



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

H.S. Lenihan ^{a,*}, S.W. Mills ^b, L.S. Mullineaux ^b, C.H. Peterson ^c, C.R. Fisher ^d, F. Micheli ^e

^a Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106-5131, USA

^b Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

^c Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC 28557, USA

^d Pennsylvania State University, University Park, PA 16802, USA

^e Stanford University, Hopkins Marine Station, Pacific Grove, CA 93950, USA

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.

© 2008 Elsevier Ltd. All rights reserved.

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

* Corresponding author. Tel.: +18058938629; fax: +18058937612.
E-mail address: Lenihan@bren.ucsb.edu (H.S. Lenihan).

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

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 H₂S 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/m² (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

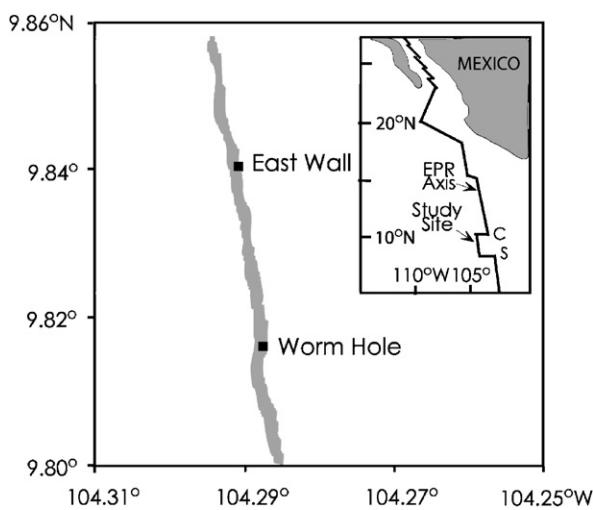


Fig. 1. Locations of hydrothermal vent study sites, East Wall and Worm Hole, along the East Pacific Rise (shaded corridor) between the Clipperton (C) and Sequidores (S) fracture zones.

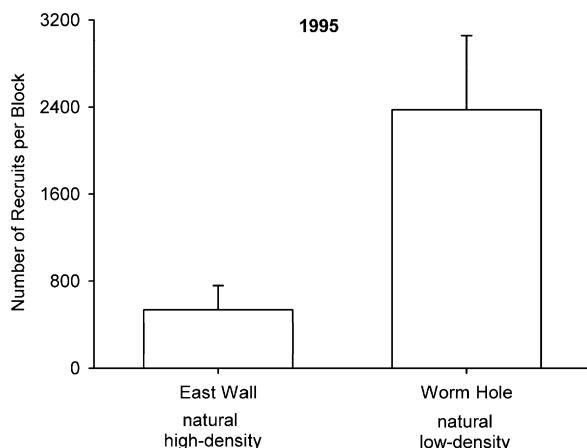


Fig. 2. Mean (+1 SE) total recruitment of invertebrates onto basalt recruitment blocks ($N = 3$) in the bivalve zone at East Wall and Worm Hole located on the East Pacific Rise in a preliminary experiment conducted in 1995. Data represent total recruitment of 29 hydrothermal vent invertebrate taxa after an 8-mo period.

other species (interference competition; Paine, 1966); inhibition of larval settlement through chemical cues (larval avoidance; Tamburri et al., 1992) or avoidance by larvae of dominant competitors (Grosberg, 1981); allelopathy (Pawlik, 1992); and the provision of microhabitat for smaller mobile predators, such as gastropods, that prey on settling larvae (enhanced predation; Suchanek, 1980). Mussels are thought to dominate areas of the rocky intertidal using combinations of these mechanisms. Whether deep-sea mussels dominate primary space around hydrothermal vents through the same processes has not been explored.

In preliminary studies conducted in 1994 and 1995, we found inverse relationships between recruitment of vent species and the density of mussels at two sites, East Wall and Worm Hole (Mullineaux et al., 2003). Mean total recruitment of 29 species measured on recruitment blocks exposed for 8 mo in the bivalve zone was five times higher at Worm Hole, where mussels were sparse, than at East Wall where mussels were dense (Fig. 2). Although recruitment in other zones was also higher at Worm Hole than East Wall, thus indicating a site difference, recruitment in the bivalve zone at East Wall (2% of total recruitment across all zones at East Wall) was much lower than at Worm Hole (37% of total recruitment across all zones at Worm Hole). Here we present results of a manipulative field experiment conducted with the deep submersible *Alvin* to test the specific hypothesis that recruitment of vent invertebrates is inhibited by mussels in mussel-dominated areas.

2. Methods

2.1. Field measurements and experiment

We tested our hypothesis by quantifying the recruitment of vent species on cubic basalt blocks (10 cm per side) placed at East Wall and Worm Hole (Fig. 1), located

on the EPR. Basalt surfaces have proved to be effective substrate for testing questions of recruitment and community interactions at hydrothermal vents (e.g., Mullineaux et al., 1998, 2000, 2003; Micheli et al., 2002). All work was conducted at ~2510 m water depth using the deep submersible *Alvin*. In May 1998, recruitment blocks were placed in each of three experimental mussel treatments located in the bivalve zone: a natural high-density patch of mussels (535 mussels/m^2) at East Wall, a natural low-density patch (114 m^{-2}) at Worm Hole, and a high-density (583 m^{-2}) patch of transplanted mussels at Worm Hole. The high-density patch at Worm Hole was created by collecting groups of mussels found in a high-density patch at East Wall using the arms of *Alvin* to pick them up and place them within the submarine's front basket (the "coffin"). These mussels were carried in several trips during one dive from East Wall to a diffusively fluxing area at Worm Hole where they were placed together in one approximately 9-m^2 patch. Mussel density in each of the three patches was quantified by counting mussels located within 0.25-m^2 quadrats ($n = 4$) delimited by laser beams projected from the submersible. This method probably underestimated the density of mussels, especially at the higher density sites, because it was not possible to see smaller mussels located beneath and between the larger ones.

We were unable to erect the ideal factorial, two-way (density \times site) experimental design to test the effects of mussel density (high vs. low) and site (East Wall vs. Worm Hole). We did establish a low-density mussel treatment at East Wall by clearing most of the mussels in an area using a scoop operated by the submersible's arm but were unable to maintain the treatment because *B. thermophilus* is highly mobile and adult mussels re-colonized the area in <48 h. We could not retry the low-density mussel treatment because the submarine *Alvin* has limited bottom time and is very expensive to operate. Instead, we made comparisons that specifically addressed our questions about processes that cause differential recruitment between a high-density mussel patch at East Wall and a low-density patch at Worm Hole. The comparison consisted of a high-density patch vs. a low-density patch at Worm Hole (a test of the effect of density) and an East Wall vs. Worm Hole comparison of recruitment in high-density mussel patches (a test of the effect of site). Constrained bottom time also prevented us from replicating each mussel density \times site treatment. Therefore, we relied on one relatively large ($\sim 9\text{ m}^2$), somewhat elliptical patch of mussels at East Wall, and two similar-sized patches at Worm Hole, one high-density and one low-density. Because we used only one large mussel patch per treatment per site, we have no information on recruitment variation between patches in a site. However, we have observed that mussel assemblages often form one large bed around active vents (Authors, personal observation).

Five basalt recruitment blocks were deployed haphazardly within each mussel patch treatment in May 1998 and were recovered 11 mo later in April 1999. The fluid microhabitat of each block was characterized upon deployment and recovery using two proxies: (1) seawater

temperature measured at the base of the block using a temperature probe manipulated by one of *Alvin*'s mechanical arms; and (2) the physiological condition of mussels measured at each experimental site. The temperature anomaly around each block was used as a proxy for physiological stress from exposure to higher temperatures, higher concentrations of potentially toxic components of vent fluids and lower oxygen levels, and, simultaneously, for chemoautotrophic primary production.

Temperature was recorded at the lowest extremity of each block because this position was closest to the fluid source, making the temperature signal less variable. Temperatures were recorded as the maximum anomaly from ambient (1.8 °C) observed during a single probe emplacement. The probe was held in place until the temperature measurements stabilized, usually within 10 s or less. This method did not allow a complete description of the temperature environment and may have underestimated the actual temperature because it was not always possible to extend the probe far enough to reach the local source of the diffuse flow. Nevertheless, our measurements provided a standardized proxy for differences in environmental conditions around each block. An assessment of the chemical composition of fluid flux was outside the scope of our study because we did not have in situ chemical sensors. At the time of the study, temperature was considered a reasonable proxy for variation in chemistry within a site on the EPR (Johnson et al., 1988), even though the correlation did not necessarily hold between sites or over time (Von Damm et al., 1995; Von Damm and Lilley, 2004). More recent in situ measurements (Le Bris et al., 2006) indicate that although the relationship between temperature and sulfide is roughly linear within some vent sites, it becomes more complex in dense mussel beds.

The physiological condition of mussels was used as another proxy for environmental conditions, as well as to determine whether healthy mussels were used in the experiment. *Bathymodiolus thermophilus* found in areas with appropriate exposure to vent fluid usually are in good condition, while mussels in areas of weak or no venting are in relatively poor condition (Smith, 1985; Fisher et al., 1988). Six mussels were collected from treatments before recruitment blocks were deployed ("before") and when the blocks were collected ("after") and analyzed for condition index (CI). CI is the ratio of ash-free dry weight of soft (i.e., somatic and gonadal) tissue to shell volume, and is a well-accepted method of determining the general physiological condition of bivalves (e.g., Smith, 1985; Lenihan, 1999). Mussels collected for CI measurements were all similar in size and, therefore, probably age. A low CI in *Bathymodiolus* sp. is generally indicative of an animal with a high tissue water content (Fisher et al., 1988; Nix et al., 1995) and therefore low tissue dry weight relative to its shell size. Such an animal is probably emaciated because of starvation or disease, or because it recently spawned. No CI data are available for mussels collected from natural mussel patches at East Wall at the end of the experiment or transplanted mussels at Worm Hole at the time they were transplanted. Because

of time constraints, we were also unable to conduct the appropriate control for the process of transplantation, moving mussels from East Wall halfway to Worm Hole and then returning them to East Wall.

Because of the lack of CI samples from the three treatments described above, we compared CI between four pairs of treatments to quantify: (1) differences between natural populations at East Wall and Worm Hole in the "before" period; (2) differences between natural and transplanted populations at Worm Hole in the "after" period; (3) change in natural low-density patch at Worm Hole over the course of the experiment; and (4) change in populations transplanted from East Wall (measured "before") to Worm Hole (measured "after"). The latter comparison represents the best estimation of the effect of transplanting mussels from East Wall to Worm Hole on CI. Measurements of CI in mussels transplanted to Worm Hole made immediately after mussels were transplanted (i.e., "before") would have been meaningless because bivalve CI would not have changed over the 6–8 h it took to transplant the mussels.

Upon termination of the experiment in April 1999, recruitment blocks were recovered by carefully lifting them from the seafloor by a rope holding an attached, floating marker. Each block was placed in a separate secure bin located on the front of *Alvin*. Once aboard ship, the blocks were removed and immediately placed whole into 70% ethanol. Remaining water within each storage bin was sieved through 64 µm mesh to capture and include in the sample all organisms that detached from blocks on the ride to the surface. Blocks were returned to Woods Hole Oceanographic Institution, where invertebrate recruits from each block were identified to lowest possible taxon under a dissecting microscope and counted.

2.2. Data analyses

To test whether temperatures varied with the mussel treatments (i.e., ambient high-density patch at East Wall; ambient low-density patch at Worm Hole; and the high-density transplanted patch at Worm Hole) and the period ("before"—May 1998 and "after"—April 1999), a two-way ANOVA was used in which mussel treatment and period were crossed, fixed factors. A one-way ANOVA was used to compare mean differences in CI among mussel treatments. Four pair-wise comparisons (described above in Methods) were made with Scheffé's post-hoc contrasts. To correct for family-wise error in the post-hoc tests, the Bonferroni procedure was used in which α (0.05) was divided by the number of comparisons in the set (i.e., α/c ; $c = 4$). The resulting level of significance for the pair-wise comparisons was 0.0125. A one-way ANOVA was also used to test whether mean total recruitment of invertebrates varied among the three mussel treatments. Prior to ANOVA, homogeneity of variances was tested using Cochran's method, and data that revealed heterogeneous variances were square-root transformed. All data in need of transformation passed a subsequent Cochran's test ($\alpha = 0.05$). After ANOVA, differences between specific

treatments were determined using Student–Newman–Keuls (SNK) post-hoc contrasts ($\alpha = 0.05$). Finally, differences in the assemblages of invertebrates on recruitment blocks were examined with ordination of samples by non-metric multi-dimensional scaling (MDS) followed by analysis of similarities (ANOSIM of the results of Bray–Curtis similarity index conducted on square-root transformed abundance data) and similarity percentages (SIMPER). SIMPER describes the proportion of difference between pairs of sample groups that are explained by each species in the groups. MDS, ANOSIM, and SIMPER are available in the statistical package PRIMER-E (Clarke and Warwick, 2001).

3. Results

In April 1999, all five blocks were recovered from the natural low-density and transplanted high-density mussel patches at Worm Hole. Four blocks were recovered at the natural high-density mussel patch at East Wall. The fifth block was lost somewhere beneath the dense assemblage of mussels and was never found. Of the four blocks recovered at East Wall, we excluded one from our analysis because it was found in an area that mussels had vacated during the experiment. Therefore, recruitment on this block was not influenced by the presence of mussels. The temperature anomaly at the base of this block (2.74°C) did not differ from the values measured at the other blocks ($2.74 \pm 0^{\circ}\text{C}$) at this site. Therefore, we have no explanation for why mussels disappeared from the area around this block, and do not know when during the experiment the mussels moved.

Temperature anomalies measured at the base of each replicate block immediately after they were deployed (the “before” period) and during recovery (“after”) were within a range (1.60 – 2.74°C ; Fig. 3) characteristic of other bivalve zones observed throughout the EPR (Micheli et al., 2002). Temperature anomaly varied with mussel treatment, the date of measurement, and their interaction (Table 1). The significant interaction reflected a complex set of differences: (1) in the before period, there was no difference in mean temperature between the natural high-density mussel patch at East Wall and the natural low-density patch at Worm Hole (SNK, $P > 0.05$); (2) mean temperature in the before period was also significantly higher within the natural high-density patch at East Wall and

Table 1

Results of a two-way crossed, fixed factor ANOVA testing whether the mean temperature anomaly (temperature in $^{\circ}\text{C}$ above ambient 1.8°C) measured at the base of recruitment blocks varied with mussel treatment (Worm Hole—natural low-density mussel patch vs. Worm Hole—transplanted high-density mussel patch vs. East Wall—natural high-density mussel patch), period [at block deployment (before) vs. at block recovery (after)], and their interaction

Source	df	ss	ms	F	P	Partial R^2
Mussel treatment (MT)	2	3.24	1.62	67.24	0.0001	0.79
Period (P)	1	0.01	0.01	0.32	0.58	0.00
MT \times P	2	0.34	0.17	7.06	0.004	0.08
Residual	23	0.55	0.02			
Total	28	4.08				

Displayed are degrees of freedom (df), sums of squares (ss), mean square errors (ms), F-ratios (F), and corresponding significance levels (P). Partial R^2 value = treatment ss/total ss.

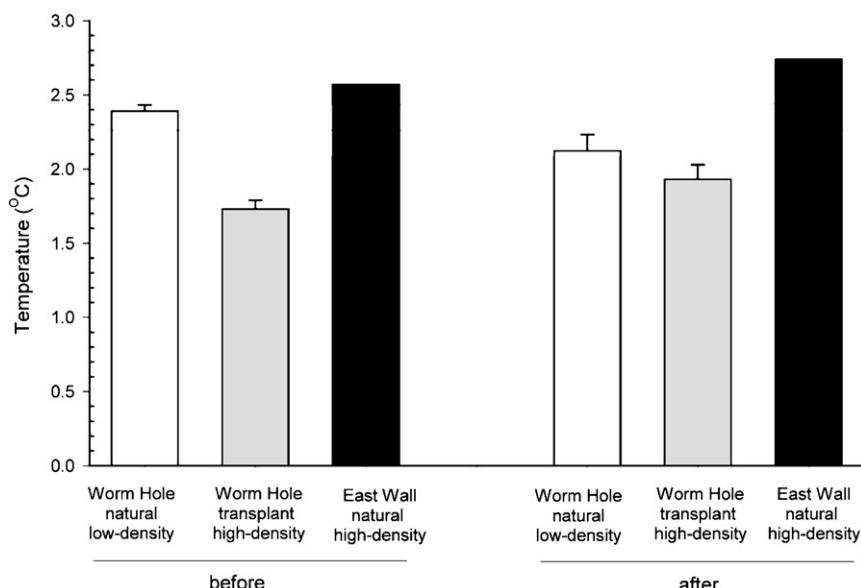


Fig. 3. Mean (± 1 SE) temperature anomaly (temperature in $^{\circ}\text{C}$ above ambient 1.8°C) measured at the bases of replicate blocks using a temperature probe operated by the mechanical arm of the submersible *Alvin*. One measurement was taken beneath each replicate block when the blocks were deployed (“before”) and when collected (“after”). See Table 1 for results of two-way ANOVA. $N = 5$ for all “before” measurements. For “after” temperature measurements, $N = 5$ within the two Worm Hole treatments, and $N = 4$ for the East Wall treatment. One block was lost at East Wall (see Methods).

natural low-density patch at Worm Hole than within the transplanted high-density patch at Worm Hole (SNKs, $P < 0.05$); (3) temperature was higher in the after period within the natural high-density patch at East Wall than in the natural low-density and transplanted high-density patches at Worm Hole (SNKs, $P < 0.05$), but there was no difference between the two treatments at Worm Hole (SNK, $P > 0.05$); (4) temperature did not differ in the natural high-density patch at East Wall before vs. after the experiment (SNK, $P < 0.05$); (5) temperature in the natural low-density patch at Worm Hole was higher before than after the experiment (SNK, $P < 0.05$); and (6) temperature was lower in the transplanted high-density at Worm Hole before the experiment than after (SNK, $P < 0.05$).

Mussel CI differed among mussel treatments (one-way ANOVA; $F_{2,30} = 28.48$, $P = 0.0001$; Fig. 4). Before mussels were transplanted, mean CI was greater in the natural high-density mussel patch at East Wall (the “source population”) than in the natural low-density patch at Worm Hole (Scheffé, $P < 0.012$). CI of mussels in the natural high-density patch at East Wall measured before the transplant (and block deployment) was higher than CI for both the natural low-density and transplanted high-density patches at Worm Hole measured after the experiment (when blocks were recovered) (Scheffé, $P < 0.012$ for both tests). When recruitment blocks were recovered, CI did not differ between natural low-density and transplanted high-density patches at Worm Hole (Scheffé, $P > 0.012$). CI was not measured after the experiment at East Wall. Finally, CI increased over the course of the experiment in the natural low-density mussels at Worm Hole (Scheffé, $P < 0.012$).

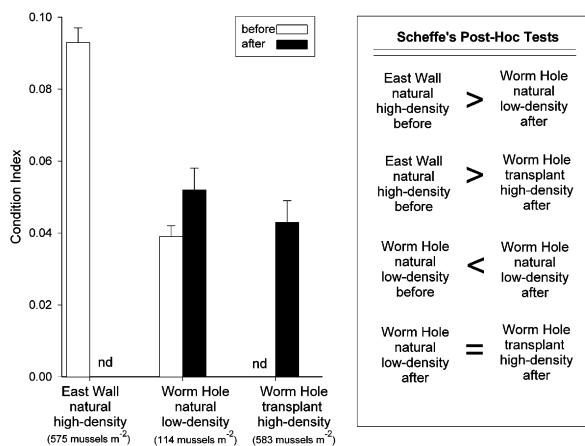


Fig. 4. Mean (± 1 SE) condition index (CI) of mussels in the three mussel density treatments located at East Wall and Worm Hole before and after the experiment. CI was calculated for mussels in (1) the natural high-density patch at East Wall before mussels were transplanted to Worm Hole and recruitment blocks were deployed (“before”); (2) the natural low-density patch at Worm Hole in the “before” and “after” (i.e., when recruitment blocks were collected) periods; and (3) the transplanted high-density patch at Worm Hole in the “after” period. $N = 6$ for all treatments. Results of Scheffé post-hoc pair-wise contrasts between different treatments are provided in the box. The corrected P -value used for Scheffé contrasts ($P \leq 0.012$) was calculated using the Bonferroni technique.

Recruitment blocks were colonized by a total of 24 taxa over the 11-mo period of the experiment. Mean total recruitment was significantly greater on blocks in the natural low-density mussel patch at Worm Hole than blocks from the high-density transplant patch at Worm Hole or the natural high-density patch at East Wall (one-way ANOVA, $F_{2,10} = 4.58$, $P = 0.04$; SNKs, $P < 0.05$; Fig. 5). There was no difference in recruitment on blocks from the two high-density treatments, the transplanted patch at Worm Hole and the natural patch at East Wall (SNK, $P > 0.05$). The foraminiferan *Abyssotherma pacifica* was the most abundant organism at each site (Table 2). *Abyssotherma pacifica* is a small (<2 mm long), sessile species that is commonly found around vents in the vestimentiferan and bivalve zones in the EPR. Of the other 23 taxa that recruited to blocks, the most abundant were the polychaetes *Amphipamytha galapagensis*, *Archinome rosacea*, *Laminatubus alvini*, and *Ophryotrocha akessoni*; the limpets *Eulepetopsis vitrea*, *Lepetodrilus elevatus*, and *L. ovalis*; and the ciliate *Metafolliculina* sp. (Table 2). Results of ANOSIM analysis revealed that there was a significant difference in the taxonomic assemblage that recruited to each treatment (Global $R = 0.50$; $P = 0.001$). A MDS plot (Fig. 6) illustrates the substantial difference in assemblages that recruited to blocks in the different mussel treatments. The assemblages on the two Worm Hole treatments were more similar to each other than they were to the East Wall assemblage. Most of the total percent variation in recruitment assemblages between pairs of treatments was explained by differences in *A. pacifica* (Fig. 6), but *Metafolliculina* sp., *L. ovalis*, *A. galapagensis*, and *O. akessoni* each accounted for >5% of the variation between pairs of treatments. The two patches at Worm Hole had relatively high numbers of *A. pacifica*, while the patch at East Wall had relatively high numbers of *A. galapagensis*. The East Wall patch also had

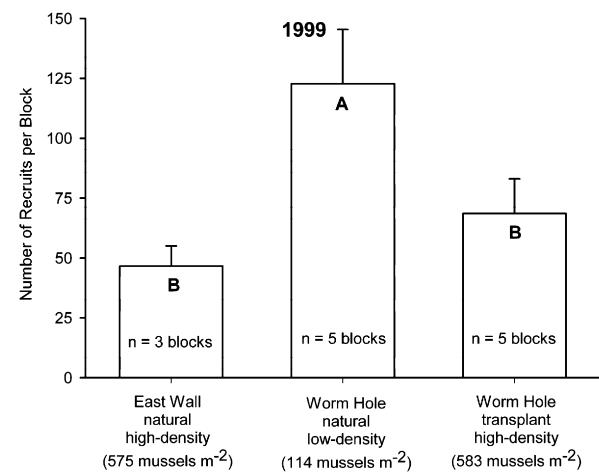


Fig. 5. Mean (± 1 SE) recruitment of invertebrates (totals across 24 hydrothermal vent taxa) on recruitment blocks placed for 11 mo in three mussel-density treatments, a natural high-density patch at East Wall, a natural low-density patch at Worm Hole, and a high-density patch of mussels transplanted from East Wall to Worm Hole. Letters inside bars represent significant differences in the SNK post-hoc contrasts: A > B at $\alpha = 0.05$.

Table 2Mean (± 1 SD) numbers of recruits from all of the faunal groups that colonized basalt recruitment blocks in each mussel treatment

Fauna	Mussel treatment			
	Worm Hole natural low-density	Worm Hole transplant high-density	East Wall natural high-density	East Wall natural high-density mussel vacated area
Bivalves				
<i>Bathymodiolus thermophilus</i>	0.2 \pm 0.4		0.3 \pm 0.6	
Vestimentiferans				
Unidentified vestimentiferans			2.7 \pm 2.3	
Polychaetes				
<i>Amphisamytha galapagensis</i>	5.8 \pm 4.4	2.0 \pm 2.0	21.7 \pm 19.4	108
<i>Archinome rosacea</i>			2.0 \pm 3.5	2
Hesionid spp.			0.3 \pm 0.5	
<i>Laminatibus alvini</i>	4.2 \pm 6.3		0.7 \pm 1.1	1
<i>Nereis</i> sp.	0.2 \pm 0.4			
<i>Nicomache</i> sp.		0.2 \pm 0.4		
<i>Ophryotrocha akessoni</i>			6.3 \pm 5.5	2
Gastropods				
<i>Clypeosectus delectus</i>	0.2 \pm 0.4			
<i>Eulepetopsis vitrea</i>	3.8 \pm 4.4			
<i>Lepetodrilus elevatus</i>			1.7 \pm 1.5	
<i>Lepetodrilus ovalis</i>	6.6 \pm 13.1		0.3 \pm 0.6	3
Unidentified limpets		0.2 \pm 0.4	0.7 \pm 0.6	
Unidentified snails	3.8 \pm 7.4		1.6 \pm 1.5	3
Aplacophorans				
Unidentified species			0.3 \pm 0.6	1
Protists				
<i>Abyssotherma pacifica</i>	88.4 \pm 27.6	60.6 \pm 37.1	7.7 \pm 9.9	317
<i>Metafolliculina</i> sp.	13.6 \pm 22.4	2.0 \pm 4.5		
Unidentified foraminiferans	1.2 \pm 0.8	1.2 \pm 1.1		
Crustaceans				
Isopods		0.2 \pm 0.4		
<i>Neolepas</i> sp.	0.2 \pm 0.4			
Miscellaneous				
Unidentified anemone	0.2 \pm 0.4	0.4 \pm 0.5		
Unidentified mites				1
Unsegmented worm			0.2 \pm 0.4	

Shown also are data from one block at the natural high-density mussel patch at East Wall from around which mussels disappeared during the experiment. Recruitment was recorded after an 11-mo deployment period.

higher numbers of limpets and small gastropods compared with the Worm Hole patches, but all sites had similar numbers of the polychaetes *L. alvini*, *O. akessoni*, and *A. rosacea*, as well as the ciliate *Metafolliculina* sp.

4. Discussion

Variation in recruitment between our high- and low-density mussel patches supports the hypothesis that naturally high densities of mussels can directly or indirectly inhibit recruitment of invertebrates at deep-sea hydrothermal vents. We present the first experimental observation of this process in this unique ecosystem. Recruitment was 44–60% higher in a low-density patch of

B. thermophilus (at Worm Hole) than in two high-density mussel patches (at Worm Hole and East Wall). The pattern in recruitment was driven largely by the foraminiferan *A. pacifica*, a commonly found species at EPR hydrothermal vents, but also by differences among patches in the recruitment of the polychaete worm *A. galapagensis*. All of the species that recruited in our experiment are thought to be those commonly associated with vent mussel beds (Micheli et al., 2002; Van Dover, 2002).

Considering that high-density mussel patches are a common feature of vents at the EPR, it is reasonable to infer that the negative relationship between *B. thermophilus* and recruitment is a potentially important process regulating the structure and dynamics of hydrothermal vent

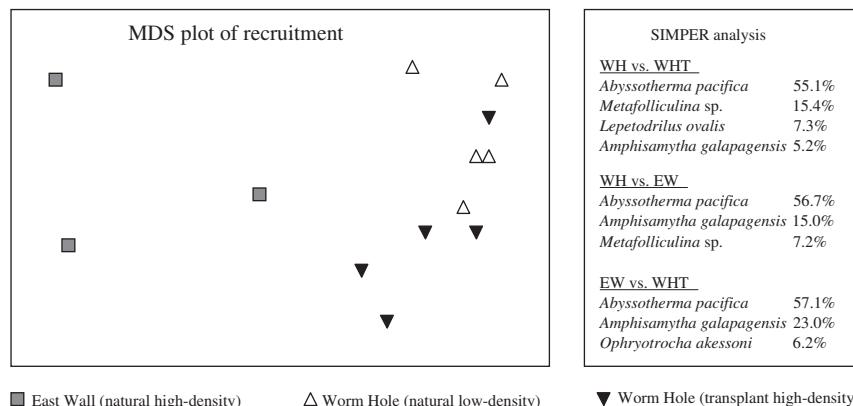


Fig. 6. A multi-dimensional scaling (MDS) plot illustrating the relative differences in the taxonomic composition of the assemblages of species that recruited to each replicate recruitment block in each treatment. The assemblages on recruitment blocks from the Worm Hole natural low-density and transplant high-density mussel treatments were more similar to each other than they were to the East Wall natural high-density mussel treatment. Displayed also are the results of a similarity percentage analysis (SIMPER; Clarke and Warwick, 2001) that relies on a Bray-Curtis similarity index to scale the average dissimilarity between the assemblages found on each recruitment block. SIMPER explains how much of the variation in species composition between pairs of treatments is caused by each species. Shown only are species that explained >5% of the variation in species composition between pairs of treatments. WH = Worm Hole: natural, low-density mussel patch; WHT = Worm Hole: high-density, transplanted mussel patch; and EW = East Wall: natural, high-density mussel patch.

communities. High-density patches of mussels (and sometimes the clam *C. magnifica*) in the bivalve zone can border and overlap the vestimentiferan zone. Recruitment within the bivalve zone is often composed of the same suite of species that recruit to the vestimentiferan zone (Mullineaux et al., 1998, 2003; Micheli et al., 2002). Our data suggest that high-density mussel beds within the bivalve zone maintain their composition and structure by inhibiting recruitment of other sessile species.

The limitation of our experimental design (see Methods) is that some factor other than mussel density could have varied among the three patches and generated the patterns we observed. One factor that influences hydrothermal vent community dynamics on the EPR is vent fluid exposure because it provides the primary energy source to the community (Childress and Fisher, 1992; Tunnicliffe, 1991). Two useful proxies for vent fluid flux are water temperature and the physiological condition of mussels, both of which usually increase within limits with the intensity of exposure to vent fluid. Water temperature co-varies with recruitment of many vent invertebrate species at various sites in the EPR (Mullineaux et al., 1998; Micheli et al., 2002). We hypothesized that reduced temperature or reduced mussel condition would indicate suboptimal abiotic conditions that might cause larvae of vent organisms, especially vestimentiferan worms, to avoid settling or indicate that the mussels were potentially not healthy enough to deter settlement through suspension feeding. However, we found that neither proxy for environmental conditions is able to provide a logical explanation of our results.

Temperature anomalies varied between our two sites but not in a manner that explains the pattern of recruitment. First, temperature varied by no more than ~1.1 °C, which is a small difference compared to the 25–30 °C range in diffuse-flow communities on the EPR (Micheli et al., 2002). Temperatures measured in *B. thermophilus* beds in the Rose Garden vent field on the

Galapagos Rift in 1985 spanned a 12 °C range, from ambient to 14 °C (Fisher et al., 1988). Temperature anomalies measured in our study were within the lower range (1.6–2.7 °C) expected for a bivalve zone (Fig. 3), so there is no reason to expect different intensity or taxonomic composition of recruitment among our treatments based on temperature. Second, if the patterns in recruitment were controlled by temperature, we would expect recruitment in the naturally low-density mussel patch at Worm Hole to be intermediate between the natural high-density patch at East Wall and the high-density transplant patch at Worm Hole. That was not the case (Fig. 5). Therefore, variation in vent fluid exposure as estimated by the proxy temperature cannot account for the differences in recruitment observed among treatments.

The second proxy for environmental conditions at each site was the CI of mussels. Previous work revealed that differential exposure to vent fluid was positively correlated to the CI of *B. thermophilus* (Smith, 1985; Fisher et al., 1988). Mussel condition can also influence the intensity of suspension feeding or water processing (Wildish and Kristmanson, 1997), so mussels in our experiment with higher CI may have been able to actively (suspension feeding) or passively (water processing) capture more larvae than mussels in poorer condition (Page et al., 1991). CI of mussels in our experiment varied among patches but not in a manner that can explain the observed recruitment pattern. The pattern of CI indicates that environmental conditions were potentially better at East Wall than Worm Hole before the experiment (Fig. 4). However, there were no significant differences between mussel patches at Worm Hole. These patterns in recruitment cannot be explained by observed differences in water temperature because environmental conditions were potentially better in patches with relatively low recruitment (the high-density transplant patch at Worm Hole) than in the

relatively high-recruitment patch (i.e., in the natural low-density patch at Worm Hole).

Based on the tests using our two environmental proxies, we are reasonably confident that inherent environmental differences between sites or between mussel density treatments did not drive the patterns of recruitment we observed. Thus, although the East Wall and Worm Hole sites differed slightly in mean temperature, and significantly in faunal composition and mussel CI, our transplant manipulation suggests that low mussel density at Worm Hole is related to the elevated recruitment observed at this site in both the present and prior study conducted in 1995. Nevertheless, a detailed description of the chemical constituents at each recruitment block was not conducted so we are not entirely certain how much of the variation in observed recruitment was caused by abiotic factors.

The biotic factors that potentially explain the patterns in recruitment we observed are: (1) inhibition of settlement through active water filtration by mussels (i.e., pre-settlement predation); (2) inhibition of settlement through larval avoidance of superior competitors or predators (Grosberg, 1981); (3) post-settlement mortality resulting from biotic interactions such as competition or predation between mussels and recruits or between recruits and other mussel-bed inhabitants; and (4) avoidance of or low survival within mussel beds by some species, including vestimentiferan worms, due to intolerance of environmental conditions, especially reduced vent fluid flux and relatively low water temperature. Evidence for larval settlement inhibition through suspension feeding has been observed in several studies conducted in shallow-water marine systems. Controlled experiments conducted on small spatial scales (cm-m) showed that bivalve (Williams, 1980; Andre and Rosenberg, 1991) and ascidian (Osman and Whitlach, 1995) suspension feeders reduce settlement through filtration. In contrast, Ertman and Jumars (1988) found that individual suspension feeders can enhance the settlement of larvae in the downstream direction because their exhalant jets create jetties that entrap passing larvae. Others have found no relationship between individual suspension feeders and settlement (Young and Gotelli, 1988; Young, 1989). The few studies that have tested whether whole assemblages of suspension feeders influence settlement and recruitment patterns (at scales of 1–10 m) also show equivocal results (Best, 1978; Black and Peterson, 1988). Nevertheless, higher densities of suspension feeders theoretically have a higher capacity to remove incoming larvae per unit area than lower-density patches because the intensity of suspension feeding per unit area increases (Ertman and Jumars, 1988; Fréchette et al., 1989). We deduce that pre-settlement predation of larvae by filtration on the scale of mussel assemblages can influence recruitment patterns, especially in situations where the filter-feeders (or in the case of *Bathymodiolus*, water processors) are densely aggregated and where the supply of larvae is also relatively low. We expect that the same process influences recruitment of *A. pacifica*, which like other foraminiferans has dispersive propagules (Mullineaux et al., 2005). Therefore, it is possible that

“filtration” by high densities of mussels reduces the concentration of larvae passing over, or attempting to settle within or near, densely assembled mussels.

Larvae of sessile vent species, such as vestimentiferan worms, may also actively avoid settling in high-density patches of mussels. Avoidance by larvae of settlement in close proximity to dominant competitors has been suggested in shallow-water invertebrate assemblages (Grosberg, 1981; but see Bullard et al., 2004). We have no direct evidence that larvae were killed before settlement or that larval settlement behavior differed between high- and low-density mussels. Such evidence could include direct visual evidence of larvae being filtered by mussels combined with mussel gut content analyses, and very fine-scale measurements of settlement within and around mussel patches.

Beds of *B. thermophilus* are inhabited by limpets, gastropods, crustaceans, and polychaetes (Van Dover and Trask, 2000; Micheli et al., 2002; Van Dover, 2002, 2003) that may graze, crush, and smother or otherwise kill newly settled larvae (Micheli et al., 2002). Work in the rocky intertidal also reveals that mussel beds harbor relatively high densities of small, mobile grazers, and predators (Suchanek, 1980; Van Dover and Trask, 2000; Menge and Branch, 2001). Larvae settling into mussel beds may attach to the substrate (e.g., a mussel shell or the seafloor) only to be killed by an invertebrate living among the byssal threads of the mussels. Mobile predators, and limpets in particular, have a profoundly negative influence on recruitment in the vestimentiferan zone (Micheli et al., 2002). However, evidence from predator-exclusion experiments in the same study also indicates that predation by both small and large grazers (e.g., crabs and eelpout fishes) does not have a biologically significant effect on recruitment outside of the vestimentiferan zone at East Wall and Worm Hole. In addition, we found no remnants of organisms (calcareous or organic residue, body parts) or scars on the recruitment blocks left by larvae that may have settled and then died. Therefore, it is not likely that post-settlement mortality caused by mussels or mussel-bed associated predators caused the large difference in recruitment that we observed among treatments. Furthermore, mussel beds at vents harbor many infaunal species (Etter and Mullineaux, 2001; Van Dover, 2002, 2003), indicating that smothering and crushing is not a mechanism that commonly excludes most vent species from the patches of dense mussels in the bivalve zone. Instead, mussels appear to out-compete other mostly sessile chemosynthetic macrofauna for access to vent fluid. How abundant and species diverse assemblages of smaller, mobile invertebrates come to occupy vent mussel beds is uncertain and a phenomenon worthy of future examination.

An interesting observation in Le Bris et al. (2006) is that within vent mussel beds, temperature and chemistry do not necessarily conform to a conservative mixing model. They suggest that mussels may be influencing chemistry by removal of H₂S by their symbionts. This is yet another intriguing way that mussels may indirectly affect recruitment in other invertebrate species (i.e., by modifying the chemical environment). This model has

even more relevance when one considers that Le Bris et al. (2006) conducted their study in the same mussel beds that we used at the East Wall site.

Results reported here provide another example of how abiotic and biotic factors can interact to regulate communities of organisms located at deep-sea hydrothermal vents. Similar to spatial patterns in competition and predation, recruitment decreases along a physical-chemical gradient of vent fluid flux (Micheli et al., 2002). Our results suggest that along such a gradient dense assemblages of a suspension feeder can influence patterns of recruitment in a wide variety of benthic invertebrates. However, the specific mechanism(s) by which vent mussels may inhibit recruitment has yet to be identified. Similar resistance to colonization by other species is found in mussel beds and other suspension-feeding assemblages located in the rocky intertidal (Menge and Branch, 2001), and in subtidal soft-sediment (Lenihan and Micheli, 2001) and hard-substrate (Witman and Dayton, 2001) communities. Recruitment inhibition by dense assemblages of suspension feeders should therefore be considered a general ecological process that helps regulate marine community composition and structure.

Acknowledgments

We thank the crew of the R/V Atlantis and ALVIN Group for making this deep-sea experiment possible. The project was funded through National Science Foundation grants to L.S. Mullenax (OCE-9315554 and OCE-9712233), C.R. Fisher (OCE-9317737 and OCE-9712808), and C.H. Peterson (OCE-9317735 and OCE-9712809). We thank S. Schaeffer, G.A. Johnson, G. Sancho, S. Kim and E. Berntson for assistance aboard the Atlantis, and M.C. Kay for a critical review of the manuscript.

References

- Andre, C., Rosenberg, R., 1991. Adult-larval interactions in the suspension-feeding bivalves *Cerastoderma edule* and *Mya arenaria*. *Marine Ecology Progress Series* 71, 227–234.
- Best, B., 1978. The effects of suspension feeding by the bivalve *Mercenaria mercenaria* on community structure. MS Thesis, University of Florida. 179pp.
- Black, R., Peterson, C.H., 1988. Absence of preemption and interference competition for space between large suspension-feeding bivalves and smaller infaunal macroinvertebrates. *Journal of Experimental Marine Biology and Ecology* 120, 183–198.
- Bullard, S.G., Whitlach, R.B., Osman, R.W., 2004. Checking the landing zone: do invertebrate larvae avoid settling near superior spatial competitors? *Marine Ecology Progress Series* 280, 239–247.
- Childress, J.J., Fisher, C.R., 1992. The biology of hydrothermal vent animals: physiology, biochemistry, and autotrophic symbioses. *Oceanography and Marine Biology: An Annual Review* 30, 61–104.
- Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. PRIMER-E, second ed. Plymouth Marine Laboratory, UK, 87pp.
- Ertman, S.C., Jumars, P.A., 1988. Effects of bivalve siphonal currents on the settlement of inert particles and larvae. *Journal of Marine Research* 46, 797–813.
- Etter, R.J., Mullenax, L.S., 2001. Deep-sea communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community Ecology*. Sinauer Associates, Inc., Sunderland, MA.
- Fisher, C.R., Childress, J.J., Arp, A.J., Brooks, J.M., Distel, D., Favuzzi, J.A., Felbeck, H., Hessler, R., Johnson, K.S., 1988. Microhabitat variation in the hydrothermal vent mussel, *Bathymodiolus thermophilus*, at the Rose Garden on the Galapagos Rift. *Deep-Sea Research* 35, 1769–1792.
- Fréchette, M., Butman, C.A., Geyer, W.R., 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder, *Mytilus edulis*. *Limnology and Oceanography* 34, 19–36.
- Grosberg, R.K., 1981. Competitive ability influences habitat choice in marine invertebrates. *Nature* 290, 700–702.
- Johnson, K.S., Childress, J.J., Hessler, R.R., Sakamoto-Arnold, C.M., Beehler, C.L., 1988. Chemical and biological interactions in the Rose Garden hydrothermal vent field, Galapagos spreading center. *Deep-Sea Research* 35, 1723–1744.
- Le Bris, N., Govorov, B., Le Gall, C., Fisher, C.R., 2006. Variability of physico-chemical conditions in 9°50'N EPR diffuse flow vent habitats. *Marine Chemistry* 98, 167–182.
- Lenihan, H.S., 1999. Physical-biological coupling on oyster reefs: how habitat form influences individual performance. *Ecological Monographs* 69, 251–275.
- Lenihan, H.S., Micheli, F., 2001. Soft-sediment communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community Ecology*. Sinauer Associates, Inc., Sunderland, MA.
- Menge, B.A., Branch, G.M., 2001. Rocky intertidal communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community Ecology*. Sinauer Associates, Inc., Sunderland, MA.
- Micheli, F., Peterson, C.H., Mullenax, L.S., Fisher, C.R., Mills, S.W., Sancho, G., Johnson, G.A., Lenihan, H.S., 2002. Species interactions at deep-sea hydrothermal vents: the role of predation in structuring communities in an extreme environment. *Ecological Monographs* 73, 365–382.
- Mullenax, L.S., Mills, S.W., Goldman, E., 1998. Recruitment variation during a pilot colonization study of hydrothermal vents (9°50'N, East Pacific Rise). *Deep-Sea Research Part II* 45, 441–446.
- Mullenax, L.S., Fisher, C.R., Peterson, C.H., Schaeffer, S.W., 2000. Vestimentiferan tubeworm succession at hydrothermal vents: use of biogenic cues to reduce habitat selection error? *Oecologia* 123, 275–284.
- Mullenax, L.S., Peterson, C.H., Micheli, F., Mills, S.W., 2003. Successional mechanism varies along a gradient in hydrothermal fluid flux at deep-sea vents. *Ecological Monographs* 73, 523–542.
- Mullenax, L.S., Mills, S.W., Sweetman, A.K., Beaudreau, A.H., Metaxas, A., Hunt, H.L., 2005. Vertical, lateral and temporal structure in larval distributions at hydrothermal vents. *Marine Ecology Progress Series* 293, 1–16.
- Nix, E.R., Fisher, C.R., Vodenichar, J., Scott, K.M., 1995. Physiological ecology of a mussel with methanotrophic endosymbionts at three hydrocarbon seep sites in the Gulf of Mexico. *Marine Biology* 122, 605–617.
- Osman, R.W., Whitlach, R.B., 1995. The influence of resident adults on larval settlement: experiments with four species of ascidians. *Journal of Experimental Marine Biology and Ecology* 190, 199–220.
- Page, H.M., Faïla-Médioni, A., Fisher, C.R., Childress, J.J., 1991. Experimental evidence for filter-feeding by the hydrothermal vent mussel, *Bathymodiolus thermophilus*. *Deep-Sea Research* 38, 1455–1461.
- Paine, R.T., 1966. Food web complexity and species diversity. *American Naturalist* 100, 65–75.
- Pawlak, J.R., 1992. Chemical ecology of the settlement of benthic marine invertebrates. *Oceanography and Marine Biology: An Annual Review* 30, 270–335.
- Sancho, G., Fisher, C.R., Mills, S., Micheli, F., Johnson, G.A., Lenihan, H.S., Peterson, C.H., Mullenax, L.S., 2005. Selective predation by the zoarcid fish *Thermautes cerberus* at hydrothermal vents. *Deep Sea Research Part I* 52, 837–844.
- Shank, T.M., Fornari, D.J., Von Damm, K.L., Lilley, M.D., Haymon, R.M., Lutz, R.A., 1998. Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9°50'N, East Pacific Rise). *Deep-Sea Research Part II* 45, 465–515.
- Smith Jr., K.L., 1985. Deep-sea hydrothermal vent mussels: nutritional state and distribution at the Galapagos rift. *Ecology* 66, 1067–1080.
- Suchanek, T.H., 1980. Diversity in natural and artificial mussel bed communities of *Mytilus californianus*. *American Zoologist* 20, 807.
- Tamburri, M.N., Zimmer-Faust, R.K., Tamplin, M.L., 1992. Natural sources and properties of chemical inducers mediating settlement of oyster larvae: a re-examination. *Biological Bulletin* 183, 327–337.
- Thorson, G., 1950. Reproduction and larval ecology of marine bottom invertebrates. *Biological Review* 25, 1–45.
- Tunnicliffe, V., 1991. The biology of hydrothermal vents: ecology and evolution. *Oceanography and Marine Biology: An Annual Review* 29, 319–407.

- Van Dover, C.L., 2002. Community structure of mussel beds at deep-sea hydrothermal vents. *Marine Ecology Progress Series* 230, 137–158.
- Van Dover, C.L., 2003. Variation in community structure within hydrothermal vent mussels of the East Pacific Rise. *Marine Ecology Progress Series* 253, 55–66.
- Van Dover, C.L., Trask, J.L., 2000. Diversity at deep-sea hydrothermal vents and intertidal mussel beds. *Marine Ecology Progress Series* 195, 169–178.
- Von Damm, K.L., Lilley, M.D., 2004. Diffuse flow hydrothermal fluids from 9°50'N East Pacific Rise: origin, evolution and biogeochemical controls. In: Wilcock, W., Cary, C., Delong, E. (Eds.), *Subseafloor Biosphere at Mid-Oceanic Ridges*. Sinauer Associates, Inc., Sunderland, MA.
- Von Damm, K.L., Oosting, S.E., Kozwloski, R., Buttermore, L.G., Colodner, D.C., Edmonds, H.N., Edmond, J.M., Grebmeier, J.M., 1995. Evolution of east Pacific Rise hydrothermal vent fluids following a volcanic eruption. *Nature* 375, 47–50.
- Wildish, D., Kristmanson, D., 1997. *Benthic Suspension Feeders and Flow*. Cambridge University Press, Cambridge.
- Williams, J.G., 1980. The influence of adults on the settlement of spat of the clam, *Tapes japonica*. *Journal of Marine Research* 38, 729–741.
- Witman, J.D., Dayton, P.K., 2001. Rocky subtidal communities. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community Ecology*. Sinauer Associates, Inc., Sunderland, MA.
- Woodin, S.A., 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. *Journal of Marine Research* 34, 25–41.
- Young, C.M., 1989. Larval depletion by ascidians has little effect on settlement of epifauna. *Marine Biology* 102, 481–489.
- Young, C.M., Gotelli, N.J., 1988. Larval predation by barnacles: effects on patch colonization in a shallow subtidal community. *Ecology* 69, 624–634.