



Impacts of anthropogenic disturbances at deep-sea hydrothermal vent ecosystems: A review



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ABSTRACT

Deep-sea hydrothermal-vent ecosystems have stimulated decades of scientific research and hold promise of mineral and genetic resources that also serve societal needs. Some endemic taxa thrive only in vent environments, and vent-associated organisms are adapted to a variety of natural disturbances, from tidal variations to earthquakes and volcanic eruptions. In this paper, physicochemical and biological impacts of a range of human activities at vents are considered. Mining is currently the only anthropogenic activity projected to have a major impact on vent ecosystems, albeit at a local scale, based on our current understanding of ecological responses to disturbance. Natural recovery from a single mining event depends on immigration and larval recruitment and colonization; understanding processes and dynamics influencing life-history stages may be a key to effective minimization and mitigation of mining impacts. Cumulative impacts on benthic communities of several mining projects in a single region, without proper management, include possible species extinctions and shifts in community structure and function.

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1. Introduction

Since the discovery of hydrothermal vents in the late 1970s, scientific research has been the primary source of anthropogenic disturbance in these ecosystems (Glowka, 2003), but there is increasing interest in commercial exploitation of seafloor massive sulfides that host vent communities (Hannington et al., 2011; Hein et al., 2013; Hoagland et al., 2010; Rona, 2008). Impacts of anthropogenic disturbances at deep-sea vents are considered here in the context of natural disturbance regimes and in more detail than has been provided elsewhere (e.g., Baker et al., 2010; Halfar and Fujita, 2007; Ramirez-Llodra et al., 2010, 2011; Van Dover, 2011a; Boschen et al., 2013).

2. General characteristics of deep-sea vent ecosystems

Hydrothermal-vent ecosystems are localized areas of the seabed where heated and chemically modified seawater exits the seafloor as diffuse or focused flow and where microbial chemoautotrophs are at the base of the food web (Van Dover, 2000). Most vent ecosystems tend to be linearly distributed on hard substrata

(basalt) associated with new ocean crust along seafloor spreading centers, though there are sites where active vents on spreading centers are sediment-hosted (e.g., Guaymas Basin in the Gulf of California, Gorda Ridge in the northeast Pacific; Van Dover, 2000). Vents are also associated with seamount volcanic systems (e.g., Loihi Seamount, Karl et al., 1988; seamounts of the Kermadec Ridge; Clark and O'Shea, 2001).

The spatial extent of any given vent field depends on the geological setting, but they tend to be at most a hundred meters or so in maximum dimension and separated from one another by 50–100 km (e.g., the TAG mound on the slow-spreading Mid-Atlantic Ridge) at one extreme or, at the other extreme, to be much smaller features (on the order of 10–50 m maximum dimension) arrayed linearly in clusters and spaced at intervals ranging from a few kilometers to 10s of kilometers on the axis of fast spreading centers (e.g., the 9°N vent field on the East Pacific Rise).

While hydrothermal fluids exiting the seafloor from black smoker chimneys reach temperatures from 330 °C to 400 °C, mixing of vent fluids with cold seawater—either in subsurface rocks or through walls of black smoker chimneys—results in habitable zones of diffuse flow with temperatures ranging from just above ambient (~2 °C) to ~50 °C (Girguis and Lee, 2006). Fluid chemistry is generally correlated with temperature at hydrothermal vents, with higher temperatures associated with a greater proportion of typically sulfide- and metal-rich and oxygen-

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depleted vent fluids (Johnson et al., 1988; Zielinski et al., 2011). The specific nature of these relationships can vary from one site to another (Beinart et al., 2012; Podowski et al., 2010).

Vent ecosystems are typically dominated by benthic invertebrate taxa (e.g., vestimentiferan tubeworms, bathymodiolin mussels, vesicomyid clams, provannid snails, rimicarid shrimp, yeti crabs) that host symbiotic, chemoautotrophic microorganisms. These symbionts require a source of electron donors (e.g., sulfide in vent fluid), a source of electron acceptors (e.g., O_2 in seawater), and a source of inorganic carbon (e.g., CO_2 or CH_4 in vent fluids, CO_2 in seawater). These so-called 'holobiont' (host-symbiont) taxa often exhibit unusual morphological, physiological, and biochemical adaptations to characteristics of vent environments, including loss of the digestive system in vestimentiferan tubeworms, novel photoreceptors in swarming shrimp on black smoker chimneys, and sulfide-binding proteins in vesicomyid clams (Van Dover, 2000). Holobiont taxa are also often foundation species, creating complex 3-dimensional habitat (e.g., worm aggregations, bivalve beds, snail aggregations) that serves as substratum for microbial growth and as refugia for juvenile invertebrates and habitat for associated organisms, including primary consumers (e.g., limpet grazers on microbial biofilms) and secondary and tertiary consumers (e.g., scavenging and predatory crustaceans and fishes).

Zonation at vents can be reminiscent of intertidal zonation, with holobiont taxa typically dominating the biomass of habitable diffuse flow regions and with abrupt transitions from one species to another that relate to differing tolerances among species for thermal and chemical regimes and to biotic interactions (facilitation, competition, predation). Total biomass of benthic organisms is typically very high at vents; beyond the periphery of a vent field, living biomass is relatively inconspicuous, punctuated occasionally by solitary large anemones, gorgonian corals, or other megafaunal organisms.

Diversity (species richness) at deep-sea hydrothermal vents is relatively low, on a par with that observed in temperate and boreal rocky intertidal systems (Van Dover and Trask, 2000), with numerical dominance (thousands of individuals per m^3) by a small number of species (<10) and with a large percentage (25%) of rare taxa (occurring as singletons or doubletons) in suites of replicate quantitative samples (Van Dover, 2002). Cryptic taxa (morphologically similar, genetically distinct) and phenotypic plasticity (genetically similar, morphologically distinct) are commonly observed. Species composition is often differentiated by habitat within a geographic region (e.g., species-abundance matrices of mussel beds are different from those of tubeworm aggregations) and varies substantially across ocean basins, with up to 11 biogeographic provinces recognized to date (Moallic et al., 2012; Rogers et al., 2012; Van Dover et al., 2002).

Growth rates of holobiont taxa at vents are among the fastest reported for marine invertebrates (Lutz et al., 1994; Shank et al., 1998). Reproductive maturation is early and gametogenesis in vent taxa is generally continuous, without a strong seasonal signal and little if any evidence for gametogenic synchrony in many vent taxa analyzed (Tyler and Young, 1999). Surprisingly, there is good anecdotal evidence of cohort phenomena occurring in at least some vent taxa (e.g., vestimentiferan tubeworms, rimicarid shrimp), where enormous numbers of juveniles have been observed in a given location (Short and Metaxas, 2010). Fertilization strategies of vent invertebrates are diverse, ranging from sperm transfer, storage, and internal fertilization [e.g., in scaleworm (polynoid) polychaetes] to broadcast spawning (e.g., bathymodiolin mussels), with nearly all taxa undergoing a dispersive larval phase with either lecithotrophic or planktotrophic development (Adams et al., 2011; Tyler and Young, 1999).

3. Natural disturbance in deep-sea hydrothermal vent ecosystems

Natural physico-chemical disturbances at hydrothermal vents range in severity from periodic tidal fluctuations in fluid flow and plume fall-out that have negligible impact on the ecosystem, to chronic disturbance regimes associated with mineralization and clogging of conduits, to systematic disturbances associated with the hydrothermal cycle. Unpredictable and catastrophic disturbance regimes result from collapse of structures either through inherent instability of mineralized structures or as a result of tectonic activity and infrequent catastrophic volcanism that paves over vent fields and result in local extinctions (Fig. 1).

Deep-sea vents have been understood to be ephemeral habitat islands from the moment of their discovery (Macdonald et al., 1980). Vent-restricted taxa are characterized by rapid growth rates, early maturation, large reproductive output, and well-developed dispersal capabilities (Grassle, 1986), characteristics shared by opportunistic marine invertebrate species that persist despite frequent local extinctions and divergent from those of deep-sea species in low-disturbance regimes (Grassle and Sanders, 1973). The documented impact of natural disturbances on vent ecosystems is reviewed here, to provide context for understanding impacts of human activities at deep-sea vents. Levels of impacts are assessed based on both the amount of change to vent ecosystems and the duration of change (Table 1).

3.1. Tidal fluctuations and plume fall-out

Diffuse vents exhibit continuous microscale temperature and chemical fluctuations due to turbulent mixing, and larger scale fluctuations (several degrees Celsius, several orders of magnitude in sulfide concentration) related to tidally induced changes in bottom flow (Tivey et al., 2002) and tidal pumping (Luther et al., 2008; Scheirer et al., 2006). The alvinellid polychaete *Paralvinella sulfincola* and other mobile invertebrate types may adjust their position in response to these fluctuations to maintain an optimal position (Robert et al., 2012). Tidal excursions of 10 °C or more are commonly tolerated by sessile or attached vent taxa (e.g., the mussel *Bathymodiolus puteoserpentis*; Zielinski et al., 2011). While tidal periodicities in shallow water are linked to a variety of periodicities in physiological processes of shallow-water invertebrates, including reproductive activities, this kind of linkage has so far not been documented for vent invertebrates. What seems clear is that many invertebrate species at vents are naturally exposed to and tolerate variable fluid chemistry and temperature regimes. What is usually not clear for most taxa is the optimal set of conditions that maximize growth and reproductive output.

Iron- and manganese-rich particulate plumes generated by black smokers typically rise 100 m or more vertically and disperse horizontally; most (99%) sedimentation of particulate iron and manganese may occur away from the vent field (e.g., Feely et al., 1994) and have little impact on benthic ecosystems through processes such as burial or clogging of feeding systems. Volcanoclastic fragments are also produced at spreading centers during deep-sea volcanic eruptions (Barreyre et al., 2011). To date, evidence for impacts of hydrothermal or volcanic plume fallout on hydrothermal vent organisms is scarce in the primary literature.

3.2. Mineralization and conduit dynamics

Time-series studies of sulfide structures at vents sites on the Juan de Fuca Ridge, Mid-Atlantic Ridge, and elsewhere emphasize the role that mineralization and clogging of conduits play in destroying and creating habitat. Cuvelier et al. (2011) describe the

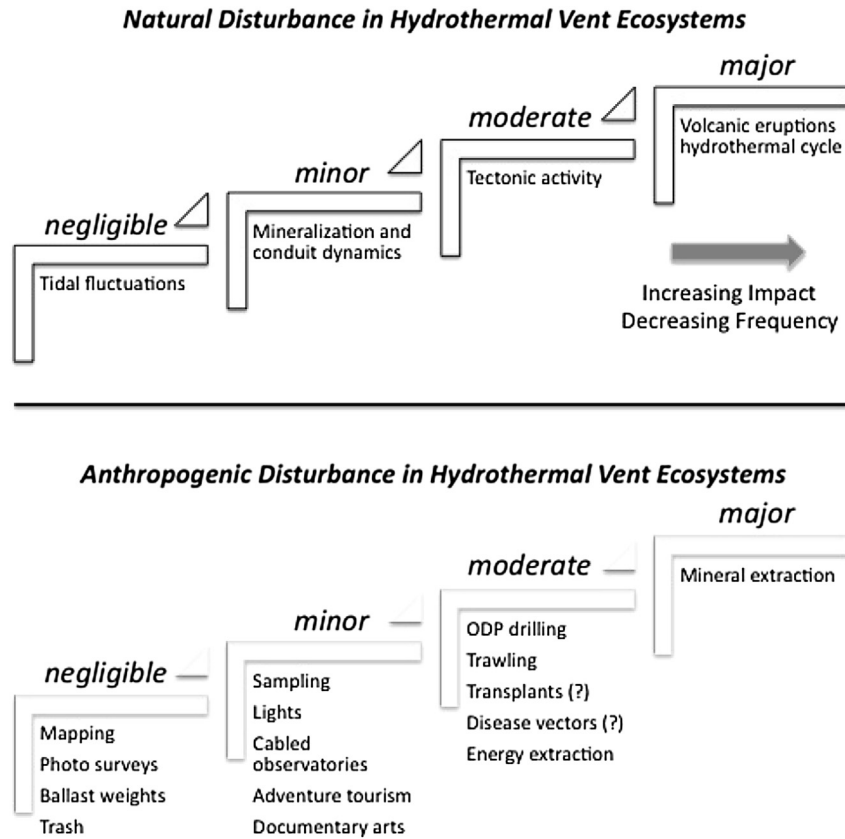


Fig. 1. Natural and anthropogenic disturbance at hydrothermal vents. Levels of disturbance are defined in Table 1. Natural disturbance occurs on a continuum of frequency and intensity of impact on vent biota. '?' indicates uncertainty associated with the classification of impact.

variability of hydrothermal activity on the Eiffel Tower edifice (Lucky Strike field, Mid-Atlantic Ridge) over a 14-year period and note the decline of hydrothermal activity at the summit and increased activity peripherally, with some corresponding reorganization of mussel beds but with overall constancy in their areal coverage.

A similar pattern of diversion of hydrothermal activity to the periphery of sulfide mounds and central clogging has also been reported for northeast Pacific vent sites (Sarrazin et al., 1997). In this Pacific setting, community structure is more dynamic than it is at the Eiffel Tower structure, with distinct faunal assemblages that occur during colonization of new 'chimlets' that form on large sulfide structures (Sarrazin et al., 2002): As early colonization of a chimlet takes place by a pioneer alvinellid polychaete species, the tubes of the polychaete allow a marcasite crust to mineralize underneath, which in turn modulates the thermo-chemical milieu and allows a second, less tolerant species of alvinellid polychaete to colonize the site. As fluid flow decreases further, other taxa move in, including limpets and tubeworms. In the senescent phase,

where clogging of the conduit becomes complete, the tubeworms, limpets, and other colonists are replaced by scavengers and detritivores. Because new chimlets open as other chimlets clog, a large sulfide edifice becomes a patchwork mosaic of assemblages representing different phases of the colonization cycle.

In the above examples of very localized and abrupt natural disturbance caused by changes in the location of fluid flow, the suite of biological responses include migration, facilitation, succession, recruitment, and trophic interactions. These disturbances do not typically result in local extinction, but community history and legacy effects can influence succession characteristics (Mullineaux et al., 2009). Biological responses to this scale of disturbance take place over periods of days to months and can promote locally enhanced species diversity as a consequence of mosaics of microhabitats in different phases of faunal succession at vents. Decadal-scale invariance in dominance, general distribution, and abundance of species at the TAG mound (Copley et al., 2007) and the Eiffel Tower edifice (Cuvelier et al., 2011) on the Mid-Atlantic Ridge remind us that processes occurring in one system may differ in others.

3.3. Tectonic activity

Vent fields occur on tectonically active regions of the seafloor, and tectonic activity can result in perturbation of fluid flow at vents through collapse of black smoker chimneys (e.g., Delaney et al., 1992) and swarm-induced rearrangement of the permeability zone (Crone et al., 2010). Documented disturbances include extended duration (weeks to months) temperature anomalies of 10 °C or more in diffuse flow zones occupied by vent invertebrates

Table 1
Levels of potential impacts to hydrothermal vent ecosystems. Modified from Cardno TEC Inc., 2013).

Impact level	Definition
Negligible	No measureable impact
Minor	Detectable change that is small, localized, of little consequence
Moderate	Readily apparent change over a relatively wide area
Major	Substantial change to the ecosystem over a large area (i.e., a vent field)

that, prior to seismic activity, had temperature records below 5 °C; the consequences of this scale of perturbation on the biological communities remains uncertain (Johnson et al., 2000).

Where chimneys collapse, there is loss of habitat, but new surfaces may form and become recolonized. Changes in fluid flow resulting from seismic activity could have many biological consequences, including mortality of taxa intolerant of the altered thermochemical conditions and enhanced growth, reproduction, and recruitment of taxa adapted to the altered conditions. Tectonic events may also generate plumes of suspended sediments that might cause burial of organisms, clog filtering mechanisms of suspension-feeding invertebrates, or otherwise interfere with biological activity (Binns and Decker, 1998), but such an event and its consequences are so far not documented.

3.4. Volcanic eruptions and hydrothermal cycles

Hydrothermal vents are associated with volcanic systems and as such are periodically subjected to volcanic eruptions and overrun. The frequency and duration of volcanic events vary depending on factors such as seafloor spreading rate and thickness of the crust (Rubin et al., 2012). Submarine volcanic eruptions may be explosive and continuous events, as evidenced by multi-year eruptions at submarine subduction zones (Embley et al., 2006; Deardorff et al., 2011; Rubin et al., 2012), or more effusive events (sometimes with explosive components; Chadwick et al., 2012; Dziak et al., 2009; Gregg et al., 1996) that take place relatively frequently (decadal or even sub-decadal time scales) and in a punctuated manner (durations of days to weeks) on fast- and intermediate spreading centers (e.g., East Pacific Rise, Juan de Fuca Ridge).

Chronic explosive volcanic activity generates an unstable benthic habitat that is colonized by only a few species. At 'Brimstone Pit', a volcanically active crater at the NW Rota-1 seamount, microbial mats and populations of mobile vent shrimp and crabs are the only persistent organisms (Embley et al., 2006). Acute effusive volcanic eruptions have acute catastrophic effects on hydrothermal vent communities. Lava flows, mass wasting, and explosive eruptions destroy vent communities, and there is typically a redistribution of venting activity associated with an eruption (Haymon et al., 1993). These events create a 'time zero', a Krakatau-like reset of the system (Whittaker et al., 2010), with well-documented 'recovery' of vent communities to pre-disturbance conditions taking place well within a decade (Marcus et al., 2009; Shank et al., 1998; Tunnicliffe et al., 1997).

Very infrequent eruptive events (repose intervals of a thousand years or more) are inferred for slow-spreading ridges (e.g., Mid-Atlantic Ridge; Rubin et al., 2012), where vent sites are long-lived and spaced at intervals of 100 km and more (Cherkashov et al., 2010). Despite the apparent longevity of venting activity in a given location, invertebrates living at Mid-Atlantic Ridge vents also display life-history characters associated with opportunistic species (Llodra et al., 2000; Tyler and Young, 1999), which suggests that factors other than volcanic eruptions may influence these life-history characters.

Genetic data can provide insight into the occurrence of catastrophic events, but any link to a singular volcanic event is so far not tenable. As an example, there is preliminary genetic evidence based on a single gene sequence for a recent bottleneck or founder event followed by demographic expansion in the shrimp *Rimicaris exoculata*, a typical dominant species at vents south of the Azores (Teixeira et al., 2011), but this genetic 'event' extended from 36°N to 4°S, far beyond the reach of a single eruptive event as we currently understand them.

In addition to the physical disturbance of lava overrun, eruptions reset the hydrothermal cycle for fluid physico-chemical parameters,

creating a longer-lasting (years), chronic effect that influences the community composition of vents. In this cycle, heat flux in the hydrothermal system increases immediately following the upwelling or eruption of magma (Butterfield et al., 1997; Von Damm, 1995). This triggers phase separation of fluids and delivery of low chlorinity fluids, heat, volatiles (e.g., sulfide, carbon dioxide, hydrogen), and dissolved metals to the seafloor. As the system cools, vent fluids may go through a brine phase, followed by decay back to chlorinities of seawater. This hydrothermal cycle affects the biological productivity, habitat quality, and community composition of diffuse flow systems.

At the 9°N vent field on the East Pacific Rise, where the hydrothermal cycle was reset by a 1991 eruption, community response to changing physico-chemical conditions was documented during a multi-year period (Shank et al., 1998). Subseafloor bacterial productivity increased immediately following the eruption (a phenomenon observed on other ridge systems as well; Marcus et al., 2009; Tunnicliffe et al., 1997) and bacterial mats and grazers on bacterial mats predominated immediately following the eruption (Marcus et al., 2009; Shank et al., 1998). The vestimentiferan tubeworm *Tevnia jerichonana* blanketed the study sites within one year and was inferred to be a pioneer species that tolerates higher temperature and sulfide conditions than giant tubeworms (*Riftia pachyptila*). Sulfide concentrations at study sites decreased 50% within two years of the eruption, and *T. jerichonana* was replaced by dense aggregations of *R. pachyptila* (Shank et al., 1998). Sulfide concentrations continued to decline in subsequent years and mussels began to colonize the seafloor diffuse flow vents along with increasing numbers of associated invertebrate taxa (Shank et al., 1998). A similar hydrothermal cycle was observed in the same area following a 2005–2006 eruption (Luther et al., 2012; Nees et al., 2008). Biological responses to eruptions at Co-Axial Volcano (Tunnicliffe et al., 1997) and Axial Volcano on the Juan de Fuca Ridge (Marcus et al., 2009) have also been monitored, and a relatively rapid succession of taxa responding to biotic and abiotic factors is reported.

Significant changes in larval supply before and after a major volcanic eruption have been reported using larval traps (Mullineaux et al., 2010). The 2006 eruption on the East Pacific Rise near 9°50'N resurfaced an area of nearly 15 km² along ~18 km of ridge crest (Soule et al., 2007). Loss of resident populations was correlated with diminished larval supply after the eruption (Mullineaux et al., 2010), a correlation consistent with population maintenance through processes that allow for larval retention. One species that was all but absent prior to the eruption—the limpet *Ctenopelta porifera*—increased in supply (Mullineaux et al., 2010), consistent with high gene flow facilitated by infrequent exchange of individuals among populations. Continued studies will document whether the changes observed in larval supply and colonization represent a phase of a successional process or whether there has been an ecological regime shift (Mullineaux et al., 2010).

Physico-chemical environments of diffuse flow habitats at hydrothermal vents evolve during the hydrothermal cycle and different taxa may be optimally adapted to or tolerate different phases of this cycle. Because there are multiple vent sites comprising a vent field at 9°N and on the eruptive segment of the Juan de Fuca Ridge, and because these sites are not all linked to the same hydrothermal system and not all affected by a given eruption event, there is always an array of habitats in different phases of the hydrothermal cycle that facilitates persistence of populations in the face of local extinctions through dispersal and colonization events. This demographic instability may be recorded in genetic data as loss of rare alleles during frequent extinction and recolonization events (Coykendall et al., 2011), with shallow, star-like genealogical networks indicating recent population expansion (Vrijenhoek, 2010).

3.5. Placing deep-sea hydrothermal vent ecosystems in an ecological-disturbance-resilience framework

As summarized above, hydrothermal-vent ecosystems are subject to a variety of spatio-temporal scales of natural disturbance and as such, they arguably occupy one extreme of a disturbance-resilience gradient relative to other deep-sea ecosystems (Fig. 1), an extreme similar to that of temperate and boreal rocky intertidal zones that experience chronic disturbance through wave action and that are periodically scoured by ice (Kelly and Metaxas, 2010).

Characteristic taxa colonizing hydrothermal vents tend to be abundant, with high biomass, rapid growth rates, and high reproductive output. The fauna of other deep-sea reducing environments (seeps and whale falls) are intermediate in this disturbance-resilience continuum (Glover et al., 2010), experiencing, for example, tectonic shifts in fluid flux (seeps: Hornbach et al., 2007; Tryon et al., 2012) and successional sequences (seeps: Bergquist et al., 2003; Cordes et al., 2009; whale falls: Smith and Baco, 2003). Taxa that live in sediments of the abyssal plain and manganese nodule beds are arguably at the other extreme of the disturbance-resilience context in the deep sea (Fig. 2). At this more stable extreme, natural disturbances tend to be biogenic and subtle compared to those experienced by vent organisms. Such disturbances include periodic pulses of phytodetritus deposition (Goody, 2002), bioturbation (Smith et al., 1997), boom–bust cycles of echinoderms (Billett et al., 2010), and climatic effects (Ruhl, 2007). In these low-disturbance, low-resilience regimes there is generally relatively low abundance, biomass, growth rates, and reproductive output of benthic invertebrates (McClain et al., 2012). Cold-water coral reefs and gardens experience biogenic reef cycles and are more productive than abyssal plain ecosystems (Roberts et al., 2006; Thiem et al., 2006; Murray et al., 2006); as such, they are at an intermediate level in the disturbance-resilience space.

4. Anthropogenic disturbance in hydrothermal vent ecosystems

4.1. Impact of scientific research and mineral exploration activities

The presence of humans at deep-sea hydrothermal vents has a relatively short history—measured in decades—since their initial

discovery in 1976 (Corliss et al., 1979). Scientific research has been the primary source of human disturbance at vents (Glowka, 2003), with more than 600 scientific research expeditions to hydrothermal vents since 1976 (Godet et al., 2011). The number of expeditions has been doubling every five years globally. Scientific research and mineral exploration activities at vents has the beneficial impact of increasing our knowledge of geophysical and hydrothermal processes, biodiversity, adaptation to extreme environments, and many other fields. The ‘knowledge value’ of hydrothermal-vent ecosystems as ‘living libraries’—as measured by both the number of publications resulting from this research and their impact factors—is high (Godet et al., 2011).

Where expeditions use remote sensing systems such as multi-beam sonar and a variety of water-column sensor systems (e.g., backscatter, Eh and other chemical sensors, magnetics), there is likely negligible impact on hydrothermal-vent communities. But most scientific or mineral exploration research uses a combination of autonomous, tethered, or human-occupied vehicles, towed camera sleds, and cabled observatories to engage in observation, sampling, and instrument deployments and recoveries. These tools and activities have varying types of impacts on vent ecosystems (discussed below). Known impacts of scientific or mineral exploration activities to date are deemed to be negligible or minor and short-term, with the possible exceptions of scientific drilling (where it extends 10s of meters and more below the seafloor in an active vent system) and damage to photoreceptors by high-intensity illumination (see discussions below).

4.1.1. Interference with vent ecosystems by tools of scientific research and mineral exploration

At the largest spatial scales, scientific and commercial exploration interference with vent ecosystems is incurred during geophysical mapping, including active multi-channel seismic studies that use air guns and other sound sources to study the subsurface structure of the seabed (e.g., Carbotte et al., 2012) and sonar methods that yield bathymetric maps with 1-m scale resolution (e.g., Caress et al., 2012). These activities are undertaken from surface ships and, in the case of multibeam sonar mapping, from autonomous, tethered, and human-occupied vehicles as well. Insonification during multibeam mapping is at low frequencies (e.g., the Reson multibeam system has dual frequencies at 200 and 400 kHz) that, together with sounds generated by the vehicle itself, could potentially alter behaviors and mask communication repertoires of, for example, vent-dwelling fish (see Codarin et al., 2009; Popper, 2003). To date there has been no study or evidence of impact of biologically relevant ambient and introduced sound in vent ecosystems. Large-scale mapping is also undertaken with magnetometers to identify magnetic anomalies associated with volcanic rocks, but the magnetic recordings are passive. Sensor surveys (e.g., conductivity, temperature, Eh, transmissivity) in the water column are benign to benthic communities. Imaging surveys are commonly undertaken at multiple spatial scales and require high-intensity light that can temporarily alter behavior of fish and invertebrates. These behavioral modifications may result in census biases resulting from attraction or avoidance (Stoner et al., 2008), but the impact of lighting during photosurveys on benthic vent communities is deemed to be minimal, the light being infrequent and of short duration, albeit of high intensity.

Rock dredge activities in support of scientific and commercial exploration of mid-ocean ridge systems result in relatively indiscriminate, destructive ‘bites’ from the seabed (the mouth of a rock dredge is typically on the order of 0.5 m in width). Scientists leading rock dredge activities generally aim to avoid hydrothermal vent sites. There is at least one celebrated example, however, where a rock dredge recovered sulfide deposits and live mussels

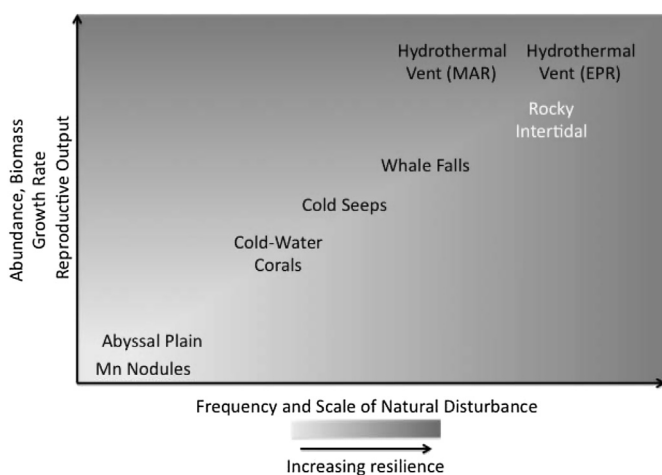


Fig. 2. Hydrothermal-vent ecosystems in an ecological (e.g., abundance, biomass, growth rate, reproductive output), disturbance (likelihood and spatiotemporal scale), and resilience framework. Vents are exposed to frequent and sometimes locally catastrophic natural disturbances and vent taxa have ecological attributes consistent with resilience (high abundance, biomass, growth rate, reproductive output); biodiversity at vents is relatively low. Vents on slow-spreading centers such as the Mid-Atlantic Ridge (MAR) experience less frequent volcanic eruptions than those on fast-spreading centers like the East Pacific Rise (EPR). White text: shallow-water ecosystem.

characteristic of vent communities, providing the first indication of a previously unknown vent field on the Mid-Atlantic Ridge, subsequently named 'Lucky Strike' (Langmuir et al., 1997). Trawlers (commercial or scientific) avoid most hydrothermal vent settings because of the hard rock nature of the seabed and the rugged terrain.

Plankton net tows and pumps may be made in the vicinity of hydrothermal vents in studies of larval distributions, pelagic food webs, and biodiversity; the 'take' of plankton nets is generally very low. Typical biomass recovered is low, although there has been at least one record of a 226 alvinocarid post-larval shrimp in 33 tows (Herring and Dixon, 1998). Given their short duration and limited sampling swath, plankton tows and pump samples are inferred to have negligible impact on vent ecosystems.

Scientific drilling in hydrothermal settings is used to study the structure of the ocean crust, hydrothermal circulation, and other deep-crustal processes and provide a subsurface dimension useful for understanding the distribution of vent faunas (Grehan and Juniper, 1996). Sediment deposition occurs during activities of the Ocean Drilling Program (ODP), where drill rigs deployed from surface ships penetrate to depths of 100 m and more below the seafloor. At the TAG hydrothermal mound on the Mid-Atlantic Ridge, ODP drilling activities in 1994 resulted in transient displacement of shrimp and burial of anemones (Copley et al., 1999). Disturbances caused by this drilling were localized and the overall ecology and productivity of the vent site has been stable on a decadal timescale (Copley et al., 2007). Bore holes can alter local hydrothermal circulation and create new 'artificial' hydrothermal vents that are often cased and capped with an outlet for subsequent study of the evolution of hydrothermal fluids and of micro- and macrofaunal development (e.g., Takai et al., 2012).

Human-Occupied Vehicles (HOVs) and Remotely Operated Vehicles (ROVs) likely do the most damage to hydrothermal-vent communities through maneuvers, light pollution, intensive and destructive sampling, intentional and unintentional transplants, abandoned materials, and potential for transport of propagules to non-native areas and spread of disease. By virtue of their relatively large size and ability to take on water ballast and achieve weighted stability on the seabed, HOVs have the greatest potential to damage vent communities by crushing seabed fauna and bashing animals living on sulfide deposits and other seafloor features with vertical relief (basalt pillars, graben walls, etc.). In the past, HOVs were intentionally used to ram sulfide chimneys for samples, but this brute tactic is now discouraged (Devey et al., 2007). Tops of chimneys are, however, often removed as part of a precision strategy to collect paired fluid/rock sampling from vent orifices and to excavate orifices to enable sampling of undiluted end-member vent fluids. Unintentional destruction seems likely to be limited to fractional areas of vent communities; the impact of unintentional habitat disturbance is rarely measured. Impacts of sampling or other human-induced disturbances that displace animals are most severe where the disturbed animals are attached holobiont taxa (such as vestimentiferan tubeworms) and relatively sessile holobiont taxa, including bathymodiolin mussels and provannid gastropods (Tunnicliffe, 1990), all of which depend on their position in diffuse flow to sustain their symbionts.

Scientific sampling equipment on HOVs and ROVs has the potential for unintentional transport of animals from one site to another, as observed in the case of Gorda Ridge limpets transported to the Juan de Fuca Ridge in a suction sampling device (Voight et al., 2012). It is not clear whether the Gorda limpet species was in fact introduced to the Juan de Fuca locale, but there is convincing evidence that it was a contaminant in samples ostensibly from the Juan de Fuca sampling site, highlighting the potential for introduction. Ballast water also has the potential to transport larval

stages from one site to another. Ballast tanks on HOVs designed to hold water at ambient seafloor pressures are often filled or dumped in the vicinity of vents, where they can take on and expel larvae and microbes. Where study sites are within a day or two-day transit from one another, it is easy to imagine ballast systems of deep-sea vehicles as effective vectors, just as they are in coastal waters. The potential role of scientific gear and vehicles in unintentional transport was also highlighted in the case of an epizootic fungal infection in mussels from sites in Fiji Basin (Van Dover et al., 2007) and for other pathogens and parasites (Voight et al., 2012).

High-intensity illumination associated with HOVs and ROVs has been implicated in photoreceptor damage in shrimp that aggregate on black smokers at vents the Mid-Atlantic Ridge, and by inference, their cognates at vents on the Central Indian Ridge and Mid-Cayman Spreading Center. Thoracic eyes in adult vent shrimp (*R. exoculata*) contain visual pigment (rhodopsin) that is light sensitive and the structure of the eyes suggests they are adapted to detecting dim light generated by high-temperature venting as a near-field remote-sensing means of avoiding thermal stress and mortality (Van Dover et al., 1989). Initial description of these thoracic photoreceptors noted degraded rhabdomeral segments inferred to result from exposure to light (Van Dover et al., 1989). Functional arhabdomeral segments in juveniles and attenuated arhabdomeral segments in adult specimens suggest that the cellular machinery to support rhabdomeric turnover (recovery from light damage) disappears during ontogeny (Chamberlain, 2000). Herring et al. (1999) brought forward further associative evidence of light-induced damage to eyes of vent shrimp, but to date, there is little to no understanding of the behavioral consequences of light-damaged photoreceptors in vent shrimp. There has also been no evidence of a decline in shrimp populations at the TAG mound during a decade of repeated exposure to scientific research, suggesting that there is no immediate conservation threat to shrimp populations resulting from high-intensity illumination (Copley et al., 2007). Other taxa with light-sensitive organs are likely susceptible to damage from submersible illumination, including bythograeid crabs (Jinks et al., 2002).

Scientific research activities intentionally and unintentionally abandon materials on the seafloor in the vicinity of hydrothermal vents, including submersible ballast (iron shot or plates), 'ghost' traps (deployed to capture crabs, fish, and other mobile scavengers and predators and abandoned on the seafloor), plastics of various kinds (milk crates, navigational markers, polypropylene line), mooring chains and anchors, etc. This scientific 'trash' has so far had negligible or possibly minor impact on vent ecosystems, but it can have a long-term impact on viewsheds of scientific research areas and the ability of documentary artists to capture images of pristine vent habitats. Cultural artifacts are occasionally purposefully placed on the seafloor at hydrothermal vents. Perhaps the best examples are installations of glass 'Planets' created by artist Josh Simpson at hydrothermal vents in Pacific, Atlantic, and Indian Oceans (Fornari, 2001) and ashes of the late Professor John Edmond, a pioneer in the study of the chemistry of hydrothermal vents, at 'Moose' (Snake Pit vent field) on the Mid-Atlantic Ridge (Van Dover, pers. obs.).

In addition to HOVs, ROVs, and AUVs, the scientific community is building cabled observatories, including the US *Regional Scale Network* (RSN) that instruments a tectonic plate, with a node at hydrothermal sites on Axial Seamount (Juan De Fuca Ridge). The funding agency for the RSN (National Science Foundation) required a site-specific Environmental Assessment of potential impacts to the natural environment for a number of resources during installation, operations, and maintenance of the RSN cabled observatory, in compliance with the US National Environmental Protection Act. Deployment and recovery of cables, nodes, and instruments were deemed to result in short-term, minor changes in water quality and

occupancy of very small patches of seabed (Cardno TEC Inc., 2013; TEC Inc., 2011) and that the threshold of impact that would require an Environmental Impact Statement (EIS) was not reached. While the installation of the cabled observatory itself may have no impact, the impact of long-term and intensified scientific studies of Axial Seamount and other vent ecosystems (e.g., the Endeavour vents, www.oceannetworks.ca) facilitated by the operation of the cabled infrastructure is of interest, but likely to be minor, i.e., resulting in detectable but small, localized, changes to vent ecosystems with little environmental consequence.

4.2. Impact of commercial (exploitation) activities

Impacts of commercial activities are informed by our knowledge of vent ecosystems, but most will remain theoretical until the activities begin and impacts are experienced and monitored. Where the tempo and scale of human activities at hydrothermal vents in a given region are intense, cumulative impacts will need to be assessed and managed as appropriate to ensure there are not regional losses of brood stock, genetic diversity, species, trophic interactions and complexity, and resilience, together with changes in community structure, genetic isolation, and the possibility of species extinctions, and species invasions.

Among the commercial activities proposed for hydrothermal vents, the most benign may be tourism and documentary arts, already underway. Genetic resources have already been developed from vent organisms in tandem with scientific research; commercial harvest of vent organisms for secondary metabolites that may serve as therapeutic agents or other commercial products are so far not widely reported, if they have taken place at all. Hydrothermal and geothermal energy sources have been considered since vents were first discovered and are still under study. One recent concept paper envisions offshore gigawatt power stations that extract minerals from hydrothermal fluids using thermo-electric generators (Parada et al., 2012), with potential for hydrogen fuel production as well (Bubis et al., 1993). Conventional, open-cut mineral extraction of seafloor massive sulfide deposits, associated with hydrothermal vents, seems the most likely commercial activity to take place in the near future (Aldhous, 2011; Hoagland et al., 2010). Each of these activities is considered below.

4.2.1. Adventure tourism and documentary arts

The UK-based Deep-Ocean Expeditions LLC (inactive since 2012) has taken more than 40 fee-paying tourists to Atlantic and Pacific deep-sea hydrothermal vents in the MIR submersibles (Leary, 2007). HOVs and ROVs have been used in the production of television, film, and video documentaries, including titles produced by Stephen Low and James Cameron (Leary, 2007; Van Dover pers. obs). Tourism and documentary arts activities are relatively infrequent and are usually integrated into marine scientific research programs; their impacts are indistinguishable from those cited above for scientific research (Section 4.1). Tourism and documentary arts have the beneficial impact of educating the public about the deep ocean and hydrothermal systems and, in the case of tourism under the auspices of Deep-Ocean Expeditions, helped to fund scientific research (Leary, 2007).

4.2.2. Genetic resources

Deep-sea hydrothermal vents are extreme environments, where organisms are adapted to temperatures, chemistries, symbiotic relationships, and other circumstances that make vent organisms of interest to drug, enzyme, cosmetic, biofuel, and other product developers (Arrieta et al., 2010; Leary, 2004; Leary et al., 2009; Thornburg et al., 2010). These products are of benefit to society as therapeutic agents and in a variety of industrial applications.

Derivatives of vent microorganisms include enzymes developed by Diversa Corporation (Pyrolase™ 60, Valley Ultra-Thin™), Invitrogen Corporation (ThermalAce™ DNA Polymerase), and New England Biolabs Inc. (Deep Vent® DNA Polymerase, among others) (Leary, 2004). The Valley Ultra-Thin™ enzyme lowers the viscosity of cornstarch, operates at high temperature and lower pH, and allows for more efficient ethanol production than other enzymes (PR Newswire, 28 February 2006), and was estimated to have an annual sales value of US\$150 million (Leary et al., 2009).

To date, interest in genetic resources from vents has involved thermophilic and hyperthermophilic prokaryotic microorganisms (Bacteria and Archaea) collected in limited quantities during scientific research for initial gene or product discovery (Leary et al., 2009; Pettit, 2011). Downstream product development often relies on laboratory cultivation, especially for microbes (Martins et al., 2013; Pettit, 2011; Thornburg et al., 2010). As such, the environmental impacts of genetic resource activities on deep-sea hydrothermal vents are currently considered to be negligible or minor.

For natural products that might eventually be derived from vent invertebrates (e.g., Andrianasolo et al., 2011), initial harvest will likely be small (Thornburg et al., 2010), but subsequent and more substantial harvests may be required (Arrieta et al., 2010). In the absence of environmental regulations, large harvests of wild vent invertebrate species to sustain a commercial enterprise are undesirable (Arrieta et al., 2010) and, if undertaken, may exceed the size of collections made during scientific sampling and have moderate to major impacts on both the target species and the vent ecosystem, including modified recruitment, size-class structure, diversity, trophic interactions, and ecosystem services. Large harvests undertaken periodically (e.g., on an annual basis) as part of a commercial production scheme would likely have a major impact on the vent ecosystem.

4.2.3. Energy and mineral harvesting

Military interest in tapping into deep-sea hydrothermal vents to power seafloor listening devices and other equipment began soon after the discovery of vents on the seafloor. Interest in using power from vents is growing (e.g., Hiriart et al., 2010), and pilot generators for scientific research are nearing the testing phase. For example, Mercury, 'a solid-state, modular, and scalable hydro-thermoelectric generator' is planned for Axial Seamount as a power source for research sensors and AUVs (MAPC: www.mapcorp.com). A more ambitious, commercial approach to a 'deep-sea energy park' includes a thermoelectric power-generating station combined with metal and mineral extraction from hydrothermal fluids, desalination, and hydrolysis and hydrogen storage (Parada et al., 2012). At least one U.S. patent has been awarded for a 'hydrothermal energy and deep-sea resource recovery system' (Marshall, 2010). Energy and mineral harvesting systems do not resurface the vent ecosystem as mineral extraction of sulfide deposits will do, but they may involve activities (e.g., establishing stable conduits), that would cause physical damage (Parada et al., 2012) and likely alter the diffuse fluid flows that support hydrothermal-vent ecosystems.

4.2.4. Mineral extraction

Technologies currently proposed for extraction of mineral deposits at hydrothermal vents involve bulk removal of minerals akin to an underwater equivalent of terrestrial open-cut mining. One proposed method is mechanical cutting and slurry transportation of ore through a riser system to a support vessel and a return water pipe which returns the seawater separated from the ore after removal of particles >8 µm (Coffey Natural Systems, 2008), to 25–50 m above the seafloor (Coffey Natural Systems, 2008; Hoagland et al., 2010; Masuda, 2011; Smith and Smith, 2010–2011). Other concepts for commercial mining under consideration include a

'grab' system (removal and transport of mineral deposits in a grab to a surface vessel), magnetic separation at the seabed, and solution mining or bio-leaching (Scott, 2007).

The impacts of mineral extraction remain theoretical in the absence of a pilot mining operation or experiment although much can be estimated based on other seafloor operations such as dredging, trenching and diamond mining. There continues to be uncertainty about whether mineral extraction will be undertaken at active hydrothermal-vent ecosystems (Hein et al., 2013), particularly given that high temperature and caustic characteristics of vent fluids of vigorously active black smokers may be incompatible with extraction technologies (Yamazaki, 2011). If extraction takes place at non-active, 'old' vent systems, there is likely to be a different set of, potentially more deleterious, impacts (Van Dover, 2011a).

Potential impacts of a mineral extraction activity on a hydrothermal-vent ecosystem fall into two broad categories: causal physico-chemical changes and biological response or consequence (Table 2). The main physical impacts expected are loss of habitat through removal of ore and associated organisms, degradation of habitat quality through reshaping of the seabed, and modification of fluid flux regimes. The intensity of impacts is expected to be major at the site scale (Fig. 1). While vent ecosystems are naturally exposed to fallout of minerals from black-smoker plumes and possibly from plumes of nearby volcanoes, the intensity of sediment plumes generated during mining activities may be in excess of natural exposures at the local scale during certain phases of operations.

Impacts to biological systems resulting from mining activities include loss of local populations where ore and organisms are removed together and the potential local extinction of rare species. The ecological significance of the rare species is uncertain, but the impact of their local loss is likely to be minor. Likely minor to moderate impacts may result from pumping water from near the seabed at vents where larvae of vent invertebrates tend to be most concentrated (Section 4.2.4.1). Minor (likely short term) impacts may also be evident in altered behaviors of vent fish and other

mobile organisms that may avoid or be attracted to light and/or noise.

In a region where there is only a single geographically constrained mining event, vent communities are predicted to re-establish within years, as they do following volcanic eruptions (Van Dover, 2011a), although they may have structure and function different from what existed prior to mining.

4.2.4.1. Impact of mineral extraction on recolonization processes. Once an impact has occurred, recovery of a vent ecosystem is dependent on both immigration of mobile species and successful colonization by larvae (Adams et al., 2012). Literature that provides insight into factors that may influence the recovery of a vent system is reviewed here in the context of extraction activities, but apply as well to any human activity that results in a similar quality and intensity of habitat alteration.

4.2.4.1.1. Maintenance of local populations: self-recruitment and near-bottom larval densities. There is gathering evidence that, at least for some hydrothermal-vent systems, invertebrate populations are maintained by local larval supply and retention during periods of habitat stability (Adams and Mullineaux, 2008; Metaxas, 2004, 2011), even while gene flow may be high from one site to another (Vrijenhoek, 2010). Characteristics that facilitate local larval supply include behavioral or other processes that retain larvae near the seafloor, effectively minimizing dilution and transport (e.g., Kim and Mullineaux, 1998; Mullineaux et al., 1995). For example, topographic basins formed by deep axial valleys (e.g., Juan de Fuca Ridge, NE Pacific) constrain circulation and trap and mix larvae (McGillicuddy et al., 2010; Thomson et al., 2003). Larval distributions estimated from net tows within axial valleys may be homogeneous i.e., no difference in larval abundance near vents (within tens of meters) or away from vents (up to 5 km; Metaxas, 2004) or heterogeneous, with higher abundances found near vents (within tens of meters) than away from vents (hundreds of meters; Mullineaux et al., 2005).

4.2.4.1.2. Timing of larval supply. A few studies have used larval traps on moorings to characterize the temporal dynamics of larval

Table 2

Types of environmental impacts resulting from mineral exploitation at deep-sea hydrothermal vents and examples of references that mention these impacts.

Impact	References
Physico-chemical impacts (cause)	
Loss of habitat	Baker et al., 2010; Coffey Natural Systems, 2008; Glover and Smith, 2003; Glowka, 2000; Halfar and Fujita, 2007; Hein et al., 2013; Ramirez-Llodra et al., 2011; Van Dover, 2007; Van Dover, 2011a,b
Degradation of habitat quality (altered topography, substrata)	Coffey Natural Systems, 2008; Halfar and Fujita, 2002, 2007; Van Dover, 2007, 2011a,b
Modification of fluid flux regimes (flow rates, distribution, chemistry)	Baker et al., 2010; Coffey Natural Systems, 2008; Glowka, 2000; Halfar and Fujita, 2007, van den Hove and Moreau, 2007; Van Dover, 2007, 2011a
Sediment plume and sedimentation	Baker et al., 2010; Coffey Natural Systems, 2008; Glowka, 2000; Halfar and Fujita, 2002, 2007; Ramirez-Llodra et al., 2011; Thiel, 2003; Van Dover, 2007; Van Dover, 2011a
Light, noise	Baker et al., 2010; Coffey Natural Systems, 2008; Van Dover, 2011a; Yamazaki, 2011
Potential biological impacts (response)	
Elimination or reduction of local populations and decreased reproductive output	Baker et al., 2010; Gena 2013; Glover and Smith, 2003, van den Hove and Moreau, 2007, Van Dover 2007, 2011a; Van Dover et al., 2011
Loss of larvae/zooplankton in lift system	Coffey Natural Systems, 2008; This paper
Local, regional, or global extinction of rare species	Van Dover, 2007, 2011a
Decreased seafloor primary production	Van Dover, 2007
Modification of trophic interactions	Van Dover, 2007
Decreased local diversity (genetic, species, habitat)	Coffey Natural Systems, 2008; van den Hove and Moreau, 2007; Van Dover 2007, 2011a
Mortality or impairment due to toxic sediments	Coffey Natural Systems, 2008; Halfar and Fujita, 2007, Van Dover, 2007, 2011a; Woodwell, 2011
Altered behaviors	This paper
Other	
Potential Cumulative effects (regional losses of: brood stock, genetic diversity, species, trophic interactions and complexity, resilience; changes in community structure, genetic isolation, species extinctions, species invasions)	Van Dover, 2007, 2011a,b; Van Dover et al., 2011; Vrijenhoek, 2010; this paper

supply in the vicinity of hydrothermal vents (e.g., [Khripounoff et al., 2008](#); [Mullineaux et al., 2005](#)). These studies suggest that supply of larvae is discontinuous and that timing of maximal supply of larval taxa varies from one taxon to another. While seasonal periodicity in reproduction is suggested as one mechanism that could account for discontinuous larval supply, alternative (non-exclusive) explanations have also been suggested, including behavioral interactions with turbulence produced by black smokers that could increase residence time ([Mullineaux and France, 1995](#); [Mullineaux et al., 2005](#)), flow conditions modulated by tidal variations and tectonic activity ([Crone et al., 2010](#)), or settlement cues ([Khripounoff et al., 2008](#)).

4.2.4.1.3. Settlement cues and gregarious settlement. Larvae of marine invertebrate taxa are selective in where they settle and they respond to inducement and deterrent cues, including those associated with chemical and physical characters of the environment and odors from conspecifics or other organisms (microbial and otherwise) in the environment (reviewed in [Hadfield, 2011](#); [Hadfield and Paul, 2001](#); [Steinberg et al., 2002](#); among others). Observations of gregarious settlement in two species of vestimentiferan tubeworms [*Lamellibrachia* sp. on the Monowai Volcanic Complex (Tonga-Kermadec Arc; [Short and Metaxas, 2010](#)), *R. pachyptila* on the southern East Pacific Rise (G Rouse, R Vrijenhoek, CL Van Dover, unpublished)] and in mussels ([Van Dover et al., 2001](#)) indicate that there can be pulsed, gregarious settlement of larvae in vent habitats.

Habitat degradation has been implicated in altered settlement cues and changes in the pattern of replenishment of coral-reef fish communities ([Feary et al., 2007](#); [McCormick et al., 2010](#)). Anthropogenic activities that interfere with inductive settlement cues or generate deterrent settlement cues at hydrothermal vents will interfere with colonization and succession processes. We understand little about how to predict the strength and duration of such interference effects, but expect that changes in characters such as fluid chemistry, substratum texture, microtopography, and microbial biofilm regeneration resulting from mineral extraction activities may not differ quantitatively from changes in these characters that take place following a volcanic eruption or other circumstances that cause new vents to form, followed by rapid colonization.

4.2.4.1.4. Major disturbances and changes in larval supply. Significant changes in larval supply before and after a major volcanic eruption have been reported ([Mullineaux et al., 2010](#)). The 2006 eruption on the East Pacific Rise near 9°50'N resurfaced an area of nearly 15 km² along ~18 km of ridge crest ([Soule et al., 2007](#)). Supply of four gastropod larval types (measured in sediment traps at 6- to 7-day intervals) declined significantly after the eruption, and one species that was all but absent prior to the eruption—the limpet *C. porifera*—increased in supply ([Mullineaux et al., 2010](#)). *C. porifera* was a successful colonist in this system (first report for the locale) and species-abundance matrices derived from colonization experiments document differences in pre- and post-eruption gastropod assemblages. The authors suggest that a combination of altered larval supply and tolerance to altered environmental conditions are not mutually exclusive and could account for the observed patterns. Loss of resident populations was correlated with diminished larval supply, a correlation consistent with population maintenance through processes that allow for larval retention. Introduction of a species previously unreported for the area is consistent with high gene flow facilitated by infrequent exchange of individuals among populations. Continued studies will document whether the changes observed in larval supply and colonization represent a phase of a successional process or whether there has been an ecological regime shift ([Mullineaux et al., 2010](#)). The extent to which the 9°50'N East Pacific Rise system—where major volcanic resets of vent habitats occur on time frames

approaching that of the life cycle of the dominant taxa—is a model for vent ecosystems in other geological settings with different frequencies of catastrophic disturbance, remains to be determined.

Although volcanic eruptions are indiscriminant and do not employ strategies to minimize impacts such as establishing set-aside areas nor do they employ strategies to restore, volcanic eruptions may be the closest natural analog to the scale of impact of mineral extraction at an active hydrothermal system. Lessons learned from larval studies following eruptions include:

- Where larval retention occurs near natal sites, larval supply will be at least temporarily diminished following an eruption or other disturbance that removes benthic adult populations ([Mullineaux et al., 2010](#)); larval supply is likely correlated with benthic population density ([Metaxas, 2011](#)).
- Changes in substratum, fluid chemistry, and other vent properties concomitant with seabed eruptions and other massive disturbances can select for subsets of species with tolerances to the changed and changing conditions, at least temporarily changing the nature of the vent community ([Mullineaux et al., 2010](#)).
- Temporal variability ([Mullineaux et al., 2005](#)) and stochasticity ([Mullineaux et al., 2010](#)) in larval supply will influence post-disturbance colonization options and outcomes.
- Colonization success by previously rare or absent species may be facilitated by natural or anthropogenic resets of the hydrothermal cycle that alter competitive interactions in the earliest stages of succession relative to established systems ([Mullineaux et al., 2010](#)).
- The relative impact of mining or similarly-scaled human activity on a vent ecosystem from the perspective of larval supply depends on the size of the local adult population that remains in the vicinity and continues to produce propagules, the degree of isolation of the site relative to larval dispersal capabilities, the degree of change in the geochemical and geophysical setting ([Metaxas, 2011](#)), and on the consequences of stochastic and deterministic processes related to succession and development of the vent community.

4.2.5. Indirect effects of human activities

Global climate change would seem decoupled from any direct impact on the ecology of hydrothermal-vent ecosystems ([Glover and Smith, 2003](#)). Variable and elevated *p*CO₂ and low pH fluids inhabited by some benthic vent organisms can provide insight into the metabolic cost of shell deposition ([Tunnicliffe et al., 2009](#)) and compensation mechanisms for acidosis ([Fabry et al., 2008](#)) under these conditions. Larvae of vent organisms disperse in the pelagic environment and some may even rely on development periods in relatively shallow water, where the biological effects of decreasing pH are expected to be evident ([Doney et al., 2009](#)) but the significance to vent ecosystems of a changing surface ocean is obscure at this time. Anthropogenically induced and shifting patterns in the timing, duration, and strength of deep-reaching mesoscale surface eddies that may transport propagules hundreds of kilometers from their source ([Adams et al., 2011](#)) could change the dynamics of long-distance dispersal and larval retention at vents. But uncertainties associated with any assessment of the impact of climate change on vent ecosystems are substantial.

5. Potential mitigation measures

While a detailed review of mitigation measures is outside the scope of this paper, it is important to recognize that there must be a balance between resource extraction and acceptable environmental impact, and that environmental impacts can be mitigated.

Approaches to mitigation of environmental impacts include avoidance, minimization, restoration, and offset measures. This mitigation hierarchy was established for wetlands mitigation (US EPA and DA, 1990) and has since been more broadly adopted as a framework for environmental management (McKenney and Kiesecker, 2010). Underlying mitigation frameworks for hydrothermal-vent ecosystems must be knowledge of the natural ecosystems, including its biogeographic context, biodiversity, community and trophic structure, connectivity, ecosystem services, disturbance regimes and community dynamics, etc. This knowledge can be acquired through scientific research and through baseline data collected as part of Environmental Impact Assessments (EIAs) (e.g., Van Dover, 2007; Collins et al., 2013). Monitoring programs at appropriate spatial and temporal scales yield additional knowledge and inform adaptive management (Boschen et al., 2013).

Avoidance is a key first step in the mitigation hierarchy and it is the approach advocated by the scientific community for mitigating the impacts of deep-sea research. Over-sampling and unintentional and intentional damage to sulfide structures are among the impacts to vent ecosystems resulting from scientific research. Concern about these impacts prompted development of a voluntary code of conduct for scientific research at vents that emphasizes avoidance of activities that might have long-lasting and deleterious effects (Devey et al., 2007). Actions to mitigate impacts of other activities, such as scientific drilling deep into the seabed, also include avoidance of sensitive areas where vent animals are particularly abundant (Juniper et al., 1992).

Marine Protected Areas (MPAs) contribute to mitigation by establish avoidance zones. To date, a number of countries have created Marine Protected Areas (MPAs) for hydrothermal vent ecosystems (Van Dover et al., 2011), including Canada (Endeavour Hydrothermal Vents MPA), Mexico (Guaymas Basin and Eastern Pacific Rise Hydrothermal Vents Sanctuary), Portugal (Azores Hydrothermal Vent MPAs, and the United States (Mariana Trench National Monument). There are currently no hydrothermal-vent MPAs in international waters, but hydrothermal-vent ecosystems are frequently cited as meeting several of the criteria of ecologically or biologically significant areas (EBSAs) in areas beyond national jurisdiction and in need of protection (e.g., Ardron et al., 2009; Taranto et al., 2012).

Marine protected areas that include hydrothermal vents and that manage human activities can implement avoidance measures with obligatory compliance (Van Dover et al., 2012). Establishment of networks of chemosynthetic ecosystem reserves as part of mining regulations has been recommended to the International Seabed Authority as a measure to address issues of population maintenance and gene flow for systems where mineral extraction or other human activities might put vent ecosystems at risk (Van Dover et al., 2011, 2012). Such an approach is modeled after the proposal for protection of Areas of Particular Environmental Interest (APEIs) for manganese nodule beds under the jurisdiction of the International Seabed Authority (Wedding et al., 2013).

The potential for self-recruitment of populations at vents suggests larval supply is at risk where anthropogenic disturbance includes removal of brood stock. In such cases, the local abundance of eggs and larvae of vent invertebrates and suitable colonization conditions would be diminished. The scale of this impact remains to be assessed for any human activity at the seabed, but mitigation measures that protect brood stocks through avoidance may prove to be an important management tool. Because hydrothermal vent ecosystems may prove to be relatively resilient to extractive activities, strategies that stagger human activities through both time and space could reduce the likelihood and degree of cumulative impacts within a region. Such a temporal strategy would require

the ecosystem to recover at an impacted vent field before activity at another vent field is permitted.

Risk management and mitigation efforts related to mineral extraction include establishment of un-mined biological corridors (temporary refuges) within a mine site to aid in recovery of the biota and site rehabilitation, as described in the voluntary Code for Environmental Management of Marine Mining (International Marine Minerals Society, 2011). These and additional approaches to minimize impacts of mineral extraction and their application to a future extractive operation are presented in Coffey Natural Systems (2008). These approaches include i) establishment of an un-mined area that can serve as both a reference site for comparative studies and as a source of colonists (Collins et al., 2012), ii) networks of permanent and temporary set-aside areas within the mine site that can also serve as sources of colonists, iii) deployment of 3-dimensional structures (artificial substrates) to provide topographic relief and structural stability for developing sulfide deposits following mining, and relocation of animals within the site to facilitate re-establishment of characteristic invertebrates. Minimization approaches may also be applied to engineering design (Coffey Natural Systems, 2008; Boschen et al., 2013), including, in the case of deep-sea mining, systems and approaches that minimize noise and sediment plumes, biodegradable lubricants, etc.

Restoration or rehabilitation of vent ecosystems and other degraded deep-sea habitats should be considered to address residual impacts as part of any mitigation hierarchy, undertaken only after all effort has been made to avoid and minimize impacts (Van Dover et al., 2014). Given the apparent natural resilience of vent ecosystems, the scope for unassisted recovery—sometimes referred to as ‘passive restoration’—should also be assessed and considered. There is scope for developing mitigation actions that time activities (e.g., to reproductive periodicity, tidal periodicity) to minimize impacts, in addition to spatial set-asides. We do not yet have a sophisticated understanding of rates of natural recovery for most vent systems or of temporal variability in larval supply at vents, but building this knowledge will help to determine whether mitigation opportunities exist that may be timed to, for example, periods of minimal larval supply.

Biodiversity offset frameworks do not yet exist for hydrothermal systems and should be an area of active discussion and engagement among stakeholders in the context of deep-sea mining. In land-based systems, offset benefits should accrue to the affected area (e.g., watershed) and should provide benefits in addition to any existing conservation value (McKenney and Kiesecker, 2010); such benefits could be challenging to develop in a deep-sea context. An alternative (or additional) offset framework has recently been proposed following a polluter-pays principle that would fund deep-sea ecosystem reserves, research, and restoration (Barbier et al., 2014).

6. Summary

Hydrothermal-vent ecosystems have been hubs for scientific activities since the moment of their discovery and they have been of commercial interest since almost the same moment because vents form metal-rich sulfide deposits. For decades, scientific activities dominated, occasionally resulting in readily apparent impacts over a localized area (i.e., within a vent field). From this scientific work, and especially from studies related to responses of vent communities to a variety of natural disturbances, vent ecosystems are inferred to be among the most resilient ecosystems in the deep sea. Despite this resilience, scientific and civil communities have paid increasing attention to detrimental impacts of scientific sampling and other activities on vent ecosystems, resulting in a code of conduct for scientific research and in

establishment of protected areas within and beyond national jurisdictions.

Most extant or proposed commercial activities (tourism, documentary arts, non-harvest genetic resource development, mineral exploration) have impacts equal to or less than those of scientific research. Because of uncertainties in the scale and technology associated with proposed energy extraction at vents, the impacts of this commercial sector are not well constrained. Mineral extraction is currently the single proposed enterprise that could have major, local, impacts on vent ecosystems; the impact of a single mining event is arguably expected to be on the scale of a volcanic eruption. Avoidance, minimization, and restoration measures during and following mining or other human activities on the seabed can mitigate impacts, and may be especially effective in systems that are naturally resilient, as in the case of hydrothermal vent ecosystems. These approaches must be informed by baseline data and monitoring efforts. Offset frameworks need to be developed for the mining sector as a key part of the mitigation hierarchy.

Of particular concern is the impact of cumulative mining events in a region, with potential for species extinctions and unanticipated changes in ecosystem structure and function if the extractive activities aren't appropriately managed. Most attention has been paid to benthic components of vent ecosystems in the face of mining activities, but most vent invertebrate species undergo a pelagic larval phase. Our understanding of the impacts of mineral extraction technologies on larval demographics and on recolonization dynamics and process is embryonic, but ensuring that there are adequate brood stocks and sources of larvae to support unassisted recovery of a vent site is a key mitigation approach.

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