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# Beyond the vent: New perspectives on hydrothermal plumes and pelagic biology



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#### ABSTRACT

Submarine hydrothermal vent fields introduce buoyant plumes of chemically altered seawater to the deep-sea water column. Chemoautotrophic microbes exploit this energy source, facilitating seafloor-based primary production that evidence suggests may transfer to pelagic consumers. While most hydrothermal plumes have relatively small volumes, there are recent examples of large-scale plume events associated with periods of eruptive activity, which have had a pronounced effect on water-column biology. This correlation suggests that hydrothermal plumes may have influenced basin-scale ocean chemistry during periods of increased submarine volcanism during the Phanerozoic eon. This paper synthesizes a growing body of scientific evidence supporting the hypothesis that hydrothermal plumes are the energetic basis of unique deep-sea pelagic food webs. While many important questions remain concerning the biology of hydrothermal plumes, this discussion is not present in ongoing management efforts related to seafloor massive sulfide (SMS) mining. Increased research efforts, focused on high-resolution surveys of midwater biology relative to plume structures, are recommended to establish baseline conditions and monitor the impact of future mining-based disturbances to the pelagic biosphere.

#### 1. Introduction

Hydrothermal vent systems exist in every ocean and are associated with a diverse range of geological and oceanographic settings (reviewed by Baker and German, 2004). Since their initial discovery in 1977, an entire research community has grown around their study, with new findings reported every year. Hydrothermal fields have characteristically diverse morphology and geochemistry, spanning the extremely deep, hot, and metal-rich 'black smoker' vent field recently discovered in the Mid-Cayman Spreading Center (Connelly et al., 2012; Kinsey and German, 2013) to the relatively shallow, lukewarm and serpentinite-hosted Lost City vent field on the Mid-Atlantic Ridge (Kelley et al., 2001, 2005). Unique fluid compositions, resulting from fluid-rock interactions occurring in the subseafloor reaction zone (Amend et al., 2011), host chemosynthetic communities with distinct biographic provinces on a global scale (Bachraty et al., 2009; Van Dover, 2011; Rogers et al., 2012). Buoyant hydrothermal plumes are just as diverse in chemistry and size, with some "megaplumes" encompassing thousands of km<sup>3</sup> in volume (Baker et al., 1987; Murton et al., 2006). Given the known global distribution of hydrothermal vents, hydrothermal

plumes are recognized as an important mechanism for thermal and chemical fluxes at the ocean basin scale (Hannington et al., 2005), as transport mechanisms for vent-endemic larvae (Tyler and Young, 2003) and tracers for major deep-sea circulation patterns (Lupton, 1995).

The influence of hydrothermal plumes on midwater biology is an embryonic research topic receiving increased attention by the oceanographic research community. While the population dynamics of deepsea pelagic faunas is poorly understood, direct measurements of enriched microbiological activity inside plumes are now paralleled with observations of elevated biomass associated with higher trophic levels. Synthesizing these results endeavors to improve our understanding of hydrothermal systems on a global scale, and draw hypotheses linking the geochronology of seafloor volcanism to the evolutionary history of pelagic fauna. Furthermore, a recent surge in efforts to promote deep-sea mining of hydrothermal vent fields has prompted numerous calls for precautionary management of these environments (Halfar and Fujita, 2002; Hoagland et al., 2010; Van Dover, 2011).

This paper presents a comprehensive synthesis of known and inferred biological and ecological processes associated with hydrother-

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mal plumes. This broad assessment is placed in context with geochronologic evidence of pulsed seafloor volcanism during the Phanerozoic eon (0–500 Mya), with present-day conditions likely driving minimal hydrothermal fluid output scenario on a global scale. Based on these considerations, the author advocates for increased research efforts to study the biology of hydrothermal plumes, particularly in the context of SMS mining. Such activities have the potential to dramatically alter natural plume-based ecosystems, which currently do not have an established baseline.

#### 2. Review: hydrothermal plumes and pelagic biology

#### 2.1. Hydrothermal plumes in space and time

The combined effects of temperature, pressure, and geologic setting drive a diverse range of fluid compositions at the approximately 600 known or inferred submarine hydrothermal vent fields in the world's oceans (Hannington et al., 2005; Beaulieu et al., 2013). Buoyant plumes originating from seafloor vents entrain background seawater as they rise, allowing them to grow in volume until they achieve a depth of neutral buoyancy where they continue to spread laterally (Baker et al., 1995; Lupton, 1995). If incidence along a ridge is high enough, singular-source plumes can combine into a larger volume; this effect is further pronounced in slow-spreading ridges with deep axial valleys and other constraining bathymetry. While off-axis, diffuse flow venting may account for heat and water flux at more than an order of magnitude higher than on-axis high temperature flow (Elderfield and Schultz, 1996), such fluid sources are not considered in this discussion based on the assumption that they do not rise high enough into the water column to influence the pelagic environment. However, the author notes that further work is required to explore the possible effects of diffuse flow venting on water-column chemistry.

Quantifying the size of hydrothermal plumes is problematic due to the non-conservative nature and/or low concentrations of many measurable properties. Hydrographic and optical tracers (temperature, salinity, optical backscatter, light attenuation), whilst easy to measure in situ, dissipate quickly and may present a low-end estimate of plume size. Suspended particles in particular are subject to precipitation and sinking mediated by both physical and biological processes (Breier et al., 2012). Chemical tracers can be used to detect hydrothermal plumes at significant distances from their source, but in most cases must also be considered non-conservative due to microbial and oxidation gradients. For example, dissolved iron is subject to rapid biogeochemical speciation in the deep-sea (Tagliabue et al., 2010, Toner et al., 2012), which complicates flux estimation and makes its utility as a tracer quite subjective. In contrast, primordial helium (<sup>3</sup>He) is a stable, non-biologically labile isotope that can be used as a conservative tracer to detect plumes thousands of km's from ridgeaxis sources (e.g. Stommel, 1982; Lupton, 1998; Rüth et al., 2000).

The relatively small size of present-day buoyant hydrothermal plumes that are measured using labile tracers compared to the total volume of the modern ocean has led to a general notion that their effect on basin-scale midwater biology is insignificant. There is, however, a line of reasoning that demonstrates this may not have always been the case. Seafloor spreading encompasses a wide range of velocities and patterns, with characteristic examples including the ultra-slow spreading Mid-Cayman Rise ( $< 20 \text{ mm yr}^{-1}$ ) and the fast-spreading East Pacific Rise (100–150 mm yr<sup>-1</sup>). Global average spreading rates for the observable lithosphere is now well established, limited by the maximum age of the seafloor to approximately 280 Mya (Müller et al., 2008). However, volcanism associated with mid-ocean spreading is characteristically episodic and spreading rates vary on multiple periodicities. These eruptive cycles are ultimately driven by mantle plumes but are also sensitive to tidal patterns on the <1 yr scale (Wilcock, 2001) and long-term variations in sea level associated with

Milankovitch cycles on the 10–100 kyr scale (Lund and Asimow, 2011; Tolstoy, 2015; Crowley et al., 2015).

Crucially, patterns of seafloor spreading and the resulting volcanism exhibit a direct correlation with hydrothermal circulation and plume incidence (Baker et al., 1995; Baker and German, 2004). Heat and mass flux calculations based on present-day observations indicate that the entire mass of the world's oceans cycles through mid-ocean ridges every ~10 My (Elderfield and Schultz, 1996), but the pulsed nature of seafloor volcanism influences hydrothermal circulation on shorter time scales (e.g. Lalou et al., 1990; Chu et al., 2006; Lund and Asimow, 2011). Recently observed "megaplumes" are examples of high-output plume events that can extend for 10 s of kilometers laterally and beyond 1000 m above the seafloor (Baker et al., 1987; Murton et al., 2006). Asymmetric sedimentation patterns on the Western ridge flank of the East Pacific Rise align with present-day <sup>3</sup>He plume signals originating from the spreading axis, and may be the result of biologically enriched plume fallout persisting for >7 Mya (Hauschild et al., 2003). Given the current observed state of suppressed global volcanism due to relatively high sea level and low orbital eccentricity, it is reasonable to hypothesize that these are minimal examples of large-scale hydrothermal plumes.

Basin-scale changes in ocean chemistry, such as oceanic anoxic and euxenic events in the past 500 Mya, exhibit correlation with submarine volcanism and hydrothermal flux. The Cenomanian-Turonian boundary, a global ocean anoxic event centered at approx. 90 Mya that led to the extinction of almost a third of marine invertebrate species, is thought to be the result of a massive hydrothermal output event that introduced enough reduced inorganic material to cause basin-scale declines in dissolved oxygen (Sinton and Duncan, 1997). This event may have persisted for up to 40 My based on magnetic reversal evidence in the South Pacific (Larson, 1991) and has been directly connected to magmatic pulsing (Turgeon and Creaser, 2008). A similar explanation has been proposed for the Jurassic oceanic anoxic event ~183 Mya (Jones and Jenkyns, 2001). Global glaciation may have compounded the effect of increased hydrothermal flux driving changes to ocean chemistry (Gernon et al., 2016), and other biologicallymediated positive feedbacks may have enhanced oxygen depletion leading to euxinic conditions (Meyer and Kump, 2008). The biogeochemistry of present-day hydrothermal vent plumes may offer a glimpse into how these environments functioned on much larger spatiotemporal scales.

#### 2.2. Hydrothermal plume ecology

While thousands of publications address the biology of hydrothermal vent systems, fewer than one hundred papers focus specifically on the role of hydrothermal plumes (Fig. 1). These reports are fairly evenly distributed among the topics of larval dispersion, microbiology, and zooplankton, but the absence of a single publication addressing tertiary consumers (such as mesopelagic fishes) in relation to hydrothermal plumes is noteworthy. The following sections synthesize the findings of the publications presented in Fig. 1.

#### 2.2.1. Microbiology

Seafloor biological communities associated with vent-derived chemoautotrophy are well documented and thoroughly reviewed by Van Dover (2000). Comparatively few studies address microbial life in hydrothermal plumes, but all evidence indicates an enrichment of chemoautotrophic biomass within these unique midwater environments. These communities may originate from the subseafloor and enter the ocean via original fluid discharge, as well as derive from background seawater entrained within the plume. Early work on the Endeavour Segment of Juan de Fuca Ridge gave the first evidence of elevated bacterial biomass in hydrothermal plumes (Winn et al., 1986). Trace metal scavenging mediated by microbial activity within a plume was observed several years later (Cowen et al., 1990; Cowen and Hui, Download English Version:

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