Cah. Biol. Mar. (1998) 39 : 345-346

Phylogenetic and functional affinities between whale-fall, seep and vent chemoautotrophic communities

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Chemoautotrophic communities on lipid-rich whale skeletons are known from a total of eight modern sites and eight fossil sites (up to 30 million years old) in the deep Pacific Ocean. We are using natural and experimentally implanted whale skeletons to study community structure, succession, and vent-seep affinities of whale-fall communities in the Northeast Pacific. With ROV's and submersibles, we sampled four lipid-rich whale skeletons at depths of 1000 - 2000 m, separated by distances of 60 - 250 km, along the California slope. Skeletons on the seafloor for more than 3 yr (n = 3) harboured similar chemoautotrophic assemblages, with at least 30-46 total macrofaunal species on each skeleton. These assemblages were dominated by large populations (10,000 - 20,000 individuals per skeleton) of the mixotrophic mussel *Idas washingtonia* (Bernard, 1978), which harbours sulphide-oxidizing endosymbionts, but also exploits non-chemoautotrophic carbon sources (based on delta C13 values of - 27 to - 34 ‰). Other prominent community components included bacteria-grazing limpets and snails, galatheid crabs, and at least four species of vesicomyid clams with sulfide-oxidizing endosymbionts.

These whale-skeleton assemblages exhibited significant phylogenetic affinities to vent and seep faunas (Table 1)

Table 1. Species Overlap with Other Reducing Habitats.

Species	Whale Skeletons	Guaymas Basin Vents*	Juan de Fuca Vents*	Northeast Pacific Seeps**	Gulf of Mexico Seeps**	Anoxic Cal. Basins	Sunken Wood
Bivalves							
Vesicomya gigas/*C. kilmeri vent*	++	++	++				
Vesicomya gigas/*C. kilmeri seep*	+			++			
Calyptogena elongata	+			++		++	
Calyptogena pacifica?	++	++	+	++			
Idas washingtonia	++		+				+
Lucinoma annulata	+					++	
Parvilucina sp.	+					++	
Gastropods							
Pyropelta corymba Mc Lean & Haszprunar, 1987	++	+					
Pyropelta musaica Mc Lean & Haszprunar, 1987	++		+				
Cocculina craigsmithi Mc Lean, 1992	++		+	+			
Mitrella permodesta	++			++		++	
Provanna lomana	++			++			
Eulimella lomana Dall, 1908	++	+		++			
Polychaetes							
Bathykurila guaymasensis (Pettibone, 1989)	+	+					
Vestimentiferans							
Escarpia spicata	+	+		++	+		
Totals		Vents = 9 spp.		Seeps = 8 spp.		4	1

* - species list from Tunnicliffe (1991)
** - species list from Sibuet and Olu (in press)
++ = abundant
\+ = present

(Bennett et al., 1994). Based on analyses of DNA sequences for the mitochondrial cytochrome oxidase 1 gene (Baco et al., submitted), the whale falls share vesicomyid clam species with Guaymas Basin vents (the "*gigas*/*kilmeri* vent" clade) (*Vesicomya gigas* (Dall, 1896)/*Calyptogena kilmeri* (Bernard, 1974)), with Guaymas, Oregon and Monterey seeps (the "*gigas*/*kilmeri* seep" clade), and with the anoxic Santa Barbara Basin (*Calyptogena elongata* (Dall, 1916)); One vesicomyid species may be unique to whale falls. Seven other species on the whale falls also occur at Juan de Fuca or Guaymas Basin hydrothermal vents (based on species list in Tunnicliffe, 1991), including a vestimentiferan: *Escarpia spicata* Jones, 1985, (see Feldman et al., in press), three limpets, and a polynoid polychaete (Table 1). In addition to vesicomyids, whale assemblages also share seven species with seeps (based on species lists in Sibuet & Olu, in press) and anoxic basins, including the snails *Provanna lomana* (Dall, 1918) and *Mitrella permodesta* (Dall, 1890), E. spicata, and the lucinid clam *Lucinoma annulata* (Reeve, 1850) .

We conclude that whale skeletons harbour similar, sulfide-based chemoautotrophic communities throughout the California slope. Some of the dominant whale-fall community components, e.g., *Idas washingtonia,* appear to specialize on whale falls, while others are found in abundance at vents (e.g., the "*gigas*/*kilmeri* vent" vesicomyid) and seeps (*Mitrella permodesta*). Thus, whale falls apparently have fostered the evolution of a characteristic fauna, while continuing to serve as refugia or stepping stones for generalized sulfophilic species at the deep-sea floor.

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