

ID: W1577451703

TITLE: Biodiversity on the Rocks: Macrofauna Inhabiting Authigenic Carbonate at Costa Rica Methane Seeps

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ABSTRACT:

Carbonate communities: The activity of anaerobic methane oxidizing microbes facilitates precipitation of vast quantities of authigenic carbonate at methane seeps. Here we demonstrate the significant role of carbonate rocks in promoting diversity by providing unique habitat and food resources for macrofaunal assemblages at seeps on the Costa Rica margin (400-1850 m). The attendant fauna is surprisingly similar to that in rocky intertidal shores, with numerous grazing gastropods (limpets and snails) as dominant taxa. However, the community feeds upon seep-associated microbes. Macrofaunal density, composition, and diversity on carbonates vary as a function of seepage activity, biogenic habitat and location. The macrofaunal community of carbonates at non-seeping (inactive) sites is strongly related to the hydrography (depth, temperature, O₂) of overlying water, whereas the fauna at sites of active seepage is not. Densities are highest on active rocks from tubeworm bushes and mussel beds, particularly at the Mound 12 location (1000 m). Species diversity is higher on rocks exposed to active seepage, with multiple species of gastropods and polychaetes dominant, while crustaceans, cnidarians, and ophiuroids were better represented on rocks at inactive sites. Macro-infauna (larger than 0.3 mm) from tube cores taken in nearby seep sediments at comparable depths exhibited densities similar to those on carbonate rocks, but had lower diversity and different taxonomic composition. Seep sediments had higher densities of ampharetid, dorvilleid, hesionid, cirratulid and lacydoniid polychaetes, whereas carbonates had more gastropods, as well as syllid, chrysopetalid and polynoid polychaetes. Stable isotope signatures and metrics: The stable isotope signatures of carbonates were heterogeneous, as were the food sources and nutrition used by the animals. Carbonate $\delta^{13}\text{C}_{\text{inorg}}$ values (mean = -26.98‰) ranged from -53.3‰ to +10.0‰, and were significantly heavier than carbonate $\delta^{13}\text{C}_{\text{org}}$ (mean = -33.83‰), which ranged from -74.4‰ to -20.6‰. Invertebrates on carbonates had average $\delta^{13}\text{C}$ (per rock) = -31.0‰ (range -18.5‰ to -46.5‰) and $\delta^{15}\text{N}$ = 5.7‰ (range -4.5‰ to +13.4‰). Average $\delta^{13}\text{C}$ values did not differ between active and inactive sites; carbonate fauna from both settings depend on chemosynthesis-based nutrition. Community metrics reflecting trophic diversity (SEAc, total Hull Area, ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and species packing (mean distance to centroid, nearest neighbor distance) also did not vary as a function of seepage activity or site. However, distinct isotopic signatures were observed among related, co-occurring species of gastropods and polychaetes, reflecting intense microbial resource partitioning. Overall, the substrate and nutritional heterogeneity introduced by authigenic seep carbonates act to promote diverse, uniquely adapted assemblages, even after seepage ceases. The macrofauna in these ecosystems remain largely overlooked in most surveys, but are major contributors to biodiversity of chemosynthetic ecosystems and the deep sea in general.

SOURCE: PloS one

PDF URL: <https://journals.plos.org/plosone/article/file?id=10.1371/journal.pone.0131080&type=printable>

CITED BY COUNT: 1716

PUBLICATION YEAR: 2015

TYPE: article

CONCEPTS: ['Authigenic', 'Cold seep', 'Carbonate', 'Geology', 'Fauna', 'Ecology', 'Petroleum seep', 'Macrobenthos', 'Intertidal zone', 'Oceanography', 'Benthic zone', 'Sedimentary rock', 'Biology', 'Paleontology', 'Methane', 'Materials science', 'Metallurgy']