and is currently
558 about 40% of pre-exploitation levels (Fig. 4). Based on the global sperm-whale trajectory,
559 whale-fall specialists may be only now approaching their greatest habitat loss, potentially
560 causing species extinctions to be occurring at their highest historical rates. Species-area
561 relationships suggest that loss of 60% of the area of a habitat, such as occurred for sperm-whale
562 falls, should yield extinction of 20% or more of its endemic fauna (e.g., Pimm and Askins 1995,
563 Ney-Nilfe and Mangel 2000).

564

565 Regional asynchrony in the extermination of great whales suggests that ocean basins may
566 be in different phases of whale-fall habitat loss and species extinction. Whale populations were
567 first reduced in the North Atlantic in the 1800's, and even now may remain at < 25% of pre-
568 whaling levels (Roman and Palumbi 2003). Because whale abundance has remained low in the
569 North Atlantic for approximately 150 yr (i.e., much longer than the lag time resulting from
570 sulfophilic community persistence), the number of whale-fall habitats have long since adjusted to
571 low whale abundance, and species extinction driven by habitat loss is likely to be well advanced
572 (e.g., Brooks et al. 1999). The loss of species may be substantial in the North Atlantic because
573 whale-fall habitat abundance has been held at 10-25% of pre-exploitation levels for an extended
574 time; species-area relationships (e.g., Pimm and Askins 1995, Ney-Nilfe and Mangel 2000)
575 suggest that such habitat reduction will extinguish 30-50% of the specialized whale-fall fauna.
576 In contrast, southern-hemisphere great whales were heavily exploited much later, i.e., between

577 1920 and 1965 (Fig. 3), with their populations remaining low to the present (e.g., Best 1993,
578 Young 2000). As consequence, sulfophilic communities in the Southern Ocean are likely only
579 now to be approaching their historic lows, with extinction of whale-fall specialists in the
580 acceleration stage. Species extinctions are probably least advanced in the northeast Pacific,
581 where the greatest depletion of most large whales did not occur until the 1970's (Fig. 3, Springer
582 et al. 2003). In addition, some species, such the gray whale, had substantially recovered by 1970
583 from depredation suffered in the 1800's (Fig. 4), with the consequence that whale-fall habitats in
584 the northeast Pacific may never have reached the relative lows experienced in the North Atlantic.
585 Thus, one can predict that species extinctions and diversity loss in whale-fall communities have
586 been greatest in the North Atlantic, have been substantial and are likely accelerating in the
587 Southern Ocean, and have been least intense in the northeast Pacific. If species extinction due to
588 whaling has dramatically altered the biodiversity of whale-fall communities, one would predict
589 that current biodiversity levels are lowest in the North Atlantic and highest in the northeast
590 Pacific.

591

592 Can we rigorously test this prediction to determine whether patterns of whale-fall
593 biodiversity are consistent with whaling induced species extinctions? A reasonable experimental
594 approach would be to emplace uniform packages of lipid-rich whale bones at similar depths in
595 the North Atlantic, Southern Ocean and northeast Pacific, and then, after a sufficient time period
596 (i.e., 2-3 yr), compare biodiversity levels of bone-colonizing assemblages across basins. This
597 experimental approach is quite feasible because bone implantations have fostered sulfophilic
598 community development on the California slope, and similar experimental approaches (i.e.,

599 using standardized colonization substrates) have been used to assess regional variations in the
600 biodiversity of fouling assemblages in shallow-water communities (e.g., Ruiz et al. 2000).

601

602 CONCLUSIONS

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

614

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

621 Atlantic, intermediate in Southern Ocean, and least intense in northeast Pacific whale-fall
622 communities.

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624

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LITERATURE CITED

- Allison, P. A., C.R. Smith, H. Kukert, J.W. Deming, and B. A. Bennett. 1991. Deep-water taphonomy of vertebrate carcasses: a whale skeleton in the bathyal Santa Catalina Basin. *Paleobiology* **17**: 78-89.
- Ashley, C. W. 1926. *The Yankee Whaler*. Boston: Houghton Mifflin.
- Baco, A. R. and C. R. Smith. 2003. High biodiversity levels on deep-sea whale skeletons. *Marine Ecology Progress Series* **260**: 109-114.
- Baco, A. R., C.R. Smith, A.S. Peek, G.K. Roderick, and R.C. Vrijenhoek. 1999. The Phylogenetic relationships of whale-fall vesicomyid clams based on mitochondrial COI DNA sequences. *Marine Ecology Progress Series* **182**: 137-147.
- Baco-Taylor, A. R. 2002. Food-web structure, succession and phylogenetics on deep-sea whale skeletons. PhD thesis, University of Hawai`i.
- Bennett, B. A., C. R. Smith, B. Glaser, and H.L. Maybaum. 1994. Faunal community structure of a chemoautotrophic assemblage on whale bones in the deep Northeast Pacific Ocean. *Marine Ecology Progress Series* **108**: 205-223.
- Best, P. B. 1993. Increase rates of severely depleted stocks of baleen whales. *ICES Journal of Marine Science*. **50**: 169-186.
- Britton, J. C., and B. Morton. 1994. Marine carrion and scavengers. *Oceanography and Marine Biology: An Annual Review* **32**: 369-434.
- Brooks, T. M., S. L. Pimm, and J. O. Oyugi. 1999. Time lag between deforestation and bird extinction in tropical forests. *Conservation Biology* **13**: 1140-1150.
- Butman, C. A., J.T. Carlton, and S. R. Palumbi. 1995. Whaling effects on deep-sea biodiversity. *Conservation Biology* **9**: 462-464.

- Butman, C. A., J.T. Carlton, and S. R. Palumbi. 1996. Whales don't fall like snow: reply to Jelmert. *Conservation Biology* **10**: 655-657.
- Coan, E.V., P. V. Scott, and F. R. Bernard. 2000. Bivalve shells of western North America: Marine bivalve mollusks from Arctic Alaska to Baja California. Santa Barbara Museum of Natural History Monographs No. 2: 1-764.
- Columbini, L., and L. Chelazzi. 2003. Influence of marine allochthonous input on sandy beach communities. *Oceanography and Marine Biology: An Annual Review* **41**: 115-160.
- Committee on Biological Diversity in Marine Systems 1995. Understanding marine biodiversity: a research agenda for the nation. Washington, D.C.: National Academy Press.
- Corkeron, P.J., and R.C. Conner. 1999. Why do baleen whales migrate? *Marine Mammal Science* **15**: 1228-1245.
- Cornaby, B.W. 1974. Carrion reduction by animals in contrasting environments. *Biotropica* **6**: **51-63**.
- Dahlgren, T. G., Glover, A. G. & Smith, C. R. 2004. Fauna of whale falls: systematics and ecology of a new polychaetes (Annelida: Chrysopetalidae) from the deep Pacific Ocean. *Deep-Sea Research*, **51**: 1873-1887.
- Dell, R. K. 1987. Mollusca of the Family Mytilidae (Bivalvia) associated with organic remains from deep water off New Zealand, with revisions of the genera *Adipicola* Dautzenborg, 1927 and *Idasola* Iredale, 1915. *National Museum of New Zealand Records* **3**: 17-36.
- Dell, R. K. 1995. New species and records of deep-water mollusca from off New Zealand. *National Museum of New Zealand Records* **2**: 1-26.
- Deming, J., A.L. Reysenbach, S.A. Macko, and C.R. Smith. 1997. The microbial diversity at a whale fall on the seafloor: bone-colonizing mats and animal-associated symbionts.

- Microscopy Research and Technique **37**: 162-170.
- Desbruyeres, D., and L. Laubier. 1988. Exploitation d'une source de matière organique concentrée dans l'océan profond: intervention d'une annelide polychete nouvelle. Comptes Rendus de L'Academie des Sciences **307**: 329-335.
- Distel, D. L., A. R. Baco, E. Chuang, W. Morril, C. Cavanaugh, and C.R. Smith. 2000. Do mussels take wooden steps to deep-sea vents? Nature **403**: 725-726.
- Gaskin, D. E. 1982. Ecology of whales and dolphins. Portsmouth: Heinemann Educational Books.
- Gibbs, P. E. 1987. A new species of *Phascolosoma* (Sipuncula) associated with a decaying whale's skull trawled at 880 m depth in the southwest Pacific. New Zealand Journal of Zoology **14**: 135- 137.
- Goedert, J. L., R.L. Squires, and L.G. Barnes. 1995. Paleoecology of whale-fall habitats from deep-water Oligocene rocks, Olympic Peninsula, Washington state. Palaeogeography, Palaeoclimatology, Palaeoecology **118**: 151-158.
- Grassle, J. F. and L. Morse-Porteous. 1987. Macrofaunal colonization of disturbed deep-sea environments and the structure of deep-sea benthic communities. Deep-Sea Research I **34**: 1911-1950.
- Guinet, C., L.G. Barrett-Lennard, and B. Loyer. 2000. Co-ordinated attack behavior and prey sharing by killer whales at Crozet Archipelago: Strategies for feeding on negatively-buoyant prey. Marine Mammal Science **16**: 829-834.
- Hessler, R. R., Ingram, C. L., Yayanos, A. A. & Burnett, B. R. 1978. Scavenging amphipods from the floor of the Philippine Trench. Deep-Sea Research I **25**: 1029-1047.
- Isaacs, J. D., and R. A. Schwartzlose. 1975. Active animals of the deep-sea floor. Scientific

- American **233**: 85-91.
- IWC. 1993. Report of the special meeting of the Scientific Committee on the assessment of gray whales. Reports of the International Whaling Commission **43**: 241-253.
- Jelmert, A, and D.O. Oppen-Bernsten. 1996. Whaling and deep-sea biodiversity. Conservation Biology **10**: 653-654.
- Jones, E. G., M.A. Collins, P.M. Bagley, S. Addison, and I.G. Priede. 1998. The fate of cetacean carcasses in the deep sea: observations on consumption rates and succession of scavenging species in the abyssal Northeast Atlantic Ocean. Proceedings of the Royal Society of London Series B-Biological Sciences **265**: 1119-1127.
- Jones, M. L., S.L. Swartz, and S. Leatherwood. 1984. The Gray Whale *Eschrichtius robustus*. San Diego: Academic Press.
- Katona, S., and H. Whitehead, H. 1988. Are cetacea ecologically important? Oceanography and Marine Biology: An Annual Review **26**: 553-568.
- Kitazato, H., and Y. Shirayama. 1996. Rapid creation of a reduced environment and an early stage of a chemosynthetic community on cattle bones at the deep-sea bottom in Sagami Bay, central Japan. Vie et Milieu **46**: 1-5.
- Levin, L. A., G.R. Plaia, and C.L. Huggett, C. L. 1994. The Influence of natural organic enhancement on life histories and community structure of bathyal polychaetes. In: Reproduction, larval biology and recruitment of the deep-sea benthos, C. Young & K. Eckelbarger (eds). New York: Columbia University Press, p. 261-283.
- Lockyer, C. 1976. Body weights of some species of large whales. International Council for the Exploration of the Sea/ Journal of Marine Science **36**: 259-273.
- Marshall, B. A. 1987. Osteopeltidae (Mollusca: Gastropoda): a new family of limpets associated

- with whale bone in the deep sea. *Journal of Molluscan Studies* **53**: 121-127.
- Marshall, B. A. 1994. Deep-sea gastropods from the New Zealand region associated with recent whale bones and an Eocene turtle. *Nautilus* **108**: 1-8.
- Moore, S.E., J. M. Grebmeier, and J. R. Davies. 2003. Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. *Canadian Journal of Zoology* **81**
- McLean, J. H. 1992. Cocculiniform limpets (Cocculinidae and Pyropeltidae) living on whale bone in the deep sea off California. *Journal of Molluscan Studies* **58**: 401-414.
- Naganuma, R., H. Wada, K. Fujioka, K. 1996. Biological community and sediment fatty acids associated with the deep-sea whale skeleton at the Torishima seamount. *Journal of Oceanography* **52**: 1-15.
- Naganuma, T., M. Hattori, K. Akimoto, J. Hashimoto, H. Momma, and C. J. Meisel. 2001. Apparent microfloral response to organic degradation on bathyal seafloor: an analysis based on sediment fatty acids. *P.S. Z. N. Marine Ecology* **22**: 1-16.
- Ney-Nilfe, M. and M. Mangel. 2000. Habitat loss and changes in the species-area relationship. *Conservation Biology* **14**: 893-898.
- Pearson, T. H., R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: an Annual Review* **16**: 229-311.
- Pettibone, M. H. 1993. Polynoid polychaetes associated with a whale skeleton in the bathyal Santa Catalina Basin. *Proceedings of the Biological Society of Washington* **106**, 678-688.
- Pimm, S. L. and R. Askins. 1995. Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Sciences (U.S.A.)* **92**: 9343-9347.

- Rouse, G. W., S. K. Goffredi, and R. Vrijenhoek. 2004. *Osedax*: bone-eating marine worms with dwarf males. *Science (NY)* **305**: 668-671.
- Robineau, D. and V. de Buffrénil, V. 1993. Nouvelles données sur la masse du squelette chez les grands cétacés (Mammalia, Cetacea). *Canadian Journal of Zoology* **71**: 828-834.
- Roman, J., and S.R. Palumbi. 2003. Whale before whaling on the North Atlantic. *Science* **301**: 508-510.
- Rose, M.D., and G.A. Polis 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. *Ecology* **79**: 998-1007.
- Rugh, D.J., M. Muto, S.E. Moore and D. P. DeMaster. 1999 Status review of the eastern North Pacific stock of gray whales. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-103, 93 pp.
- Ruiz, G.M., P. Fofonoff, J.T. Carlton, M.J. Wonham and A.H. Hines. 2000. Invasions of Coastal marine Communities in North America: Apparent Patterns, Processes, and Biases. *Annual Review of Ecology and Systematics* **31**: 481-531.
- Schafer, W. 1972. *Ecology and Palaeoecology of marine environments*. 1972. University of Chicago Press.
- Schuller, D., D. Kadko, and C. R. Smith. 2004. Use of $^{210}\text{Pb}/^{226}\text{Ra}$ disequilibria in the dating of deep-sea whale falls. *Earth and Planetary Science Letters*, in press.
- Sibuet, M. and K. Olu. 1998. Biogeography, biodiversity, and fluid dependence of deep-sea cold seep communities at active and passive margins. *Deep-Sea Research II* **45**: 517-567.
- Silber, M.W. Newcomer, and M. Perez-Cortes. 1990. Killer whales (*Orcinus orca*) attack and kill a Bryde's whale (*Balaenoptera edeni*) *Canadian Journal of Zoology* **68**: 1603-1606.
- Smith, C. R. 1992. Whale falls: chemosynthesis on the deep-sea floor. *Oceanus* **36**: 74-78.

- Smith, C.R. and A.R. Baco. 1998. Phylogenetic and functional affinities between whale-fall, seep, and vent communities. *Cahiers de Biologie Marine* **39**: 345-346.
- Smith, C.R. and A. R. Baco. 2003. The ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology: an Annual Review* **41**: 311-354.
- Smith, C.R., Baco, A. R. & Glover, A. 2002. Faunal succession on replicate deep-sea whale falls: time scales and vent-seep affinities. *Cahier de Marine Biologie* **43**: 293-297.
- Smith, C. R. and A.W.J. Demopoulos. The deep Pacific Ocean floor. In: *Ecosystems of the World Volume 28: Ecosystems of the Deep Ocean*, P. A. Tyler, ed., Elsevier, Amsterdam, pp. 179 – 218.
- Smith, C. R., H. Kukert, R. A. Wheatcroft, P.A. Jumars, J.W. Deming. 1989. Vent fauna on whale remains. *Nature* **34**: 27-128.
- Snelgrove, P. V. R., J.F. Grassle, and R.F. Petrecca. 1994. Macrofaunal response to artificial enrichments and depressions in a deep-sea habitat. *Journal of Marine Research* **52**: 345-369.
- Snelgrove, P.V.R. and C. R. Smith. 2002. A riot of species in an environmental calm: the paradox of the species-rich deep-sea floor. *Oceanography and Marine Biology: an Annual Review* **40**: 311-342.
- Springer, A.M., J. A. Estes, G.B. van Vliet, T. M. Williams, D. F. Doak, E. M. Daner, K.A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences (U.S.A.)* **100**: 12223-12228.
- Squires, R. L., J.L. Goedert, J. L. and L.G. Barnes. 1991. Whale carcasses. *Nature* **349**: 574 only.

- Stockton, W. L. T.E. DeLaca. 1982. Food falls in the deep sea: occurrence, quality, and significance. *Deep-Sea Research I* **29**, 157-169.
- Tonnenssen, J. N., and A.O. Johnson. 1982. The history of modern whaling. University of California Press, Berkeley.
- Tunnicliffe, V., A.G. McArthur, and D. McHugh. 1998. A biogeographical perspective of deep-sea hydrothermal vent fauna. *Advances in Marine Biology* **34**: 353-442.
- Turner, R.D. 1973. Wood-boring bivalves, opportunistic species in the deep sea. *Science* **180**: 1377-1379.
- Turner, R. D. 1977. Wood, mollusks, and deep-sea food chains. *Bulletin of the American Malacology Union* **213**: 13-19.
- Van Dover, C. L. 2000. The ecology of deep-sea hydrothermal vents. Princeton: Princeton University Press.
- Wada, H., T. Naganuma, K. Fujioka, H. Ditzato, K. Kawamura, K., and Y. Akazawa. 1994. The discovery of the Torishima whale bone animal community and its meaning – the results of revisit dives by the “Shinkai 6500”. *Japan Marine Science & Technology Center/ Deep-Sea Research* **10**: 38-47.
- Warén, A. 1989. New and little known Mollusca from Iceland. *Sarsia* **74**: 1-28.
- Warén, A. 1993. New and little known Mollusca from Iceland and Scandinavia. Part 2. *Sarsia* **78**: 159-201.
- Warén, A. 1996. New and little known Mollusca from Iceland and Scandinavia. Part 3. *Sarsia* **81**: 197-245.
- Weston, D. P. 1990. Quantitative examination of macrobenthic community changes along an organic enrichment gradient. *Marine Ecology Progress Series* **61**: 233-244.

Whitehead, H. 2002. Estimates of the current global population size and historical trajectory for sperm whales. *Marine Ecology Progress Series* **242**: 295-304.

Williams, A.B., C. R. Smith, and A.R. Baco. 2000. New species of *Paralomis* (Decapoda, Anomura, Lithodidae) from sunken a whale carcass in the San Clemente Basin of southern California. *Journal of Crustacean Biology* **20**: 282-285.

Zmarzly, D. L., Stebbins, T. D., Pasko, D., Duggan, R. M. & Barwick, K. L. 1994. Spatial patterns and temporal succession in soft-bottom macroinvertebrate assemblages surrounding an ocean outfall on the southern San Diego shelf: relation to anthropogenic and natural event. *Marine Biology* **118**: 293-307.

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 vesicomid 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 \pm 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).

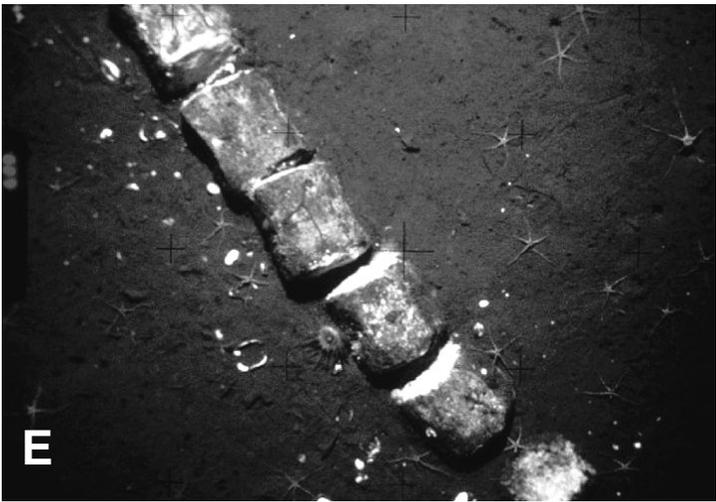


Figure 1

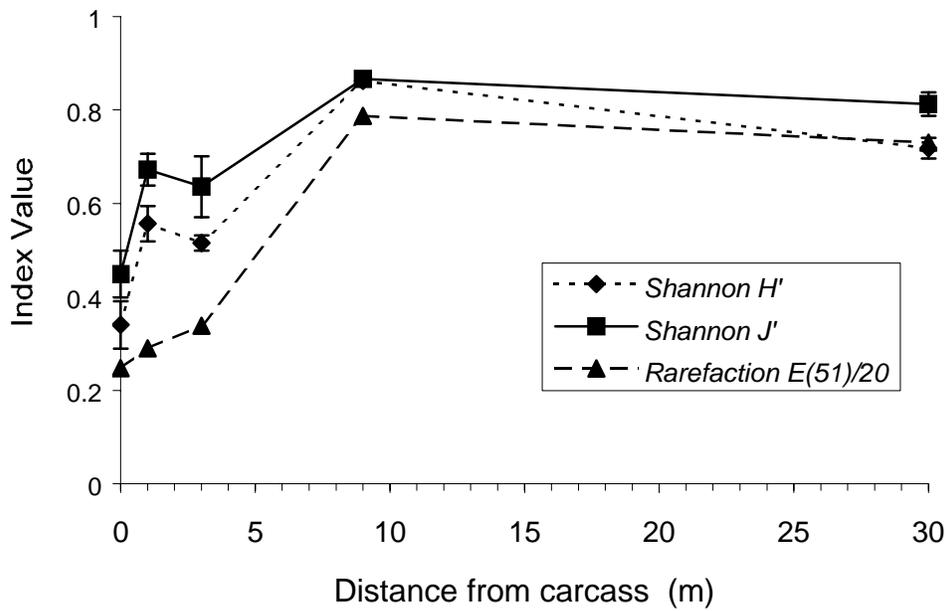
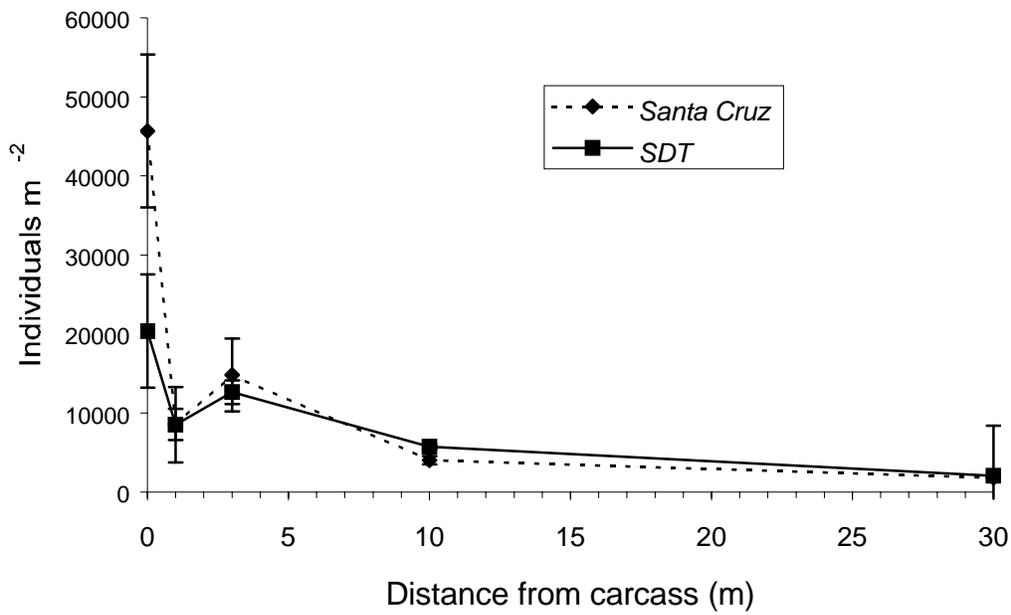
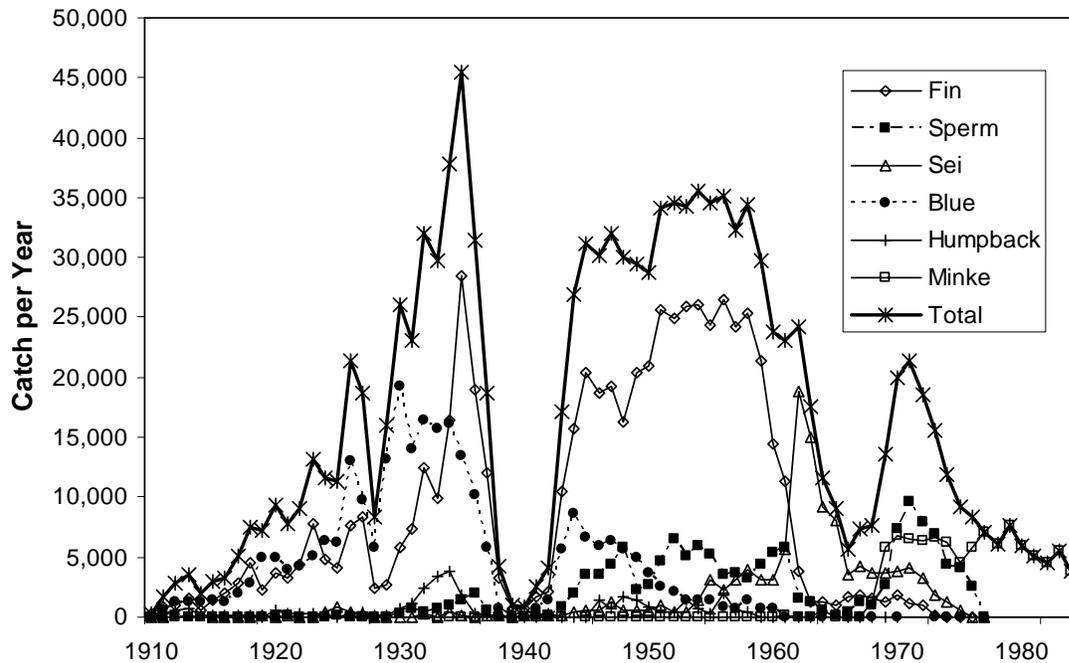


Figure 2

Southern Hemisphere Catch of Great Whales



Northern North Pacific Modern Catch of Great Whales

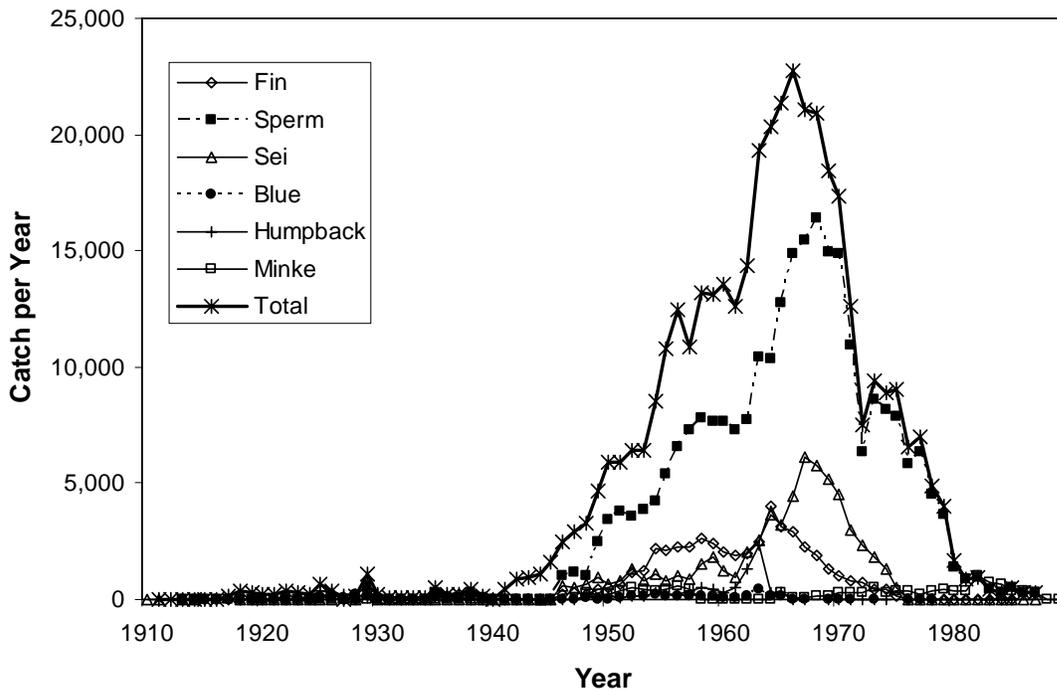


Figure 3

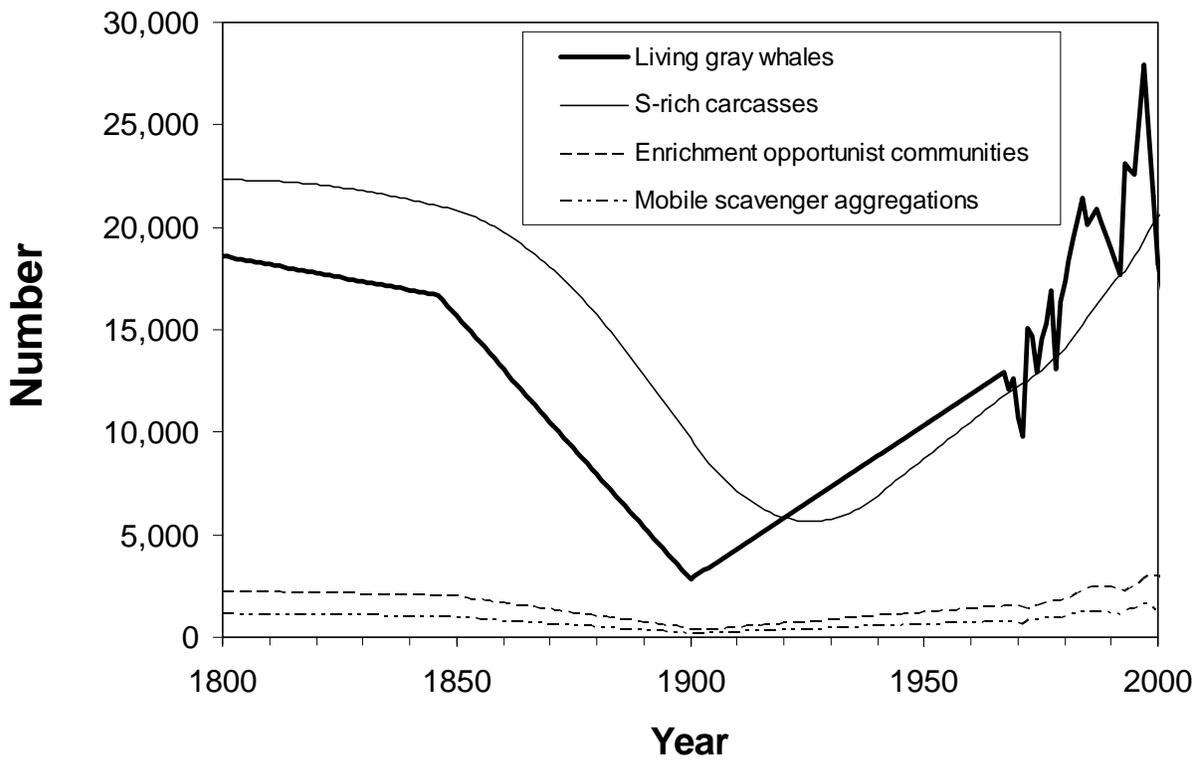
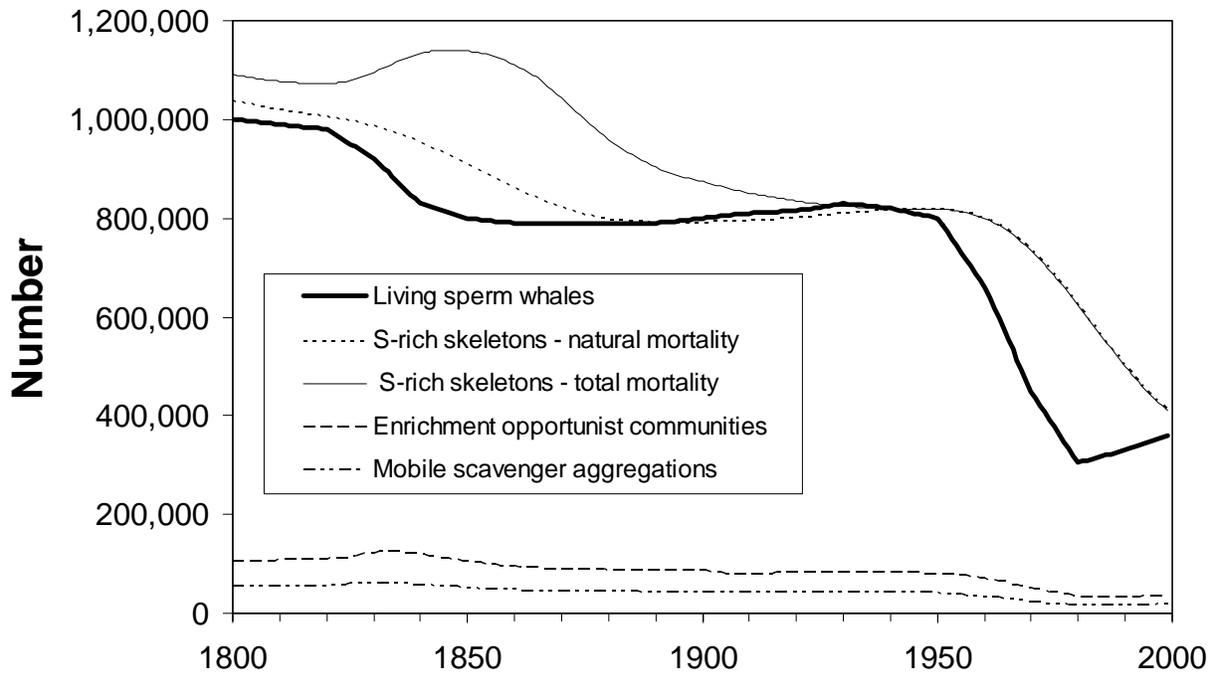


Figure 4

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).

HigherTaxon	Species	Known only at whale falls	Estimated pop. Size	Location	Reference
Mollusca					
Archaeogastropoda	<i>Pyropelta wakefieldi</i>	X	>100	California	McLean 1992
	<i>Cocculina craigsmithi</i>		300-1100	California	McLean 1992
	<i>Paracocculina cervae</i>			New Zealand	Marshall 1994
	<i>Osteopelta praeceps</i>	X	>200	New Zealand	Marshall 1994
	<i>Osteopelta ceticola</i>			Iceland	Warén 1989
	<i>Osteopelta mirabilis</i>	X		New Zealand	Marshall 1987
	<i>Protolira thorvaldsoni</i>			Iceland	Warén 1996
Gastropoda	<i>Bruciella laevigata</i>	X		New Zealand	Marshall 1994
	<i>Bruciella pruinosa</i>	X		New Zealand	Marshall 1994
	<i>Xylodiscula osteophila</i>	X		New Zealand	Marshall 1994
	<i>Hyalogyrina</i> n.sp.			California	McLean and Warén pers. comm.
Bivalvia					
Bathymodiolinae	<i>Adipicola pelagica</i>	X		South Atlantic	Dell 1987
	<i>Myrina (Adipicola) pacifica</i>	X		Japan, HI	Dell 1987
	<i>Adipicola (Idas) arcuatilis</i>			New Zealand	Dell 1995
	<i>Adipicola osseocola</i>			New Zealand	Dell 1995
	<i>Idas pelagica</i>	X		North Atlantic	Warén 1993
	<i>Idas ghisottii</i>			North Atlantic	Warén 1993

Vesicomylid	New species?	X		California	Baco et al. 1999
Thyasiridae	<i>Axinodon</i> sp. nov.	X		California	P. Scott pers. comm.
Aplacophora	New genus	X		California	Scheltema in prep.
Arthropoda					
Anomura	<i>Paralomis manningi</i>	X		California	Williams et al. 2000
Annelida					
Polychaeta					
Polynoidae	<i>Harmathoe craigsmithi</i>	X		California	Pettibone 1993
	<i>Peinaleopolynoe santacatalina</i>	X		California	Pettibone 1993
Chrysopetalidae	<i>Vigtorniella flokati</i>	X	1000 – 100,000	California	Smith et al. 2002, Dahlgren et al., 2004
Ampharetidae	New genus	X	>10	California	B. Hilbig pers. comm.
	<i>Asabellides</i> sp. nov.	X	>10	California	B. Hilbig pers. comm.
	<i>Anobothrus</i> sp. nov.	X		California	B. Hilbig pers. comm.
Siboglinidae	<i>Osedax frankpressi</i>	X	>1,000	California	Rouse et al., 2004
	<i>Osedax rubiplumus</i>	X	>1,000	California	Rouse et al., 2004
	<i>Osedax</i> , 3 sp. nov.	X	> 1,000	California	Pers. obs.
	<i>Osedax</i> , sp. nov.	X	>1,000	Sweden	Dahlgren and Glover, pers. comm.; pers. obs.
Dorvilleidae*	<i>Palpiphitime</i> sp. nov.	X	>10,000	California	B. Hilbig pers. comm.
	Dorvilleid sp. nov.	X		California	B. Hilbig pers. comm.
Sipuncula	<i>Phascolosoma saprophagicum</i>	X	>20 - >200	New Zealand	Gibbs 1987

* 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).

Species	Population Size on Whale Skeletons	Number Collected in Other Habitat(s)
Bivalvia		
<i>Idas washingtonia</i>	>10,000 - >20,000	1 – 10 (wood, vents, seeps)
Gastropoda		
<i>Cocculina craigsmithi</i>	300 - 1100	1 – 10 (vents)
<i>Pyropelta corymba</i>	>1000	1 – 10 (vents)
<i>Pyropelta musaica</i>	>250	1 – 10 (vents)
Crustacea		
<i>Ilyarachna profunda</i>	500 - 1800	1 – 90 (sediments, seeps)