Evidence for a chemoautotrophically based food web at inactive hydrothermal vents (Manus Basin)

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ABSTRACT

Hydrothermal vents are ephemeral systems. When venting shuts down, sulfide-dependent taxa die off, and non-vent taxa can colonize the hard substrata. In Manus Basin (Papua New Guinea), where hydrothermally active and inactive sites are interspersed, hydroids, cladorhizid sponges, barnacles, bamboo corals, and other invertebrate types may occupy inactive sites. Carbon and nitrogen isotopic compositions of animals occupying inactive sites are consistent with nutritional dependence on either chemoautotrophically or photosynthetically produced organic material, but sulfur isotopic compositions of these animals point to a chemoautotrophic source of sulfur from dissolved sulfide in vent fluids rather than sulfur derived from seawater sulfate through photosynthesis. Given that suspension-feeding and micro-carnivorous invertebrates are the biomass dominants at inactive sites, the primary source of chemoautotrophic nutrition is likely suspended particulates and organisms delivered from nearby active vents.

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1. Introduction

Invertebrate communities associated with active deep-sea hydrothermal vents have been the focus of considerable research since the first report of the Galapagos hot springs in 1977 (Corliss et al., 1979). The life cycle of active hydrothermal vent communities is reasonably well understood for a number of sites that have been intermittently studied for years to decades, but little is known about the ecology of organisms colonizing inactive sulfide substrata or other nearby hard surfaces.

Vent formation begins as seawater seeps below the ocean seafloor, reacts with hot rock, and eventually builds up enough thermal buoyancy to rise through conduits to mix with cold, oxygen-rich water (e.g., Fornari and Embley, 1995; Parson et al., 1995; Tolstoy et al., 2008). Dissolved metals precipitate at the mixing zone to form sulfide chimneys and mounds (i.e., polymetallic sulfide deposits; Haymon, 1983). These polymetallic

sulfide deposits continue to build during the lifetime of an active vent, providing substratum for a variety of invertebrates and metabolically diverse microbes that nourish life in hydrothermal environments (e.g., Karl, 1995).

In time, hydrothermal activity terminates and sulfide chimneys often topple, leaving piles of metal-rich mounds on the seafloor and an environment that no longer delivers the fluid flux required by endemic vent organisms. Absence of noxious concentrations of dissolved hydrogen sulfide opens a hospitable new environment to a different suite of invertebrate species. While it is routine to observe megafaunal and macrofaunal invertebrates associated with inactive sulfide mounds along mid-ocean ridges and spreading centers of back-arc basins, little is known about the role of chemoautotrophic primary production in the nutrition of these animals.

Stable-isotope analysis is a valuable tool for generating or constraining hypotheses about trophic resources in systems where direct observations of feeding interactions and samples are difficult to obtain, such as at hydrothermal vents (Conway et al., 1994; Van Dover, 2000, 2007). Carbon and nitrogen stable-isotope compositions have been used to advance our understanding of food and energy flow in a variety of marine settings (e.g., Rau and Hedges, 1979; Rau et al., 1992; Van Dover et al., 1992; Wainright et al., 1993). Characterization of patterns of isotopic compositions among individuals and among species at vents permits development of hypotheses regarding trophic issues such as changes in diet during growth within species

(Pond et al., 1997, 2000; Polz et al., 1998; Rieley et al., 1999), site-specific differences in diet within species (Trask and Van Dover, 1999; Colaço et al., 2002), and trophic interactions among species (Van Dover and Fry, 1989, 1994; Fisher et al., 1994; Southward et al., 1994; Vereshchaka et al., 2000; Colaço et al., 2002; Van Dover, 2002). Isotopic techniques also have been used to infer the importance of free-living chemoautotrophic microorganisms in the diet of heterotrophic invertebrates within vent communities (e.g., Van Dover and Fry, 1994). Sulfur isotopes are less frequently employed in trophic studies, but where organic sulfur may be derived from seawater sulfate or dissolved sulfide through autotrophic processes, sulfur isotopes can be useful dietary discriminators (Fry et al., 1983; Peterson and Fry, 1987; Vetter and Fry, 1998).

In this study, we report the results of stable-isotope analysis ($\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$) of dominant taxa at hydrothermally inactive sites at Solwara 1 (also known as the Suzette vent field) in Manus Basin, Papua New Guinea. Inactive sites were defined as massive sulfide (or, in one instance, volcanic rock) deposits without evident warm- or hot-water fluxes and by the absence of characteristic vent-endemic taxa for the region. To provide an isotopic context for biological samples (non-vent-endemic taxa) from inactive sites, we also sampled and analyzed dominant biota (vent-endemic taxa) from hydrothermally active sulfide mounds. Our objective was to provide insight regarding the primary source of nutrition for invertebrates at inactive sites at Solwara 1. At least three non-exclusive conditions were deemed possible:

(1) Sinking photosynthetically derived particles provide all or nearly all of the nutrition for the invertebrates colonizing inactive sulfide mounds.
(2) In situ production of organic carbon from acid-labile sulfides mobilized by microbial activity (or low-level, inconspicuous venting) may support chemoautotrophic primary production within the boundary layer overlying the substratum.
(3) Proximity of inactive sites (sometimes within 10 s of meters) to active vent sites within Solwara 1 suggests that allochthonous, chemoautotrophically derived organic material may be readily available to suspension feeders.

2. Material and methods

A research cruise to the Solwara 1 hydrothermal vent field (3°47.45′S, 152°5.65′E; ~0.8 km^2) was undertaken 31 Dec 2005 through 30 Jan 2006 on the M/V DP Hunter using the Perry Slingsby Remotely Operated Vehicle (ROV) TST212. Solwara 1 lies approximately 50 km northwest of Rabaul (East New Britain Province, Papua New Guinea), within Manus Basin. The crest of Solwara 1 is at ~1460 m and is characterized by the presence of active and inactive massive sulfide chimneys. Active chimneys and inactive sites were a variety of shapes and sizes: from small deposits with <0.5 m relief above the seafloor, to slender, finger-like sulfide branches reaching >10 m above the seafloor, to extensive fields of chimneys with diameters of 3 m or more. Inactive sulfide chimneys (~2 m height, 0.5 m diameter) and clear diffuse vents dominated the Solwara 1 field, with interspersed black smokers (116–296 °C), grey smokers, and white smokers (95–119 °C). There were three main discrete sites of activity: Williamson (also referred to as 'Far West' and 'West' by Nautilus Minerals) to the west, Binns and Paine to the north (also referred to as 'Central'), and Kowalczyk to the east (also referred to as 'East'). In most areas where active hydrothermal venting was observed, there were also remnants of old sulfide chimneys (no longer actively venting).

'Inactive' and 'active' sampling sites with substantial invertebrate biomass were selected during reconnaissance video transects. Animals were collected from six inactive sites at areas known as Binns and Paine, Williamson, Fullagar Extended (also known as 'Far East'), Nat Nat, and 99, and from four active sites at Kowalczyk, Binns, Williamson, and Fullagar Extended (Fig. 1, Table 1). The substratum of the inactive sites was massive sulfide deposited by hydrothermal processes, except at 99, where the substratum was volcanic rock and not a sulfide deposit. Of the six inactive sites sampled, the westernmost part of Williamson and 99 supported the largest areas of inactive substratum and the greatest biomass and abundance of non-vent-endemic taxa (cladorhizid sponges, Keratoisis sp. bamboo corals, stalked barnacles, and hydroids; Table 1, Fig. 2). Fullagar Extended, Kowalczyk, and Binns were characterized by active sulfide deposits interspersed with inactive sulfide deposits. Paine, 99, and Nat Nat were characterized by large areas of sedimented seabed with discrete patches of inactive substratum (Table 1). At the time of sampling, Binns and Kowalczyk were the most active of the four active sites sampled and supported the highest biomass and abundance of vent-endemic taxa (Fig. 2). At Fullagar Extended there were only a few localized areas of active venting with high biomass and abundance of vent-endemic taxa.

Specimens were collected using a suction sampler, 'biological scoop', or the ROV manipulator claw. Invertebrates were preserved for laboratory identification in 10% buffered formalin (24 h) and stored in 70% ethanol. Consultants verified taxonomic identifications (see acknowledgements). Mode of feeding for each invertebrate taxon is inferred based on literature review and functional anatomy. Voucher specimens are archived at the Duke University Marine Laboratory (Beaufort, NC). Samples of sulfide rocks from hydrothermally active and inactive sites were collected for sulfur isotopic analysis of associated organic material and stored dry. Whole animals and tissues for isotope analysis were stored frozen, dried at 60 °C, and processed in the laboratory.

2.1. Stable-isotope analysis

Muscle tissue was preferentially used for isotopic analysis. For smaller organisms, multiple individuals were homogenized using a mortar and pestle as a single sample. For certain small taxa, we analyzed pooled samples of individuals assumed to be in the same taxonomic and trophic category (e.g., hydroids, limpets, isopods, or amphipods). Animal tissues and the outer surface of sulfide samples were acidified to remove carbonate, and dried. Carbonate-free residues were weighed into tin capsules and converted to CO_2, N_2 and SO_2 for isotope analysis using a Carlo Erba elemental analyzer coupled to an OPTIMA stable-isotope-ratio mass spectrometer (GV Micromass, Manchester, UK). Carbon and nitrogen isotopic compositions were determined simultaneously on each sample using a dual furnace system composed of an oxidation furnace at 1020 °C and a reduction furnace at 650 °C. Using the Carlo Erba elemental analyzer, samples for sulfur were separately pyrolyzed at 1050 °C by means of a combination oxidation and reduction single furnace system. The resulting gases were chemically dried and directly injected into the source of the mass spectrometer. Isotopic composition of stable isotopes is based on the standard expression as a delta value (δ):

$$\delta^n X = (R_{sample}/R_{standard} - 1) * 1000‰ \text{ (per mil)},$$

where X is the heavy isotope (^{13}C, ^{15}N, or ^{34}S), and R is the abundance ratio of the heavy to light isotopes ($^{13}C/^{12}C$, $^{15}N/^{14}N$, or $^{34}S/^{32}S$).