Marine Environmental Research xxx (2014) 1–14

Contents lists available at ScienceDirect

Marine Environmental Research

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

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

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ARTICLE INFO

Article history:
Received 20 September 2013
Received in revised form
25 February 2014
Accepted 11 March 2014
Available online xxx

Keywords:
Scientific research
Mitigation
Deep-sea mining
Cumulative impacts
Resilience
Commercial activities
Larval dynamics
Colonization processes

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.

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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http://dx.doi.org/10.1016/j.marenvres.2014.03.008

Please cite this article in press as: Van Dover, C.L., Impacts of anthropogenic disturbances at deep-sea hydrothermal vent ecosystems: A review, Marine Environmental Research (2014), http://dx.doi.org/10.1016/j.marenvres.2014.03.008

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 substantively across ocean basins, with up to 11 biogeographic provinces recognized to date (Moalic 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 plankotrophic 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

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