Cah. Biol. Mar. (2002) 43 : 293-297

Faunal succession on replicate deep-sea whale falls: time scales and vent-seep affinities

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Introduction

In 1987, a chemoautotrophic community containing vesicomyid clams, mussels and bacterial mats was discovered on the lipid-rich skeleton of a 21 m baleanopterid in the Santa Catalina Basin (Smith et al., 1989). Subsequently, chemoautotrophic assemblages have been recovered from eight deep-sea whale skeletons off California (Smith, 1989; Smith & Baco, 1998; Baco et al., 1999), from at least four sites in the western Pacific (Naganuma et al., 1996; Baco et al., 1999), and from 8 fossil skeletons from ~30 mya (Goedert et al., 1995). Whale-fall communities appear to be widespread in the modern ocean, and have occurred at the deep-sea floor for at least 30 million years.

A fresh whale fall is an intense point source of organic enrichment: a single 40-ton carcass contains as much organic carbon as reaches a typical hectare of deep-sea floor in roughly 200 y. Since 1988, we have conducted time-series studies of natural and experimentally implanted whale falls with two general goals in mind: (A) To evaluate deep-sea community response to intense pulses of organic enrichment; (B) To elucidate the importance of whale falls as organic- and sulphide-rich habitat islands at the deep-sea floor. Based on previous studies of deep-sea scavengers (e.g., Smith, 1985), analogies with shallow-water organic-enrichment communities (e.g., Pearson & Rosenberg, 1978), and our initial whale-fall finds (Smith et al., 1989), we predicted that large whale falls at bathyal depths off California would pass through four successional stages (Smith et al., 1998):

(1) A *mobile-scavenger stage,* during which soft tissue would be removed from the carcass by large, mobile necrophages;

(2) An *enrichment opportunist stage,* during which opportunistic polychaetes and crustaceans would colonize organically enriched sediments surrounding the whale fall;

(3) A *sulphophilic (or "sulphur-loving") stage,* during which a chemoautotrophic assemblage would colonize the bones as they emitted sulphide during anaerobic decomposition of internal lipid, and

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

Here we report initial data collected from four deep-sea whale falls (two natural and two artificial) suggesting the presence and duration of the first three successional stages. In addition, we present the species overlap between the fauna on each of these whale-fall stages, and the fauna of hydrothermal vents and cold seeps.

Methods

Four whale carcasses were studied for this paper: two skeletons from natural whale falls, and two whale carcasses experimentally implanted at the bathyal seafloor. The natural whale falls consisted of two large baleanopterids: a 21 m blue or fin whale in Santa Catalina Basin at 1240 m (estimated fresh weight ~ 70,000 kg) and a baleanopterid of unknown species on the slope west of San Nicolas Island at a depth of 1100 m (fresh weight roughly estimated to be 40,000 kg) (Fig. 1). The two implanted carcasses were (1) a headless, juvenile grey whale, *Eschrichtius robustus* (Lilljeborg, 1861) (estimated fresh weight at sinking = 5000 kg) sunk with ~1000 kg of ballast at 1220 m in the San Diego Trough, and a subadult grey whale (estimated fresh weight = 35,000 kg) sunk with 3000 kg of ballast at 1670 m depth in the Santa Cruz Basin (Fig. 1).

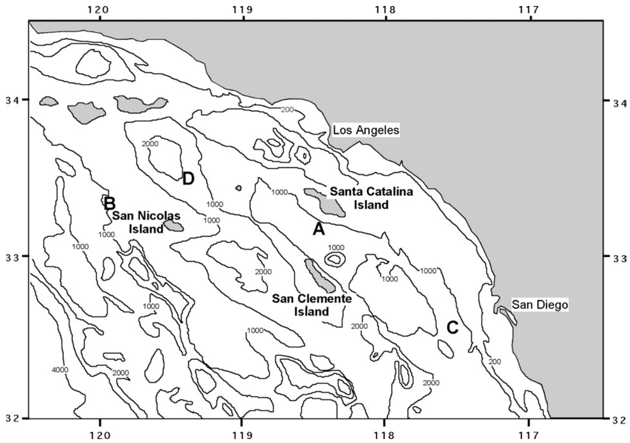

Figure 1. Location of whale carcasses discussed in this paper. **A.** Natural whale fall in Santa Catalina Basin, depth = 1240 m. **B.** Natural whale fall on slope near San Nicolas Island, depth = 1100 m. **C.** Implanted whale fall in San Diego Trough, depth = 1220 m. **D.** Implanted whale fall in Santa Cruz Basin, depth = 1670 m.

To describe succession on whale falls, time since carcass arrival at the seafloor must be known or estimated. Time since arrival for the two natural carcasses could be estimated only very roughly. Based on the size of vesicomyid clams at time of discovery, Smith et al. (1989) estimated that the Santa Catalina carcass had been at the seafloor for at least 3 yr in 1987. Thus, seafloor arrival for this carcass is taken to be 1984 or earlier. When visited in 1995, bones of the San Nicolas skeleton appeared to be significantly more eroded than were those of the Santa Catalina Basin in 1987. We thus assume that the San Nicolas skeleton had been at the seafloor for at least 5 years in 1995.

Visual observations, survey photographs, and video footage were collected on each carcass at various times (Fig. 2), using the submersible *Alvin* and the remotely operated vehicle ATV with the methods described in Bennett et al. (1994). Bone samples were also collected and associated fauna sorted and identified as in Bennett et al. (1994). Sediment macrofauna were collected with 7-cm diameter tube cores (35 cm^2 in area) or 100-cm^2 Ekman cores at distances of 0,1, 3, ~10 and $\geq$ 30 m from carcass, along transects starting from random points around the carcass. The top 10 cm of sediment were extruded from each core, fixed in 4% formaldehyde-seawater solution, washed on a 300 mm sieve, stained in rose Bengal, and then sorted under dissecting microscope as in Smith et al. (1998).

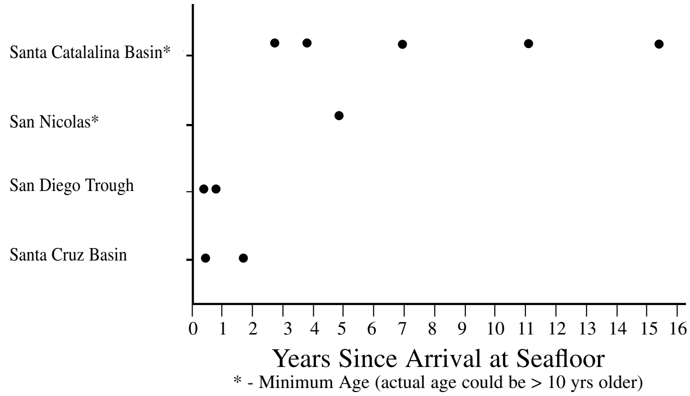

Figure 2. Time points at which whale carcasses were visited. Dates corresponding to time zero are as follows: Santa Catalina Basin ~1984; San Nicolas ~1990; San Diego Trough, June 1996; Santa Cruz Basin, April 1998.

Results

Carcasses at the seafloor for 0.5 – 1.5 months

We visited two carcasses that had been at the seafloor for 0.5 – 1.5 months: the San Diego Trough carcass and the Santa Cruz Basin carcass. When visited, each carcass appeared to be largely intact (i.e., only a small percentage of the soft tissue had been removed), but each had attracted a large aggregation of actively feeding scavengers (Table 1). Each carcass was covered with hundreds of hagfish (predominantly *Eptatretus deani* (Evermann & Goldsborough, 1907) but including *Myxine circifrons* Garman, 1899, that were consuming soft tissue. Sleeper sharks (*Somniosus pacificus* Bigelow & Schroeder, 1944) ranging in size from approximately 1.5 to 3.5 meters in length, were observed feeding voraciously on the Santa Cruz carcass, and at least one large sleeper shark was

Table 1. Estimated total megafaunal abundance, and megafaunal abundance per metric tonne of carcass wet weight, on whale carcasses at the seafloor for 0.5 and 1.5 months. Note that the original wet weight of the San Diego Trough carcass was 5000 kg, and that of the Santa Cruz carcass was 35,000 kg. Estimated abundances of lysianassid amphipods are extremely rough.

Megafauna species	San Diego Trough carcass (t = 0.5 months)		Santa Cruz Basin Carcass (t = 1.5 months)	
	Total	No. per tonne	Total	No. per tonne
Eptatretus deani	~ 300	~60	400 – 800	11.4 –22.8
Macrourid fish	1-2	0.2 – 0.4	0	0
Lithodid crabs	2-4	0.4 – 0.8	0	0
Small lysianassid amphipods	0	0	10^5 - 10^6?	3000 – 30,000
Somniosus pacificus	1 observed on periphery	0.2	1-3	0.029 – 0.086

observed near the San Diego Trough carcass. Because *S. pacificus* appeared to be wary of the submersible and ROV, its abundance on carcasses is likely to be underestimated by our video surveys and visual observations. Based on the feeding activities and bite marks visible on the Santa Cruz carcass, it seems likely that *S. pacificus* had removed more soft tissue from the carcass at 6 wk than had any other species.

There are notable differences in the list of scavengers attracted to the whale carcasses in the two different basins. The most remarkable is the apparent absence of lysianassid amphipods on the San Diego Trough carcass; this is surprising because lysianassids have been attracted to baitfalls at 1200 m depths off southern California over time scales of days (e.g. Smith, 1985) and the San Diego Trough does not appear to contain an unusual (e.g. oxygen-stressed) community (Levin & Gage, 1998).

None of the species found on the whale carcasses in this time frame are known to occur routinely at hydrothermal-vent or cold-seep habitats, although *E. deani* has been observed feeding on carrion at cold seeps within its bathyal depth range in Monterey Canyon (James Barry, MBARI, personal communication).

Carcasses at the seafloor for 4 -18 months

Two carcasses were studied during the 4-18 month time frame: the San Diego Trough carcass at 4 months and the Santa Cruz carcass at 18 months. In each case, the carcass had been nearly completely stripped of soft tissue to expose the skeleton. Small concentrations of soft tissue remained in a few locations (e.g. as meter-scale accumulations on the seafloor around the San Diego Trough carcass and beneath large vertebrae on the Santa Cruz carcass), but less then 10% of the original soft tissue mass was visible. The dominant megafaunal species around each carcass was the hagfish *E. deani*, although few of the individuals were visibly feeding on the carcass. Macrourid fish and lithodid crabs were present on the San Diego Trough skeleton at 4 months.

The sediment-water interface within 1-3 m of each carcass was visibly colonized by high densities of epibenthic macrofauna. Around the San Diego Trough skeleton, a dense bed of free-living, centimeter-long, white polychaetes undulated in the near-bottom flow; the worms were oriented vertically with one end in contact with the seafloor. Large numbers of minute white mollusk shells were visible around the Santa Cruz skeleton, and some bones of this skeleton were densely covered with writhing masses of polychaetes. Sediment macrofaunal densities around both carcasses were extremely high, attaining mean abundances of 20,000 - 45,000 m^{-2} within 1 m of the skeletons (Fig. 3); in contrast, species richness was extremely low (typically ≤ 5 species collected per 35 cm^2 core sample) within 1 m. Dominant macrofauna common to both skeletons included a new species of chrysopetalid polychaete (abundant on sediments around the San Diego Trough skeleton and on bone surfaces at the Santa Cruz skeleton), the dorvilleid polychaete *Ophryotrocha* sp. A, and the cumacean *Cumella* sp. A, all of which achieved densities > 3000 m^{-2} within 3 m of the carcass (Table 2).

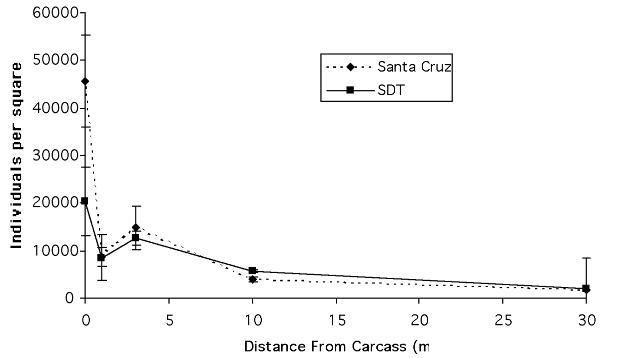

Figure 3. Total macrofaunal abundance in sediment cores as a function of distance from San Diego Tough (SDT) and Santa Cruz Basin whale carcasses. Abundances at 30 m on the x-axis are for samples collected from 30 to ~100 m from the skeleton and reflect background conditions in the basins. Mean numbers of macrofauna (>300 mm) per core ± 1 standard error are given. N for each distance and whale range between 3 and 9.

Table 2. Dominant macrofauna species at each of the whale carcasses sampled at 4 – 18 months. Species are listed in rank order of maximum abundance for each carcass, with maximum abundance and distance from carcass at which maximum abundance occurred. The last species given (BG) is the dominant background species in surrounding sediments.

Rank	San Diego Trough Carcass (t = 4 months)	Santa Cruz Carcass (t = 18 months)
1	*Ophryotrocha* sp. A, >11,000 m-2 at 0 m	Juv. Gastropod sp. J, >22,000 m^{-2}, 0 m
2	Chrysopetalid n. sp., > 8700 m^{-2} at 0 m	Juv. Bivalve sp. A, >20,000 m^{-2}, 0 m
3	*Cumella* sp. A, > 5200 m^{-2} at 3 m	*Ophryotrocha* sp. A, > 7000 m^{-2}, 3 m
4	Dorvilleid sp. B, > 1000 m^{-2} at 3 m	Tie: *Cumella* sp. A, > 3000 m^{-2}, 3 m and Cumacean sp. K, > 3000 m-2, 3 m
BG	*Tharyx tesselata,* ~ 400 m^{-2}, > 10 m	Cirratulid sp. A, ~ 770 m^{-2}, > 30 m

Several of the species abundant at the whale carcasses during this time frame may be shared with cold-seep habitats on the California slope. In particular, three undescribed dorvilleid species, including one in the genus *Ophryotrocha,* are reported from soft sediments at cold seeps near the Eel River at 500 m depths (Levin et al., 2000). Confirmation of species overlap must await direct comparison of the undescribed whale and seep dorvilleids.

Carcasses at the seafloor for ≥ 5 to ≥ 15 years

Data are presented from two carcasses that had been at the seafloor for > 5 yr: The San Nicolas Island skeleton (≥ 5 yr) and the Santa Catalina Basin skeleton in 1999 (≥ 15 yr). During these sampling times, no soft tissue was visible on the bones, no megafaunal scavengers were observed in skeleton vicinities, and bone surfaces were substantially colonized by microbial mats and macrofaunal invertebrates. No opportunistic species were visible on sediments surrounding the skeletons, and macrofaunal densities near skeletons differed little from background assemblages (data not shown). In contrast, bone surfaces were heavily colonized by diverse assemblages of invertebrate macrofauna, with at least 30,000 individuals belonging to at least 180 species occurring on each skeleton (Table 3). The numerically dominant macrofaunal species on each skeleton was the mussel *Idas washingtonia* (Bernard, 1978) which harbors sulphur-oxidizing, chemoautotrophic endosymbionts (Deming et al., 1997). Both skeletons also shared substantial populations of three limpet species and an isopod, indicating a common species assemblage among the skeletons (Table 3).

Table 3. Estimated population sizes of dominant bone-associated macrofauna on the San Nicolas and Santa Catalina skeletons > 5 yr and > 15 (respectively) after carcasses reached the seafloor. More detailed data are presented in Baco & Smith (submitted).

Taxon	San Nicolas (>5 yr.)	Santa Catalina (>15 yr.)
Mytilid		
Idas washingtonia	> 10,000	> 10,000
Limpets		
Cocculina craigsmithi	300	1,100
Pyropelta corymba	1,200	1,000
Pyropelta musaica	280	1,000
Other Limpets	1,800	1,200
Snails		
Mitrella permodesta	1,800	1,800
Provanna lomana	1,500	-
Juveniles and Others	1,700	800
Crustaceans		
Illyrachna profunda	500	1,800
Amphipods	800	500
Galathaeids	~50	~100
Misc. crustaceans	8,000	4,000
Polychaetes		
Nereid sp. 1	~50	~50
Ampharetids	2,500	100
Misc. polychaetes	10,000	8,000
Total Individuals	>40,000	> 30,000
Total Species	>191	>180

The macrofaunal assemblages on both skeletons during this time frame show significant affinities to hydrothermal-vent and cold-seep faunas (Table 4). Together, the whale skeletons share nine species with vent communities, including two vesicomyid clams that are abundant at vents (Baco et al., 1999). In addition, the whale skeletons share 18 species with northeast Pacific cold seeps, including eight species that are abundant at seeps. It should be noted, however, that the species shared among the whale-skeletons and vents and seeps constitute a small proportion of the hundreds of species found in each of these habitats in the north Pacific (Tunnicliffe, 1998; Sibuet & Olu, 1998).

Discussion

Our results are highly consistent with the prediction that whale falls at the bathyal seafloor would pass through at least three, overlapping succession stages: (1) A *mobile scavenger stage,* (2) an *enrichment opportunist stage,* and (3) a *sulphophilic stage.* Carcasses studied 0.5 - 1.5 months after reaching the seafloor appeared to exclusively harbour mobile necrophages, and clearly were in the mobile scavenger stage. All of these scavengers have been experimentally attracted to much smaller baitfalls of fish (Isaacs & Schwartzlose, 1975; Smith, 1985), indicating that they are generalized feeders on carrion. By 4 mo for the 5000 kg carcass, and 18 mo for the 35,000 kg carcass, most soft tissue had been removed and only a few scavengers remained, indicating that the mobile scavenger stage was drawing to a close. Thus, the duration of this stage at 1200 - 1700 m depths off California appears to range from somewhat longer than 4 mo to somewhat longer than 18 months, almost certainly depending on carcass size.

At 4 and 18 months, the small and large carcasses (respectively) were also surrounded by dense assemblages of polychaetes and cumaceans, suggesting the development of an enrichment opportunist stage. Within 1 m of the skeletons, macrofaunal sediment assemblages exhibited the extreme abundance and low species richness typical of communities of enrichment opportunists (e.g, Pearson & Rosenberg, 1978). Several of the most abundant species near the skeletons (e.g. *Ophryotrocha* sp. A and Dorvilleid sp. B) belong to taxa known to respond to organic enrichment (Levin et al., 2000) and thus are likely to be generalized enrichment respondents. We cannot estimate the duration of this enrichment opportunist stage without additional times-series data from whale falls.

The skeletons studied after >5 - >15 yr at the seafloor clearly contained major components (e.g., *Idas washingtonia)* of the chemoautotrophic assemblage described by Bennett et al. (1994); These whale-skeleton communities may thus be considered to be in the sulphophilic successional stage. A chemoautotrophic community was first observed on the Santa Catalina skeleton in 1987 when the skeleton was assumed to have been at the seafloor for ≥ 5 yr. The presence of a robust sulphophilic assemblage on this skeleton in 1999 indicates that the duration of this stage may easily exceed 15 years on a large skeleton. A functionally and taxonomically related community was described from a whale skeleton on the Toroshima Seamount at 4037 m depth in the western Pacific (Naganuma et al., 1996), suggesting that the sulphophilic stage occurs widely on whale skeletons at the deep-sea floor.

Table 4. Species shared among the San Nicolas and Santa Catalina Basin whale falls (at the seafloor for > 5 yr and > 15 yr respectively) ("Whale"), hydrothermal vents at Guaymas Basin and on the Juan de Fuca Ridge ("Guay." and "JdF", respectively) Northeast Pacific seeps at various locations ("NEP Seep") and Gulf of Mexico seeps ("GOM Seeps"). For details see: Bennet et al., 1994; Baco et al., 1999; Baco & Smith, unpublished data). One cross = species present; two crosses = species abundant.

	Species	Whale	Guay.	JdF	NEP seep	GOM seep
Bivalves	*Vesicomya gigas*	++	++	++		
	Calyptogena kilmeri	+			++	
	Calyptogena elongata	+		+	++	
	Calyptogena sp.	++	++		++	
	Idas washingtonia	++	+	+	+	
Gastropodes	*Pyropelta musaica*	++		+	++	
	Cocculina craigsmithi	++		+	+	
	Neoleptosis sp. ?	+			+	
	Astyris permodesta	++			+	
	Provanna lomana	++			++	
Isopodes	*Illyrachna profunda*	++			+	
	Janiridae sp.	+			++	
Polychaetes	*Bathykurila sp.*	+	+			
	Syllid sp. A	+			++	
	Sabellid sp. A	+			+	
	Maldanid sp. C	+			+	
	Dorvilleid sp. B	+			+	
	Scale Worm sp.	++			+	
Vestimentiferans	*Escarpia spicata*	+	+		++	+
Endoprocts	Endoprocts sp. B	+			+	
TOTALS			VENTS 9		SEEPS 18	

In conclusion, whale falls at bathyal depths off southern California appear to pass through at least three successional stages: a *mobile-scavenger stage*, an *enrichment-opportunist* stage, and a *sulphophilic stage*. The entire successional process may take decades, with carcasses providing habitat for potential whale-fall specialists (e.g., the chrysopetalid polychaete), enrichment opportunists, and a selection of vent/seep species during the latter two successional stages.

Acknowledgements

We thank Iris Stowe, Bryce Glaser and numerous others for help in the laboratory and at sea. This work was generously supported by NURC-Alaska grant no. UAF 97-0038, and a National Geographic Society grant, to CRS. This is contribution no. 6063 from SOEST, University of Hawaii.

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