ARTICLE IN PRESS

Deep–Sea Research II xx (xxxx) xxxx–xxxx

Contents lists available at ScienceDirect

Deep–Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

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

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ARTICLE INFO

Keywords:
Hydrothermal springs
Hydrothermal plumes
Hydrothermal solutions
Zooplankton
Water column
Deep-sea mining

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^3 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 deep-sea 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

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http://dx.doi.org/10.1016/j.dsr2.2016.10.005

Please cite this article as: Phillips, B.T., Deep–Sea Research II (2016), http://dx.doi.org/10.1016/j.dsr2.2016.10.005

inferred biological and ecological processes associated with hydrothermal 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 (^{3}He) is a stable, non-biologically labile isotope that can be used as a conservative tracer to detect plumes thousands of km's from ridge-axis 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 mm yr^{-1}) and the fast-spreading East Pacific Rise (100–150 mm yr^{-1}). 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 ^{3}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 biologically-mediated 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,

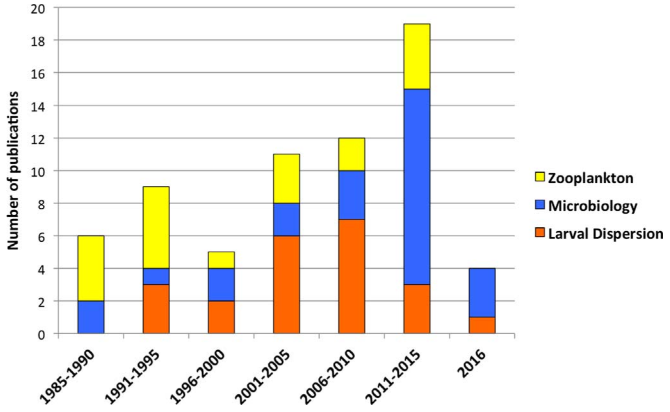

Fig. 1. The number of primary journal articles published since 1985 that associate midwater biology and hydrothermal plumes. "Larval Dispersion" papers are restricted to studies on vent-endemic larvae. Based on a survey of Web of Science, Google Scholar and references therein.

1991), closely followed by evidence of an associated increase in methane oxidation (De Angelis et al., 1993). At the same site, sinking biogenic particulate matter from the surface appeared to scavenge hydrothermally-sourced Fe within the midwater plume (Bertram et al., 2002). A major eruptive event on the nearby Gorda Ridge allowed for observations of 2–3 fold increases of bacterial abundance in the resulting plumes (Juniper et al., 1998) largely associated with manganese-precipitating bacteria (Cowen et al., 1998). Observations following the 1998 eruption of Axial Seamount delivered similar results, with significantly higher counts of bacteria measured relative to background seawater (Cowen et al., 1999).

Evidence of plume-associated microbiology has now been observed in several oceanic basins. Sunamura et al. (2004) found a permanent sulfur-reducing microbial population within a plume physically constrained by an active submarine volcano's caldera in the Izu-Bonin Arc. Recently, Bennett et al. (2013) reported on three distinct zones of primary production occurring in the plume overlying the Von Damm vent field in the Cayman Spreading Center, largely driven by methanotrophic bacteria. A range of enriched chemoautotrophic processes associated with plumes in the Guaymas and Lau Basins is described by Dick et al. (2013), notably mediated by diverse communities similar to background seawater but with higher specific abundances (Dick and Tebo, 2010) and largely dominated by sulfur-reducing microorganisms (Anantharaman et al., 2016). Inconclusive evidence of vent-associated pelagic microbiology over Nordic Sea vents is presented in Olsen et al. (2015). The interplay of microbial activity relative to an ephemeral hydrothermal plume was recently examined by an integrated monitoring program following the submarine eruption of El Hierro (Canary Islands). The massive discharge of acidic fluids enriched in dissolved Fe, reduced sulfur species, and CO_2 led to a completely anoxic condition in the core of the midwater plume (Santana-Casiano et al., 2013), followed by increased abundance and decreased species richness of heterotrophic bacteria throughout the water column (Ferrera et al., 2015). When the eruption ended approximately 6 months later, the water column returned to normal conditions.

2.2.2. *Vent-associated larvae*

Vent-endemic larvae and their post-larval forms present another source of biological enrichment within hydrothermal plumes (Mullineaux et al., 1995). The planktonic stages of these species can live for weeks to months, facilitating dispersal over 100 s of kilometers and directly influencing the global biogeography of hydrothermal vent communities (reviewed in Tyler and Young, 2003). While estimates of larval abundance in plumes are orders of magnitude lower than microbial abundance (e.g. Mullineaux et al., 2005; Bennett et al., 2013), individual larvae are much larger than bacteria and these energy-rich food sources may be specifically targeted by larger midwater predators that do not filter feed (Lindsay et al., 2015). Given the distinct vent-associated biogeographic provinces now defined on a global scale for benthic communities (Bachraty et al., 2009; Van Dover, 2010; Rogers et al., 2012) such ecologic diversity may also be true for plume-associated biological communities and their larval constituents. The known hydrologic barriers and corridors governing larval dispersion among hydrothermal vent faunas (Thomson et al., 2003; Adams et al., 2012) may offer a first-order evaluation of these pelagic provinces.

2.2.3. *Zooplankton*

Pathways of plume-mediated chemosynthetic production to higher trophic levels have not been directly observed, but there is growing evidence that such connections exist. Enriched, upward-directed lipid and POC flux associated with secondary production was first measured at the Endeavour Segment of Juan de Fuca Ridge using moored inverted sediment traps (Cowen et al., 2001; Wakeham et al., 2001). Burd and Thomson (1995, 2012, 2015) have repeatedly observed a broad enrichment of biomass and secondary production in the water column above the Endeavour Vent Field using towed multiple-net equipment paired with backscatter measurements from acoustic Doppler current meters. Some of this research has also pointed to an increased abundance of predacious gelatinous zooplankton that may be associated with enriched microzooplankton biomass within plumes (Burd and Thomson, 2000). Early work on the East Pacific Rise and within Guaymas Basin also indicate enriched benthopelagic zooplankton populations directly above and surrounding active hydrothermal vent fields (Smith, 1985; Berg and Van Dover, 1987; Wiebe et al., 1988).

Visual-based methods to observe zooplankton distribution relative to hydrothermal plumes have produced largely inconclusive results, despite the extensive deployment of ROV's and manned submersibles to hydrothermal vent sites. Video-based quantification of zooplankton and nekton populations at Juan de Fuca Ridge revealed a complex system heavily influenced by physical circulation patterns, with distinct clustering of major organism groups relative to plume and bathymetric zones (Skebo et al., 2006). Total abundances of macroplankton relative to the Lost City and Broken Spur hydrothermal vent fields appear unrelated to these features (Vinogradov and Vereshchaka, 2006), but dense aggregations of salps have been observed at Lost City offset from their expected diel vertical migration pattern and near the maximum of their known depth range (Fig. 2; author, personal observations). A diverse community of gelatinous zooplankton was observed in waters overlying a vent field in the Okinawa Trough (Lindsay et al., 2015); notably, appendicularian larvaceans were measured in high abundances relative to turbid plume waters. Similarly, larvaceans were seen in dense aggregations inside a hot (> 43 °C), acidic (< 6.1 pH) and turbid plume at a shallow-water volcanic vent in the Solomon Islands (Fig. 2). Given that filter-feeding appendicularians have the ability to capture suspended picoplankton (Bedo et al., 1993; Gorsky et al., 1999), they are uniquely suited to exploit chemosynthetic bacteria as an energy source.

2.2.4. *Tertiary consumers*

Associations between hydrothermal plumes and tertiary consumers are hypothesized based on several noteworthy reports and observations. Coincident acoustic backscatter and deep-water trawl data give evidence of enriched fish biomass relative to the Mid-Atlantic Ridge (Sutton et al., 2008). While a recent review concluded that seafloor biological productivity likely had no influence on these observations (Priede et al., 2013), the studies were not targeting specific geographic regions of hydrothermal venting. Burd and Thomson (2015) present a strong hypothesis for an associative pattern of whale feeding and hydrothermal plume-associated zooplankton at the Endeavour Segment of the Juan de Fuca Ridge; this is best supported by acoustic

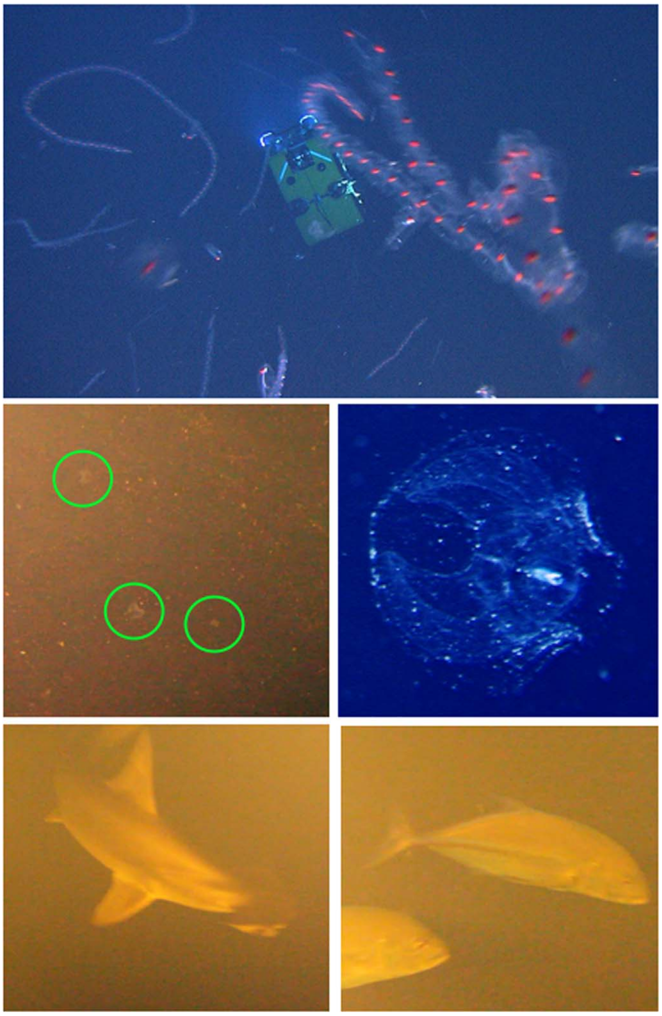

Fig. 2. *Top row*: Down-looking view of a *Salpa* sp. swarm with the *HERCULES* ROV in center frame, taken from ~30 m altitude above the Lost City vent field at a depth of ~750 m (image courtesy of NOAA Ocean Exploration/Institute for Exploration/Inner Space Center). *Middle row*: larvaceans inside the Kavachi volcano crater circled in green (left, image copyright The National Geographic Society) and a close-up view of a similar larvacean observed in dense numbers at the Hatoma Knoll hydrothermal vent field (right, image courtesy of D. Lindsay). *Bottom row*: A hammerhead shark, *Sphyrna lewini* (left) and bluefin trevally, *Caranx melampygus* observed inside the Kavachi volcano crater (both images copyright The National Geographic Society).

behavior studies on fin whales in the region (Soule and Wilcock, 2013). In addition to swarms of larvaceans, two species of reef fish and two species of shark appeared to be living within the hydrothermal plume of the Solomon Islands submarine volcano, where catastrophic eruptions occur on a monthly basis (Fig. 2; Phillips et al., in press). Tagged leatherback turtles have been repeatedly observed circling the same volcano in a pattern consistent with feeding behavior (Albert et al., 2014). These collective observations, while lacking definitive conclusions, inspire further questioning and highlight the potential influence of hydrothermal plumes to the pelagic biosphere.

3. Discussion

The spatiotemporal boundaries of hydrothermal plumes are characteristically ephemeral and span broad biogeochemical gradients. In contrast, most methodology used to observe the biology inside and around plumes do not adequately address this dynamic nature. The temporal patterns of hydrothermal venting at specific study sites, a nascent research topic of its own, must be considered to place future biological observations in proper context. With the notable exception of work presented by Burd and Thomson (2015), which includes observations made over two decades at the Juan de Fuca Ridge, most investigations into plume-associated biology have taken place on singular oceanographic cruises. In several instances published conclusions have been made based on a single submersible or ROV dive.

Observing pelagic populations in high spatial resolution is a characteristic challenge in biological oceanography. The approximate 100-meter depth intervals that most surface-controlled multiple net systems can achieve may be too coarse to adequately resolve spatial patterns associated with hydrothermal plumes. The extreme bathymetry generally associated with active spreading centers further complicates the use of towed nets to assess zooplankton distribution. New methods centered on advanced acoustic and video-based technology may address this issue; for example, AUV-based high-resolution acoustic surveys have demonstrated an approximate 5-meter critical scale necessary to resolve patchiness in deep-sea zooplankton (Benoit-Bird et al., 2013). The video transects made in Endeavour Axial Valley approach the 10-meter scale (Skebo et al., 2006), and are a good example of a high spatial resolution survey applied to a hydrothermal plume. More studies such as these, conducted on multiple time scales, are needed; highly maneuverable autonomous platforms and long-term deployment ocean observatories may be critical to achieving success in this regard.

Despite worldwide interest from a diverse set of stakeholders, the potential impact of deep-sea seafloor massive sulfide (SMS) mining on existing plume-associated pelagic biology has essentially been ignored. An important distinction must be made: the introduction of sediment plumes from SMS mining, whether from seafloor extraction or from surface processing, is a completely different consideration than the potential disturbance of altering and/or removing existing hydrothermal fluid sources to the water column. The former topic of sediment plumes has received much attention in recent policy literature (Boschen et al., 2013) and has been the subject of at least three deep-sea experiments related to SMS and manganese nodule mining (Fukushima, 1995; Borowski and Thiel, 1998; Sharma et al., 2001). Paradoxically, there appears to be no mention of hydrothermal plume-associated biology in SMS mining policy literature, and all published work on plume-associated biology (Fig. 1) fails to draw connections to the long-standing threat of SMS mining. Given the observations and hypotheses presented in this work regarding secondary and tertiary consumer associations with hydrothermal plumes, and the relatively unexplored nature of hydrothermal systems in general, it appears that an entire ecosystem is being overlooked by SMS policy stakeholders.

The International Seabed Authority (ISA) has long recognized the need to establish a proper baseline from which to judge the potential impacts of SMS mining to deep-sea ecosystems (e.g. ISA Technical Study #9 2011, ISA Technical Study #10 2011). Potential disturbance to the natural hydrothermal plume environment is missing from these high-level discussions, and existing scientific evidence is insufficient to properly define a baseline for the ISA to adopt. This presents a compounded problem: to put it simply, we do not know what is out there, and if SMS mining proceeds with the current level of oversight, we will not know if it is gone. Furthermore, efforts to create Marine Protected Areas that include deep-sea vent sites (i.e. the Endeavour Hydrothermal Vents Marine Protected Area, Department of Fisheries and Oceans Canada) may also wish to include the plume environment in spatial management efforts.

4. Conclusion

This paper reviews a growing body of evidence portraying hydrothermal plumes as a distinct, biologically rich environment in the deep-sea water column. Chemoautotrophic microbial food webs have been observed in association with every plume that has been examined, and a positive relationship with secondary consumers appears to be a common occurrence. A connection between hydrothermal plumes and tertiary consumers, such as midwater fish, sharks, and marine mammals, is hypothesized based on limited observations. The influence of plumes to ocean chemistry on large spatiotemporal scales is inferred based on the geochronology of submarine volcanism. Despite these wide-ranging considerations, the pelagic biology associated with hydrothermal plumes appears to be excluded from deep-sea management efforts, specifically within the context of SMS mining. The author recommends increasing research efforts to incorporate dedicated surveys of pelagic biology relative to plume structure in high spatio-temporal resolution, and an inclusion of hydrothermal plume biology in discussions at the policy and management level for the deep-sea.

Acknowledgements

This paper is the result of a special session on deep-sea mining held at the 14th Deep Sea Biology Symposium in Aveiro, Portugal in September 2015. The author wishes to thank Richard Thomson, Karen Wishner, and two anonymous reviewers for their critical reviews of this manuscript. Dhugal Lindsay, Steven Carey, and Paraskevi Nomikou contributed helpful discussions and imagery.

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