Seven-year enrichment: macrofaunal succession in deep-sea sediments around a 30 tonne whale fall in the Northeast Pacific

Craig R. Smith^{1,*}, Angelo F. Bernardino², Amy Baco³, Angelos Hannides¹, Iris Altamira¹

¹Department of Oceanography, University of Hawaii at Manoa, 1000 Pope Road, Honolulu, Hawaii 96822, USA ²Departamento de Oceanografia, CCHN, Universidade Federal do Espírito Santo, Vitória, ES, 29055-460, Brazil ³EOAS/Oceanography, Florida State University, 117 N Woodward Ave, Tallahassee, Florida 32306-4320, USA

*Corresponding author: craig.smith@hawaii.edu

Marine Ecology Progress Series 515:133-149 (2014)

Supplement. (1) Results of post-hoc *t*-tests for significant Kruskal-Wallis tests on macrofaunal abundance versus distance around the whale fall (Table S1). (2) The mean absolute and relative abundances of the dominant macrofaunal species as a function of time and distance from the whale fall (Table S2). (3) A detailed description of the patterns of sediment macrofaunal community composition around the whale fall in space and time. (4) Photomosaics of the whale carcass at times of 1.5 y and 6.8 y after implantation (Fig. S1). (5) Rarefaction curves for pooled macrofaunal samples illustrating patterns of species diversity around the whale carcass as a function of time and distance (Fig. S2).

Table S1. Student's post-hoc t-tests of significant (p < 0.05) Kruskal-Wallis tests on macrofauna abundance around the whale carcass. Values not presented indicate no statistical difference from background sediments.

	0.12 yr	•		1.5	yr		4.5	yr		5.8 yr			6.8 y	r
Distance from whale-fall (m)	0 m	1 m	0 m	1 m	3 m	9 m	0 m	1 m	0 m	0.5 m	1 m	0 m	0.5 m	1 m
0														
0.5														
1									0.05					
3		0.05					0.001	0.03	0.05			0.04		
9							0.02		0.01			0.01		
20–100			< 0.001	0.001	0.001	0.003	0.001	0.05	0.001	0.03		0.001	0.01	0.03

Table S2. Mean abundance m^{-2} (SE) and relative abundances of macrofaunal species as a function of time and distance from the whale fall, and in the background community. Species constituting $\geq 2.8\%$ of community abundance at any time-distance combination are included. Ranks indicated are for 0 m distances or background sediments. (P) Polychaeta, (Cr) Crustacea, (M) Mollusca. Dashes indicate no samples taken at that distance/time point

					Whale	0.12 yr					
Rank											
0 m	0 m			0.5 m		1 m		3 m		9 m	i
		Mean density	%	Mean density	%	Mean density	%	Mean density	%	Mean density	%
1 2	Lysianassid sp. A (Cr) Idas washingtonia	1565 (234)	86.0%	-	-	4034 (1476)	85.6%			424.7 (92)	41.7%
	(M)	127.4 (23.5)	7.0%	-	-					127.4	
	Laonice sp. A (P) Monoculodes sp. A			-	-	169.9 (24.5)	3.6%	84.9 (24.5)	40.0%	(55.2)	12.5%
	(Cr) Cumella sp. A (Cr)			-	-	127.4 (73.6) 127.4 (42.5)	2.7% 2.7%				
	Cossura rostrata (P)			-	-			84.9 (49)	40.0%	127.4 (55.2)	12.5%

	Aphelochaeta sp. A (P)			-	-			42.5 (24.5)	20.0%	254.8 (55.2)	25.0%
	Total percentage		93.0%	-	-		94.6%		100.0%		91.7%
Rank 0 m					Whale	1.5 yr					
1	Juvenile vesicomyid?										
2	bivalve (M)	25112 (3550)	48.8%	-	-	1094 (186.2)	11.0%				
2	Hyalogyrina n. sp.	22((2 (1051)	46.00/			2057 (570)	20.00/				
3	(M) CRS Ampharetid sp.	23662 (1851)	46.0%	-	-	3956 (568)	39.9%				
3	14 (P)	1400 (168)	2.7%	_	_	527.2 (21.7)	5.3%				
		1400 (100)	2.770	_	_	994.9	3.370			229.3	
	Parougia sp. A (P)			_	_	(155.2)	10.0%	6985 (932)	40.1%	(33.2)	2.6%
	Cumella sp. A (Cr)			_	_	2552 (348.9)	25.8%	3990(658)	22.9%	203 (42.6)	2.3%
	Cumacea sp. K (Cr)			-	_	,		3654(507)	21.0%	615 (76.3)	6.9%
	Prionospio sp. B (P)			-	-			590.6(118.2)	3.4%	382 (86.4)	4.3%
	CRS Ampharetid sp.										
	2 (P)			-	-					1070 (205)	12.0%
	Chaetozone sp. E (P)			-	-					918 (112)	10.3%
	Cossura rostrata (P)			-	-					408 (48.8)	4.6%
	Subadyte mexicana									254.8	2 00/
	(P)			-	-					(113)	2.8%
	Gastropod sp. K		07.50/	-	-		92%		02.80/	280 (125)	3.1%
Rank	Total percentage		97.5%	-	-		92%		92.8%		
0 m					Whale	4.5 yr					
1	Ophryotrocha sp. A										
1	(P)	6803 (962)	39.4%	_	_						
2	CRS Ampharetid sp.	(, , , ,									
	14 (P)	2513 (298)	14.6%	-	-						
3	CRS Ampharetid sp.	, ,									
	12 (P)	1343 (250)	7.8%	-	-	52.0 (23.2)	1.2%				
4	Ophryotrocha										
	platykephale (P)	1256 (218)	7.3%	-	-						
5	Cumella sp. A (Cr) Samytha cf.	780 (219)	4.5%	-	-						
	californiensis (P)	260 (54.8)	1.5%	-	-						
	Cumacea sp. K (Cr)			-	-	2288 (551)	53.0%				
	Tharyx sp. A (P)			-	-	260 (63.7)	6.0%	104 (28.5)	16.7%	260 (90)	16.7%
	Parougia sp. A (P)			-	-	208 (43.5)	4.8%			52 (23.2)	3.3%

	Monticellina sp. A (P)			-	-			104 (28.5)	16.7%	156 (46.5)	10.0%
	Idas washingtonia (M) Total percentage	260 (106)	1.5% 76.6%	-	-		65.0%	52 (23.2)	8.3% 33.4%		26.7%
Rank	Total percentage		70.070				03.070		33.470		20.770
0 m					Whale	5.8 yr					
1	Ophryotrocha sp. A										
	(P)	4003 (996)	22.6%	4246 (1883)	23.1%						
2	Cumacea sp. K (Cr)	3692 (988)	20.9%	1300 (750)	7.1%			52 (23.3)	2.3%		
3	Ophryotrocha sp. E			346.6							
	(P)	1924 (803)	10.9%	(132.4)	1.9%						
4	Cumella sp. A (Cr)	1039 (285)	5.9%	1387 (727)	7.5%			52 (23.3)	2.3%		
5	CRS Ampharetid sp.										
	14 (P)	728 (216)	4.1%	1993 (1150)	10.8%						
	Parougia sp. A (P)	312 (67.8)	1.8%	780 (378)	4.2%	208 (23.3)	9.8%	156 (46.5)	7.0%		
	Chaetozone cf.										
	commonalis (P)					208 (67.8)	9.8%	156 (69.8)	7.0%	130 (37.5)	9.1%
	Monticellina sp. A (P)					52 (23.3)	2.4%	208 (43.5)	9.3%	260 (75)	18.2%
	Cossura cf. rostrata										
	(P)							52 (23.3)	2.3%	325 (97.5)	22.7%
	Total percentage		66.2%		54.6%		22%		30.2%		50.0%
Rank					Whale	6 8 vr					
0 m											
1	Cumacea sp. K (Cr)	4524 (861)	19.4%	1872 (476)	15.4%	312 (57)	8.6%				
2	Ophryotrocha sp. A										
	(P)	2652 (334)	11.4%	572 (182)	4.7%	51.9 (23.3)	1.4%				
3	CRS Ampharetid sp.										
	14 (P)	2184 (571)	9.4%	416 (186)	3.4%						
4	CRS Ampharetid sp.										
	12 (P)	1976 (245)	8.5%	884 (340)	7.3%						
5	Parougia sp. A (P)	1664 (499)	7.1%								
6	Exallopus sp. A (P)	728 (297)	3.1%	1040 (465)	8.5%						
	Cumella sp. A (Cr)	104 (28.5)	0.4%	623 (203)	5.1%	156 (46.5)	4.3%				
	Cossura cf. rostrata										
	(P)			208 (23.3) 364 (78.9)	1.7%	416 (130)	11.4%	52 (23.3)	2.8%	260 (90)	15.6%
		Chaetozone cf. commonalis (P)			3.0%	468 (43.5)	12.9%	156 (46.5)	8.3%	156 (28.5)	9.4%
	<i>Ophryotrocha</i> sp. E										
	(P)			2444 (1093)	20.1%						
	Samytha cf.										
	californiensis (P)	260 (52.0)	1.1%	416 (78.0)	3.4%	52 (26.0)	1.4%				

	Monticellina sp. A (P)		104 (46.5) 0.9% 260 (52				260 (73.5)	<i>13.9%</i> 260 (73.5	260 (73.5)	15.6%
	Total percentage	60.7%		70.1%		45.7%		25.0%		40.6%
Rank Bkgc			Bac	ckground	(>9–20 m)					
			Mean	density			%			
1	Cossura cf. rostrata (P)		214 (81.1)				16.9%	_		
2	Chaetozone sp. D (P)		183 (53.5)				14.5%			
3	Monticellina sp. A (P)		168 (58.7)				8.4%			
4	Tharyx sp. $A(P)$		76.5	(29.6)			6.0%			
	Total percentage						45.8%			

Patterns of macrofaunal community composition around the carcass in space and time

Macrofaunal community composition exhibited strong, time-dependent responses to the whale carcass. At 0.12 yr, the sediment within 1 m of the carcass was dominated by amphipods, with 1 species of mobile scavenger, Lysianassid sp. A, constituting >85% of community abundance (Table 2); this amphipod also was dominant at 9 m and was absent from background community samples.

Based on mean amphipod densities in core samples at 0 and 1 m distances (2800 m⁻²) and the seafloor area (>40 m²) within 1 m of the carcass (Treude et al. 2009), the total population size of Lysianassid sp. A at the carcass exceeded 100000 individuals. Other macrofaunal species occurring near the carcass at this time were rare or absent in the background community and included juveniles of the bivalve *Idas washingtonia* (a bone-inhabiting species with sulfur-oxidizing endosymbionts; Smith & Baco 2003), the omnivorous enrichment opportunist cumacean *Cumella* sp. A (Smith 1986, Smith et al. 2002, Bernardino et al. 2010), and the omnivorous oedicerotid amphipod, *Monoculodes* sp. A (Table 2).

By 1.5 yr, the sediment macrofaunal community around the carcass had changed dramatically, with the high abundances at 0 to 1 m dominated by bivalve juveniles and a single species of gastropod, which were absent from background sediments (Fig. 6; Table 2). The bivalve juveniles, most likely in the family Vesicomyidae, and the gastropod Hyalogyrina n. sp. constituted 50 to >90% of total macrofaunal abundance (Table 2). The vesicomyid bivalves appear to have recruited in response to high sulfide levels in sediments adjacent to the carcass (Fig. 4). Hyalogyrina n. sp. is known from microbial mats at kelp falls in Santa Cruz Basin (Bernardino et al. 2010), and this genus is common in other habitats supporting sulfur-oxidizing bacterial mats, including hydrothermal vents, cold seeps, wood falls, and whale falls (Smith & Baco 2003, Warén & Bouchet 2009), so this gastropod likely was attracted to microbial mats around the Santa Cruz whale carcass. At 3 m at this time, the sediment community was dominated by a dorvilleid polychaete, a spionid polychaete, and cumacean crustaceans (Fig. 6); the dorvillied, *Parougia* sp. A, and the 2 cumaceans (*Cumella* sp. A and Cumacea sp. A; Table 2) are attracted to organic enrichment around fish, kelp, and wood falls and are considered enrichment opportunists feeding on microbial mats and/or labile sediment organic matter (Smith 1986, Smith et al. 2002, Bernardino & Smith 2010). The spionid, *Prionospio* sp. B, also falls in a family with many enrichment opportunists (Smith & Baco 2003). At 9 m at this time (1.5 yr), non-background taxa continued to dominate the macrofaunal community (Table 2), including many species apparently responding to organic enrichment, such as the cumaceans Cumella sp. A and Cumacea sp. K, dorvilleid polychaetes (Parougia sp. A and Subadyte mexicana), spionids, and ampharetid polychaetes (Table 2).

After 4.5 yr, the sediment macrofauna at 0 m was dominated (>75%) by high abundances of dorvilleids, cumaceans, and ampharetids (Table 2, Fig. 6). The dominant species at this distance included the omnivorous enrichment opportunists *Ophryotrocha* sp. A, *Cumella* sp. A, and other apparently opportunistic ampharetids and dorvilleids (e.g. *Parougia* sp. A, *Ophryotrocha platykephale*), which were all absent from the background community. At 1 m, the enrichment opportunist Cumacea sp. K and some dorvilleids were still dominant, but dominant background species (the cirratulids *Tharyx* sp. A and *Monticellina* sp. A) had become common. By 3 to 9 m, the cirratulids common in the background community had become dominant, with a few dorvilleids present (Fig. 6, Table 2).

Macrofaunal community composition at 5.8 and 6.8 yr was quite similar. Sediments with enhanced macrofaunal abundances at distance of 0 to 0.5 m (Fig. 5) were dominated (55 to 75%) by dorvilleids, cumaceans, and ampharetids (Fig.

6). Species dominant at these distances included the omnivorous opportunists *Ophryotrocha* sp. A, *Cumella* sp. A (Bernardino et al. 2010), and other apparently opportunistic ampharetids and dorvilleids (e.g. Ampharetid sp. 14, *Parougia* sp. A, *Ophryotrocha* sp. E, *Exallopus* sp. A), all absent from background community samples. At a distance of 3 m, background community cirratulid and cossurid polychaetes had become common, with a few presumably opportunistic dorvilleids still present. By 9 m, the macrofaunal community at 5.8 and 6.8 yr resembled the background community in terms of higher-level taxa and dominant species (Fig. 6, Table 2).

In summary, the macrofaunal community exhibited strong successional patterns in space and time around the whale carcass in both higher taxonomic composition and dominant species. The sediment macrofaunal community near the whale carcass was dominated (1) initially (0.12 yr) by patches of mobile lysianassid scavenging amphipods to distances of 1 to 9 m, (2) then (at 1.5 yr) by sulphophilic juvenile vesicomyids and hyalogyrinid gastropods near the carcass (≤1 m) and enrichment opportunists including dorvilleids (Menot et al. 2009), cumaceans, and ampharetids at greater distances (3 to 9 m), and (3) finally by enrichment opportunists in a diminishing zone extending outward from the carcass to 3, 1, and 0.5 m after 4.5, 5.8, and 6.8 yr, respectively.

LITERATURE CITED

- Bernardino AF, Smith CR (2010) Community structure of infaunal macrobenthos around vestimentiferan thickets at the San Clemente cold seep, NE Pacific. Mar Ecol (Berl) 31:608–621
- Bernardino AF, Smith CR, Baco AR, Altamira I, Sumida PYG (2010) Macrofaunal succession in sediments around kelp and wood falls in the deep NE Pacific and community overlap with other reducing habitats. Deep-Sea Res I 57:708–723
- Menot L, Crassous P, Desbruyeres D, Galéron J, Khripounoff A, Sibuet M (2009) Colonization patterns along the equatorial West African margin: implications for functioning and diversity maintenance of bathyal and abyssal communities. Deep-Sea Res II 56:2313–2325
- Smith CR (1986) Nekton falls, low-intensity disturbance and community structure of infaunal benthos in the deep-sea. J Mar Res 44:567–600
- Smith CR, Baco AR (2003) Ecology of whale falls at the deep-sea floor. Oceanogr Mar Biol Annu Rev 41:311-354
- Smith CR, Baco-Taylor AR, Glover AG (2002) Faunal succession on replicate deep-sea whale falls: time scales and vent-seep affinities. Cah Biol Mar 43:293–297
- Treude T, Smith CR, Wenzhofer F, Carney E and others (2009) Biogeochemical processes at a deep-sea whale fall: rates of sulfate reduction, sulfide efflux and methanogenesis. Mar Ecol Prog Ser 382:1–21
- Warén A, Bouchet P (2009) New gastropods from deep-sea hydrocarbon seeps off West Africa. Deep-Sea Res II 56:2326–2349

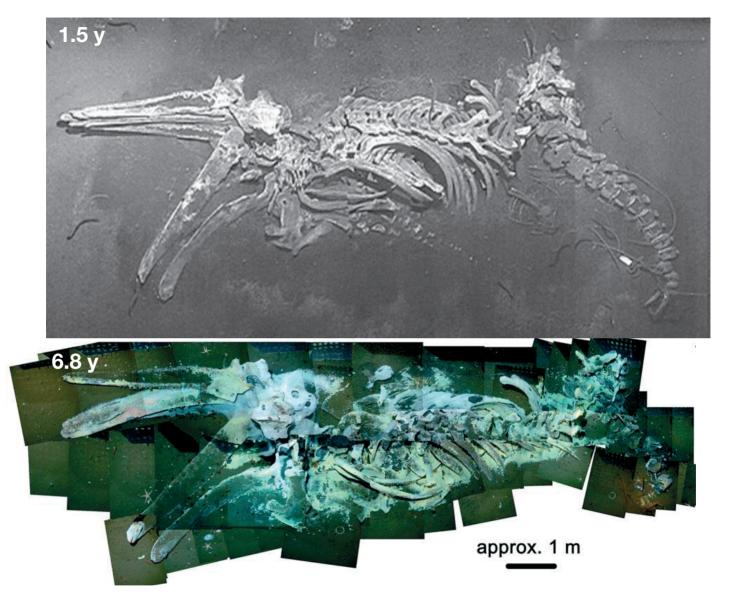


Fig. S1. Photomosaics of the grey whale skeleton in the Santa Cruz Basin at 1.5 yr (top) and 6.8 yr (bottom) after emplacement. The photo-mosaic at 1.5 yr is black and white because the down-looking camera in the HOV 'Alvin' in 1999 was black and white. Note the darkened area of sediment around the skeleton at 1.5 yr. At 6.8 yr, the skeleton is essentially intact and largely covered with white microbial mats

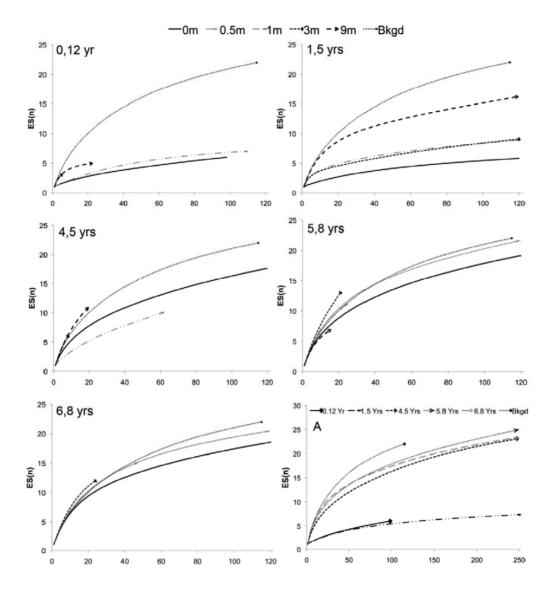


Fig. S2. Rarefaction curves $(ES_{(n)})$ for pooled macrofaunal samples as a function of time and distance from the whale carcass. The first 5 panels show rarefaction curves for each time point separately, with curves based on samples pooled at each distance. Panel A for 'all time points' (bottom right) shows rarefaction curves for 0 m pooled samples across all time points and pooled background community samples