FOOD-WEB STRUCTURE, SUCCESSION, AND PHYLOGENETICS ON DEEP-SEA WHALE SKELETONS

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ABSTRACT

Macrofaunal communities associated with sunken whale skeletons are now known from numerous deep-sea locations. Whale falls may be important as organic enrichment, sources of deep-sea biodiversity, havens for specialized fauna, and as dispersal and evolutionary stepping-stones. These roles are addressed in the context of successional stages in the whale-bone epifaunal community.

Based on $\delta^{13}C$ and $\delta^{15}N$ stable isotopes, macrofaunal species composition and abundance, there is evidence for the predicted "mobile scavenger", "organic enrichment", and "sulphophilic" stages on whale skeletons. The "mobile scavenger" stage was characterized by a low diversity assemblage dominated by mobile macrofauna. The "organic enrichment" stage was characterized by a less mobile, very low diversity assemblage of enrichment respondents. Isotope analyses revealed that species in both these stages are dependent on whale organic material.

Skeletons on the bottom for ≥ 2 years ("sulphophilic" stage) showed a clear difference in community structure and trophic complexity between large and small skeletons, implying a minimum whale skeleton size is required to sustain chemoautotrophic production. Species on small skeletons were dependent on whale organics and were part of a diverse, low mobility assemblage. Whale-fall communities on large skeletons exhibited complex trophic structure and extremely high diversity.

Species richness in three "sulphophilic" stage whale skeleton communities was compared to assemblages from vents, seeps, and other deep-sea hard substrates. The whale-fall community average *local* species richness is greater than any other deep-sea

hard substrate habitat, approaching known levels of *global* cold-seep macrofaunal diversity. This high species richness may be explained by unusually high trophic diversity in chemoautotrophic whale-fall communities.

Phylogenetic analyses of whale-fall vesicomyid clams provide support for the role of whale falls as dispersal stepping stones for species dependent on chemoautotrophic production, with at least three whale-fall clam species conspecific with vent and/or seep vesicomyids. Mitochondrial genes of mussels provide support for the role of whale falls as evolutionary stepping stones, with an evolutionary sequence from organic remains to seeps to vents. There is also a pattern of evolution from shallow-water to the deep sea. Carbon isotope values imply increasing dependence on chemoautotrophy and later methanotrophy over evolutionary time.