Deep-Sea Research I 55 (2008) 1707–1717

Contents lists available at ScienceDirect

Deep-Sea Research I

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

Biotic interactions at hydrothermal vents: Recruitment inhibition by the mussel *Bathymodiolus thermophilus*

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ARTICLE INFO

Article history:
Received 1 August 2007
Received in revised form
20 July 2008
Accepted 23 July 2008
Available online 25 July 2008

Keywords:
Adult–larval interaction
Bathymodiolus thermophilus
Deep-sea
East Pacific Rise
Hydrothermal vents
Mussels
Recruitment
Zonation

ABSTRACT

The structure and dynamics of marine communities are regulated in part by variation in recruitment. As in other ecosystems, recruitment at deep-sea hydrothermal vents is controlled by the interplay of propagule supply and behavior, gradients in physical–chemical conditions, and biotic interactions during pre- and post-settlement periods. Recent research along the East Pacific Rise indicates that inhibition of recently settled larvae by mobile predators (mainly limpets) influences patterns of recruitment and subsequent community succession. We conducted a manipulative experiment at the same sites (~2510 m water depth) to test whether high-density assemblages of the mussel *Bathymodiolus thermophilus* also inhibit recruitment. In a preliminary study, recruitment of vent invertebrates within the faunal zone dominated by *B. thermophilus* was strikingly different at two sites, East Wall and Worm Hole. East Wall had high densities of mussels but very low total recruitment. In contrast, Worm Hole had few mussels but high recruitment. Using the submersible *Alvin*, we transplanted a large number of mussels from East Wall to Worm Hole and quantified recruitment on basalt blocks placed in three treatments: (1) naturally high densities of mussels at East Wall; (2) naturally low densities of mussels at Worm Hole; and (3) high densities of transplanted mussels at Worm Hole. After 11 months, a total of 24 taxa had recruited to the basalt blocks. Recruitment was 44–60% lower in the transplanted high-density mussel patch at Worm Hole and the natural high-density patch at East Wall than within the natural low-density patch at Worm Hole. Biotic processes that may have caused the pattern of recruitment observed included predation of larvae via water filtration by mussels, larval avoidance of superior competitors, interference competition, and enhanced predation by species within the mussel-bed community. Our results indicate that biotic interactions affecting recruitment must be understood to explain patterns of invertebrate community organization and dynamics at hydrothermal vents.

1. Introduction

Recent discoveries indicate that communities of invertebrates inhabiting deep-sea hydrothermal vents are regulated through complex ecological processes that involve both biotic and abiotic factors. Vent communities are unique because they are fueled largely by

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0967-0637/$ - see front matter © 2008 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr.2008.07.007

chemosynthetic microbial production, and population persistence is dependent on the variable and ephemeral flux of sulfide-rich vent fluids. Distance from the source of vent fluids imposes steep gradients in temperature and vent chemical constituents, which have many direct effects on benthic invertebrates (Tunnicliffe, 1991). However, recent ecological experiments reveal that variation in biotic interactions along this physical–chemical gradient, especially competition and predation, also plays a prominent role in regulating species abundance and community composition (Mullineaux et al., 1998, 2003; Micheli et al., 2002). Here we extend study of the role of biological interactions in deep-sea vents through a test of whether mussel beds, which can dominate space near active vents, resist invasion by propagules of other invertebrates.

At the East Pacific Rise (EPR) (near 9°50′N, 104°17′W; Fig. 1), vent communities display a common but dynamic pattern of species distribution along gradients of vent fluid exposure. Vestimentiferan worms (*Tevnia jerichonana* and *Riftia pachyptila*) are often the most abundant megafaunal species nearest to active, diffuse vent flow (Johnson et al., 1988; Childress and Fisher, 1992). Areas around diffusely flowing vents dominated by vestimentiferan worms are referred to as the vestimentiferan zone (Micheli et al., 2002). Two other invertebrates commonly found with vestimentiferans at many vents on the EPR and elsewhere are the mussel *Bathymodiolus thermophilus* and clam *Calyptogena magnifica*. As exposure to vent fluid declines, as a function of (1) distance away from a vent opening, (2) time as vents age and flux or chemistry change, or (3) because fluid flux is obstructed and diffused by increasing densities of vestimentiferan worms, bivalves usually increase in number, tending to displace other sessile megafaunal species and dominating the assemblage (Shank et al., 1998; Mullineaux et al., 2003). Areas dominated by bivalves are referred to as the bivalve zone. This zone often has relatively high biodiversity and total

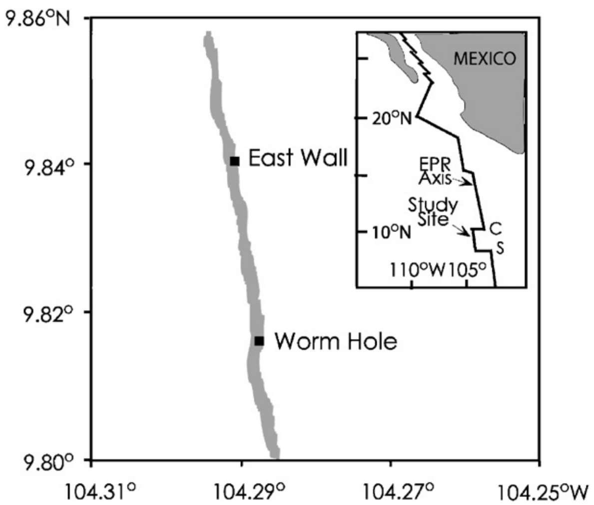

Fig. 1. Locations of hydrothermal vent study sites, East Wall and Worm Hole, along the East Pacific Rise (shaded corridor) between the Clipperton (C) and Sequieros (S) fracture zones.

invertebrate abundance because patches of vent mussels provide interstitial habitat and refuge for a number of smaller mobile species such as limpets, polychaetes, amphipods, isopods, and small crabs (Van Dover and Trask, 2000; Van Dover, 2002, 2003). Beyond the bivalve zone, where vent flux is weak and very diffuse, various suspension feeders, including especially barnacles and serpulid worms, create the suspension-feeder zone (Mullineaux et al., 2003).

Vent biologists initially concentrated on physiological tolerances to extreme physical conditions (i.e., high temperature, sulfides, and heavy metal toxicity) and nutritional requirements to explain patterns of distribution of the dominant symbiont-containing megafauna at hydrothermal vents. For example, Childress and Fisher (1992) found that the distribution of *R. pachyptila* and *C. magnifica* at the EPR is largely determined by their narrow range of physiological tolerances for temperature and toxic chemistry, as well as strict requirements concerning concentrations of H_2S necessary for their endosymbiotic bacteria. Subsequent work by community ecologists indicates that mechanisms underlying patterns of species distribution are more complex. Utilizing manipulative field experiments, we have shown that spatio-temporal variability in larval settlement (Mullineaux et al., 1998), competitive interactions among initial colonists (Mullineaux et al., 2000), and complex predator–prey interactions (Micheli et al., 2002) combine with physiological and nutritional gradients to influence species abundance and distribution. These studies indicate that models used to explain community patterns and zonation along environmental stress gradients in other marine habitats, including the rocky intertidal and subtidal, also operate in the deep sea (see reviews by Menge and Branch, 2001; Witman and Dayton, 2001; Etter and Mullineaux, 2001). In the vestimentiferan zone, the zoarcid fish *Thermarces cerberus* influences the recruitment of other vent species through a trophic cascade (Micheli et al., 2002). *Thermarces cerberus* plays a key role in structuring vent communities near to active diffuse-fluid vents because the fish preys directly on small snails, limpets, and amphipods, which otherwise control recruitment of many typically sessile species, including vestimentiferan worms, through grazing and other forms of biotic disturbance (Sancho et al., 2005). It has yet to be determined what role other predators and dominant competitors play in controlling larval settlement, recruitment, and community structure in other vent bio-zones.

Here we examine whether the presence of the chemosymbiotic and suspension-feeding mussel *B. thermophilus* influences recruitment within the bivalve zone. Beds of *B. thermophilus* around vents often reach densities of 300–1000 individuals/m^2 (Van Dover, 2002). The mechanism(s) that *B. thermophilus* employs to dominate other species near vents are poorly understood but potentially include fast growth to large size facilitated by chemoautotrophic endosymbionts; high mobility; inhibition of larval settlement through filtration during the processing of water (for respiration and chemosynthesis), and suspension feeding (e.g., Thorson, 1950; Woodin, 1976; Page et al., 1991); the physical removal, crushing, or smothering of