

# Imprint of past environmental regimes on structure and succession of a deep-sea hydrothermal vent community

Lauren S. Mullineaux · Fiorenza Micheli ·  
Charles H. Peterson · Hunter S. Lenihan ·  
Nilauro Markus

Received: 13 August 2008 / Accepted: 22 May 2009  
© Springer-Verlag 2009

**Abstract** Dramatic perturbations of ecological communities through rapid shifts in environmental regime do not always result in complete mortality of residents. Instead, legacy individuals may remain and influence the succession and composition of subsequent communities. We used a reciprocal transplant experiment to investigate whether a legacy effect is detectable in communities experiencing an abrupt increase or decrease in hydrothermal fluid flux at deep-sea vents. Vent habitats are characterized by strong gradients in productivity and physico-chemical stressors, both of which tend to increase with increasing vent fluid flux. In our experiments, many species survived transplan-

tation from cool (water temperatures  $<2^{\circ}\text{C}$  above ambient) to warm ( $4\text{--}30^{\circ}\text{C}$  above ambient) habitats, resulting in significantly higher species richness on transplanted than remaining experimental substrata. A legacy effect was much less apparent in transplantation from warm to cool habitat, although a few vestimentiferan tubeworms, normally restricted to warm habitat, survived transplantation. The asymmetry in influence of legacy individuals suggests that productivity enhancement may outweigh potential physiological stress in setting limits to distributions of vent invertebrates. This influence of biological processes contrasts with theory developed in the rocky intertidal that predicts the predominance of physical control at the high-stress end of an environmental gradient. Prediction of successional transitions in vents and other habitats experiencing regime shifts in which remnant species may survive must take into account the possible influence of historical effects.

Communicated by Tony Underwood.

L. S. Mullineaux (✉)  
Woods Hole Oceanographic Institution, MS34,  
Woods Hole, MA 02543, USA  
e-mail: lmullineaux@whoi.edu

F. Micheli  
Stanford University, Hopkins Marine Station,  
Pacific Grove, CA 93950, USA  
e-mail: micheli@stanford.edu

C. H. Peterson  
Institute of Marine Sciences,  
University of North Carolina at Chapel Hill,  
Morehead City, NC 28557, USA  
e-mail: cpeters@email.unc.edu

H. S. Lenihan  
Bren School of Environmental Science and Management,  
University of California, Santa Barbara, CA 93106-5131, USA  
e-mail: Lenihan@bren.ucsb.edu

N. Markus  
Version3 Inc, 5345 Madison Ave, Sacramento,  
CA 95841, USA  
e-mail: nmarkus@version3.com

**Keywords** Benthic community structure · Vestimentiferan tubeworm · East Pacific Rise · Reciprocal transplant · Legacy species

## Introduction

The concept of succession as a deterministic sequence that depends on strong species interactions and culminates in a predictable climax community guided early theoretical studies (Clements 1928; Drury and Nisbet 1973; Connell and Slatyer 1977). More recent work has emphasized alternative processes and outcomes that are observed in a variety of ecosystems, shifting our perspectives regarding the organization of ecological communities from a deterministic view where successional sequences are highly predictable

to a more complex view where multiple processes contribute to variable outcomes (reviewed in McCook 1994; Sousa 2001). Unraveling the contribution of different processes to such variability for different communities and disturbance types is crucial for producing expectations about community responses to natural and anthropogenic disturbance. Especially important are the initial conditions—environmental conditions, availability of propagules, and presence of grazers or predators—when colonization of a disturbed habitat begins. These types of historical effects may initiate successional trajectories that are difficult to predict and perhaps lead to very different outcomes (Berlow 1997). For example, if a particular species spawns seasonally, or its main consumer varies in abundance, the timing of a disturbance will influence whether that species can colonize successfully. If it does colonize, and its presence preempts other possible recruits, then successional changes and eventual species composition will be contingent on those initial conditions. This type of priority effect has been observed in many systems, both terrestrial and marine (Paine 1977; Huston and Smith 1987; D'Antonio et al. 2001).

Communities that inhabit highly variable environments often experience dramatic changes in response to shifts in environmental regimes. If the shift is sufficiently severe and spatially extensive, recolonization after the disturbance-induced mortality may occur through a primary successional sequence starting with species that may differ entirely from the former community. Perhaps more often, a regime shift allows some individuals to survive within or near the disturbed area and influence recolonization (reviewed in Platt and Connell 2003). This type of historical influence on community succession occurs in a wide variety of terrestrial and marine habitats. On slopes of terrestrial volcanoes, buried seeds and root fragments remain and re-grow after eruptions (del Moral 1983); in old-growth forests, fires leave remnant live trees (Keeton and Franklin 2005); in temperate coastal habitats storms remove large algal fronds but leave their holdfasts (Lubchenco 1980); and in the tropics, hurricanes may partially damage coral colonies leaving live sections to regrow (Connell et al. 1997). The influence of these remnant individuals, also known as legacies (Franklin et al. 1988), on post-disturbance community development likely depends on their life-history traits and competitive abilities relative to those of new recruits (Platt and Connell 2003). They may accelerate or impede recovery of the community back to its pre-disturbance state, and reduce the likelihood of directional species replacement.

We might expect historical effects on succession to be particularly apparent in ecosystems undergoing environmental regime shifts. One such type of habitat is found at deep-sea hydrothermal vents on the East Pacific Rise, where abrupt tectonic and magmatic events can strongly

alter the physico-chemical environment experienced by inhabitants (reviewed in Fornari and Embley 1995). New vents form when tectonic movements open conduits in the crust, and during volcanic eruptions, such as those observed in 1991 (Haymon et al. 1993) and 2006 (Tolstoy et al. 2006). Established vents close when seafloor conduits are blocked by tectonic shifts, geochemical clogging (e.g., mineral precipitation as temperatures cool), lava flows, or basaltic-pillow collapses and rockfalls (Haymon et al. 1991). Over the course of an individual vent's existence, the magnitude and character (temperature, chemical composition) of hydrothermal fluid flux may change substantially (Butterfield et al. 1997; von Damm 2000). The species living at vents subsist largely on chemoautotrophic production fueled by reduced chemicals in the hydrothermal vent fluids (Karl 1995), so a disruption in venting results directly in a change in food production and community composition (e.g., Shank et al. 1998; Sarrazin et al. 1999). The tectonic and magmatic events that alter vent fluid flux occur on time scales similar to species' generation times (years to decades). At newly formed vents, colonists arrive within months, and establish extensive communities within a year (Shank et al. 1998). Because conditions at vents can shift suddenly and dramatically, and successional sequences occur rapidly, vents are an intriguing system in which to investigate the possible role of past biological imprints on community development.

Our primary question in the present study is if, and under what circumstances, a community that develops after a major and persistent transformation of the physico-chemical environment carries a past imprint of the earlier fauna. In particular, is there a legacy of earlier fauna on post-transformation recruitment and community structure? Does the possible legacy of earlier fauna depend on the direction of change in the physico-chemical environment? Thus, is the successional sequence more or less predictable depending on whether the change consists of an increase or decrease of hydrothermal fluid flux? And finally, what mechanisms may underlie an observed past imprint at vents? Using reciprocal transplant experiments, we simulated an abrupt, then persisting, increase or decrease in vent fluid flux that corresponds to natural perturbations at vents along the East Pacific Rise. If community development at vents were shaped solely by physico-chemical conditions, we would not expect any remaining biological imprint of prior conditions. Under this scenario, we should be able to predict the diversity and composition of the community based on current environmental conditions at sites characterized by those same environmental regimes. In contrast, some species may survive drastic environmental change, thereby representing a persisting legacy of past conditions. A legacy effect may occur in one direction of the environmental shift but not the other, depending on what factors limit

survival. Vigorously venting environments have elevated concentrations of  $\text{H}_2\text{S}$  (Le Bris et al. 2006) and other reduced chemicals that support primary production, but also elevated water temperatures and levels of trace metals that are potentially toxic to benthic invertebrates (Childress and Fisher 1992). Species limited by primary productivity may survive an increase, but not a decrease, in vent fluid flux, whereas species limited by physico-chemical stress (i.e., from high temperature or trace element concentrations) may exhibit the reverse response. Thus, asymmetry in legacy effects could provide additional insight into processes structuring vent communities and, by implication, other communities experiencing environmental regime shifts.

## Materials and methods

### Study site

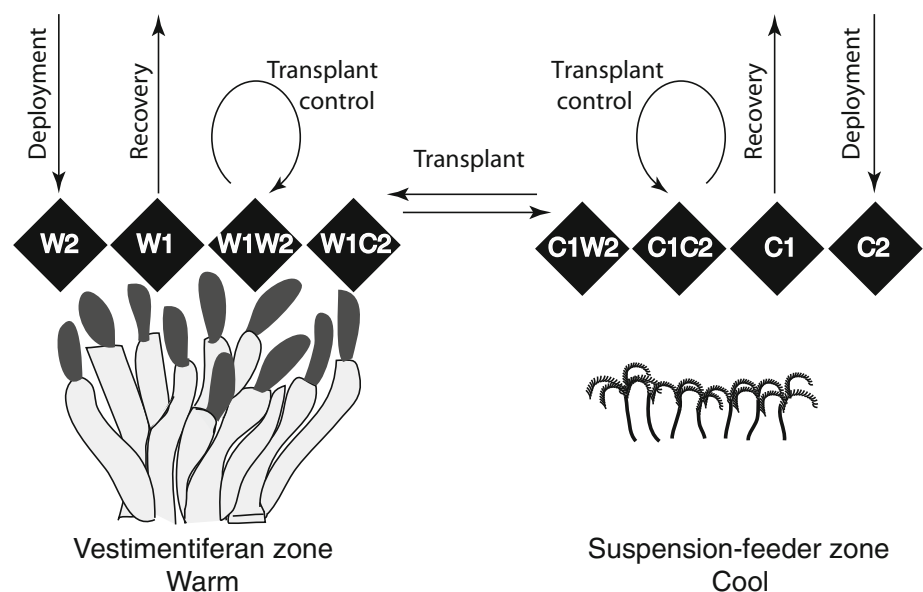
The study was conducted in a hydrothermal vent community (the 'East Wall' site) located at 2,500 m water depth on the East Pacific Rise at  $9^\circ 50.6' \text{N}$ ,  $104^\circ 17.5' \text{W}$ . The hydrothermal fluid venting at the site extended over tens of square meters, reached temperature anomalies of  $30^\circ\text{C}$  above ambient ( $1.8^\circ\text{C}$ ), and extended from the floor of the axial valley, up the 15 m high wall and onto the ridge crest. Two distinct environmental and faunal zones (Micheli et al. 2002) were identified for the experiments: the vestimentiferan zone where vent fluids exited the seafloor at temperatures ranging from 4 to  $30^\circ\text{C}$  above ambient, and the suspension-feeder zone, where vent fluid temperatures were  $<2^\circ\text{C}$  above ambient. When the experiments were initiated in December 1995, the vestimentiferan zone was characterized

by dense clumps of large vestimentiferan tubeworms (*Riftia pachyptila* Jones, Siboglinidae). Over the course of the experiment, average temperatures in this zone changed only slightly ( $<2^\circ\text{C}$ , Hunt et al. 2004). Throughout the experiment, the dominant visible species in the suspension-feeder zone were serpulid polychaetes and barnacles. A variety of smaller invertebrate species, mostly polychaetes and gastropods, inhabited each of these zones. Although a few species have been found exclusively in one zone or the other (Hessler et al. 1985; Jollivet 1996; Mullineaux et al. 2003; Mills et al. 2007), many occur in both.

### Experimental design

We exposed existing communities of vent organisms experimentally to an abrupt change in physico-chemical environment simulating the natural and frequent cessation or onset of vent fluid flux by transplanting them either from the vestimentiferan zone to the suspension-feeder (30 m away) or vice versa (Fig. 1). These transplants were accomplished in two steps using the deep-sea research submersible Alvin. First, organisms were allowed to colonize cubic basalt blocks placed on the seafloor in each zone in November 1995. Each block was roughly 10 cm on a side, and had a thin polypropylene line with a coded float looped through a hole in one corner for deployment and retrieval. After an initial interval of 29 months (May 1998), randomly selected blocks were placed gently into individual compartments on the Alvin's working platform and moved to the other zone, where they remained for another 11 months. Species composition of the communities immediately before transplantation was determined by retrieving subsets of blocks from each zone at the end of the initial interval and examining the specimens in the laboratory. The composition of the

**Fig. 1** Diagram of design for reciprocal transplant experiment from vestimentiferan zone to suspension-feeder zone, and vice versa. Labels on blocks indicate thermal environment (*W* warm, *C* cool) and interval of deployment (initial interval, *I* = December 1995 to May 1998; end interval, *2* = May 1998 to April 1999). Arrows movement of block during May 1998 cruise as indicated. Three replicate blocks were used in each treatment. Note that transplant control corresponds to transplant block from the same end-interval, not start-interval



community developing on new substratum during the second (end) interval was determined by examining colonists of new blocks placed in each zone for the duration of the end interval (11 months, from May 1998 to April 1999). The durations of deployment were dictated by Alvin's schedule, but both the 11- and 29-month intervals were sufficiently long to develop a community that resembled the nearby natural fauna. Prior colonization studies indicate that abundance and species composition do not change substantially on blocks that are left for longer than 8 months (Mullineaux et al. 2003) when the environment is undisturbed. Three replicate blocks were used in each treatment.

Composition of communities retrieved on the transplanted blocks was compared to those retrieved on the newly exposed end-interval blocks in order to test for legacy effects. Effects of handling and transport by the submersible were evaluated by comparing communities colonizing transplant-control blocks (transferred into the Alvin's working platform after the initial interval but then replaced during the same dive back into their original zone for the duration of the end interval) to communities on the end-interval blocks. We indicate each treatment by codes for temperature of the habitat and deployment interval. For example, the vestimentiferan to suspension-feeder zone transplant block was labeled W1C2 (i.e., warm habitat in interval 1 to cool habitat in interval 2), the corresponding transplant control was C1C2, and the end-interval block in the suspension-feeder (cool) zone was simply C2. In each zone, the blocks were arranged in three replicate clusters, with all treatments represented in each cluster, and the clusters separated from each other by 2 m or more. The transplant, transplant control, and end-interval blocks all were recovered in April 1999.

Close-up video images were taken of each block prior to recovery or transplantation, as a qualitative record of the composition and condition of resident fauna. A few highly mobile species (amphipods, copepods, the bythograeid crab) were observed to abandon blocks when they were disturbed, and these species were eliminated from our analyses. We saw no evidence of damage (crushing, falling off) of individuals during transport but cannot exclude the possibility that the transport process may stress or kill some individuals.

Upon recovery, each block was placed in a separate closed compartment on the submersible's working platform to prevent organisms from moving between blocks or from escaping. When the submersible was secured on board ship, the blocks and their fauna were removed and preserved in 80% ethanol. Colonists on the blocks were counted and identified to the lowest possible taxon (species if possible) under a dissecting microscope. Any individuals larger than 63  $\mu\text{m}$  (the mesh size of sieves used to retrieve organisms from holding compartments) that had fallen off the block

into the container during sample processing were included in these counts.

## Data analyses

The reciprocal transplant experiment was designed to mimic an abrupt shift in physico-chemical environment, while assessing some of the effects of transplantation (Schoen et al. 1986; Arnett and Gotelli 1999; Forrester et al. 2003). Because of the logistical constraints associated with conducting experiments in a deep-sea environment, we were not able to include the full set of experimental artifact controls (e.g., Chapman 1986) but instead included the treatments most critical for appropriately addressing our main questions. We tailored the design to investigate two specific questions about species composition of a community that has experienced a dramatic, persisting change in physico-chemical environment. First, we posed the question of whether a past imprint from initial residents was apparent in the community after the environmental regime shift, and whether such a legacy effect depended on the direction of the shift (i.e., a simulated cessation or onset of vent fluid flux). If a past imprint was evident, we then explored its underlying mechanisms, specifically whether it appeared to be a consequence of survival of pre-existing residents, or whether residents might have influenced subsequent recruitment. We categorized possible effects of initial residents on potentially recruiting species as facilitation, inhibition, or tolerance, following Connell and Slatyer (1977). We discriminated among these possible successional effects using the following comparisons of communities on transplanted blocks with those on transplant controls and single-interval blocks.

To detect a past imprint, we compared species abundance, species richness, and community structure on the transplanted blocks (C1W2 and W1C2) with those from the corresponding end-interval blocks (W2 and C2). If the number of species or individuals on the transplanted blocks was no different than in the end interval, then no past imprint was indicated; i.e., the community appeared as if it had started anew after the transplantation. If the number was greater on the transplanted blocks, a past imprint was indicated in the form of a remnant of colonization that occurred during the start interval. This remnant might result simply from accumulation of individuals over time (the transplanted blocks were exposed for a longer period), or from interactions of early residents with later colonists.

To explore mechanisms potentially responsible for the past imprint, we then compared values on the transplanted blocks (C1W2 and W1C2) to the summed values from the start- and end-interval blocks (C1 + W2 and W1 + C2; for species richness comparisons, a species was counted only once in the sum). If values on the transplanted blocks were

greater ( $C1W2 > C1 + W2$  or  $W1C2 > W1 + C2$ ), then facilitation of new recruits by residents was the simplest explanation. If the opposite pattern was apparent, then inhibition of new recruits or mortality of residents (e.g., due to competition) could be inferred. In most cases, it was not possible to distinguish between recruitment inhibition and resident mortality, because physical evidence of mortality, such as empty tubes or scars of former residents, was rare and difficult to interpret. When no difference was found between the transplanted and summed-interval blocks, the simplest explanation was independence (tolerance) between new recruits and surviving residents (i.e., individuals accumulated over time without interacting). In each of these cases, more complicated combinations of facilitation, inhibition and/or competition could have produced the same result, so we do not consider our mechanistic explanations as definitive.

If species richness or abundance on the transplanted blocks was not significantly different from the end-interval blocks ( $C1W2 = W2$  and  $W1C2 = C2$ ), then no past imprint was evident. This pattern could result, however, from different processes. The most parsimonious explanation is that the residents did not survive in the new environment after transplantation. A viable alternative is that the residents did not survive the transport process itself. To evaluate this alternative for each habitat, we compared abundances in the end intervals ( $W2$  and  $C2$ ) with those on blocks transported from that habitat and placed back into it ( $W1W2$  and  $C1C2$ ). If abundance on this transplant control was no greater than on the end interval blocks, then we could not exclude the possibility that substantial mortality had occurred during transport. The transplant-control does not allow us to distinguish what aspect of transport—disturbance or translocation (*sensu* Chapman 1986)—is responsible for the mortality. One additional control treatment that we did not use in our study consists of leaving blocks undisturbed in each habitat for the duration of the experiment. Although this treatment is a standard component of many transplantation experiments, and would have been informative (a comparison with the transplant control provides a quantitative measure of transport mortality), we did not include it because we were limited by payload and operating time of the submersible. We judged our transport control to be more informative because it addressed directly the question of whether a ‘no-imprint’ interpretation could have been caused by mortality induced by the transportation disturbance itself.

Patterns of species composition and abundance were compared qualitatively between the transplanted blocks and other treatments using a metric multidimensional scaling analysis (MDS) of Pearson’s correlations, evaluated with Kruskal’s stress (Systat v. 11). The relative contributions of abundant and rare species to the patterns were explored by

using both raw and fourth-root transformed abundances in the MDS, where the fourth-root transformation gives more weight to rare species and reduces influences of abundant taxa. Alternative analyses using nonmetric and metric MDS also were explored, using different correlations, distance measures, and goodness of fit measures (Pearson, Bray-Curtis, QSK, Euclidian and Spearman). Each analysis produced results qualitatively similar to metric MDS with Pearson correlation and Kruskal stress, such that we present only one set of results. Statistical significance of patterns of variation in community structure revealed by MDS was assessed using MANOVA (see below). A SIMPER analysis (similarity percentage analysis, Primer 5) of raw abundances was used to identify the top five species that were responsible for most (>70%) of the variation in pairwise comparisons between treatments.

The total number of species was compared between treatments in a two-way analysis of variance (ANOVA; Systat v. 11), with the environment on recovery (cool or warm) and the history (transplant, control, start interval, end interval) as fixed factors. Subsequent analyses of abundances of individual species, using the same fixed factors as above, were conducted with a two-way MANOVA (Systat v. 11) on all but the rarest species (i.e., those with ten or more individuals in the entire sample set), followed by univariate ANOVAs of the five species that contributed most to the MDS analysis. Rare species were not included in the MANOVA to reduce the number of zeros in the dataset and avoid problems of multicollinearity. Abundances were  $\ln(x+1)$  transformed, to achieve homogeneity of variance. Pairwise, post-hoc comparisons between transplant treatments (transplant, control and end interval) were conducted with Tukey contrasts. The start interval was excluded from these post-hoc comparisons because it was not needed to answer our main questions, and we wanted to retain as much power as possible.

When the Tukey contrasts showed significantly greater numbers in the transplant than in the end-interval treatments (no cases of the reverse were found), a past imprint was indicated. In these cases, a second one-way ANOVA was used to compare abundances between the transplant treatment and the summed abundances from the corresponding start and end intervals to discriminate between facilitation, inhibition or tolerance effects of residents on later recruitment. This second ANOVA could not be combined with the first because summed values were not independent of end-interval values.

## Results

Thirty-one sessile species or taxa colonized the set of blocks (Table 1). All but one, an unidentified kinorhynch,

**Table 1** Mean number of individuals of species or taxonomic groups quantified on blocks ( $n = 3$ ) in cool-to-warm and warm-to-cool transplant experiments

| Species/taxon                     | Cool-to-warm |       |       |       | Warm-to-cool |      |       |        |
|-----------------------------------|--------------|-------|-------|-------|--------------|------|-------|--------|
|                                   | C1W2         | W2    | W1W2  | C1    | W1C2         | C2   | C1C2  | W1     |
| <b>Polychaete</b>                 |              |       |       |       |              |      |       |        |
| <i>Vestimentiferans</i>           | 9.3          | 88.3  | 56.3  | 0     | 1.7          | 0    | 0     | 24.7   |
| <i>Amphisamytha galapagensis</i>  | 200.0        | 109.7 | 107.7 | 25.0  | 20.3         | 0    | 1.3   | 212.3  |
| <i>Laminatubus alvini</i>         | 9.7          | 0     | 2.0   | 11.0  | 12.0         | 0    | 1.0   | 102.7  |
| <i>Ophryotrocha akessoni</i>      | 4.0          | 12.7  | 5.3   | 0     | 0            | 0    | 0     | 9.3    |
| <i>Paralvinella</i> spp?          | 0            | 1.7   | 4.3   | 0     | 0            | 0    | 0     | 0      |
| <i>Nicomache</i> sp               | 0            | 0     | 0     | 1.3   | 0            | 0    | 0     | 1.3    |
| <i>Nereis</i> sp                  | 2.7          | 0     | 0     | 0.3   | 0.3          | 0    | 0     | 3.0    |
| <i>Prionospio</i> sp              | 0            | 0     | 0.3   | 0     | 0            | 0    | 0     | 0      |
| Brown papillated worm             | 0            | 0     | 0     | 0     | 0            | 0    | 0.7   | 0      |
| Polynoid polychaetes              | 0            | 0     | 0     | 0.7   | 0            | 0    | 0     | 0.3    |
| <i>Archinome rosacea</i>          | 3.0          | 0     | 0     | 5.7   | 0            | 0    | 0     | 1.0    |
| Other polychaetes                 | 0.3          | 0.3   | 0     | 0     | 0            | 0    | 0     | 0.3    |
| <b>Mollusc</b>                    |              |       |       |       |              |      |       |        |
| <i>Bathymodiolus thermophilus</i> | 7.0          | 15.3  | 12.3  | 3.0   | 2.7          | 0    | 0.3   | 82.3   |
| <i>Bathypecten vulcani</i>        | 0            | 0     | 0     | 0     | 0            | 0    | 0.3   | 0      |
| <i>Lepetodrilus elevatus</i>      | 5.0          | 83.0  | 1.7   | 0     | 1.3          | 0    | 0.3   | 9.0    |
| <i>Lepetodrilus ovalis</i>        | 7.0          | 0.7   | 0.3   | 4.3   | 0            | 0    | 0     | 3.3    |
| <i>Pachydermia laevis</i>         | 0            | 0     | 0.3   | 0     | 0            | 0    | 0     | 0      |
| <i>Eulepetopsis vitrea</i>        | 4.0          | 0     | 0     | 1.3   | 0            | 0    | 0     | 0.3    |
| <i>Rhynchopelta</i> sp.           | 0.3          | 0.7   | 0.7   | 0     | 0            | 0    | 0     | 0      |
| Other gastropods                  | 0            | 0     | 0     | 0     | 1.7          | 0    | 0     | 0      |
| Aplacophora                       | 8.7          | 0     | 0     | 0     | 0            | 0    |       | 5.7    |
| <b>Arthropod</b>                  |              |       |       |       |              |      |       |        |
| <i>Neolepas zeviniae</i>          | 0            | 0     | 0     | 0     | 0            | 0    | 0.3   | 26.3   |
| Barnacle cyprids                  | 0            | 0     | 0     | 0     | 0            | 0    | 0     | 0.3    |
| Mites                             | 0.3          | 0     | 0.3   | 0     | 0            | 0    | 0     | 0.3    |
| <b>Other</b>                      |              |       |       |       |              |      |       |        |
| Hydroids                          | 0            | 0     | 0     | 0     | 0            | 0    | 0.3   | 0      |
| Anemones                          | 0.7          | 0     | 0     | 0     | 0            | 0    | 0     | 0.3    |
| Unsegmented worm                  | 1.3          | 0     | 0     | 0     | 0            | 0    | 0     | 0      |
| Kinorhynch                        | 4.3          | 0     | 0     | 0     | 0            | 0    | 0     | 0      |
| <i>Metafolliculina</i> sp.        | 814.0        | 5.0   | 329.0 | 390.0 | 112.3        | 0    | 141.0 | 2000.0 |
| <i>Abyssotherma pacifica</i>      | 759.7        | 10.0  | 33.0  | 340.0 | 363.7        | 12.3 | 713.7 | 52.0   |
| Benthic foraminifers              | 0            | 0.3   | 0     | 0     | 0.3          | 0    | 1.7   | 0      |

The four different block manipulations were transplant (C1W2 and W1C2), end interval (W2 and C2), transplant-control (W1W2 and C1C2), and initial interval (C1 and W1)

had been observed previously as colonists on blocks deployed at the East Wall site (e.g., Micheli et al. 2002; Mullineaux et al. 2003; Lenihan et al. 2008). Most of the taxa (9 of 11) that settled in the cool habitat (C1) appeared capable of surviving the transition to warm conditions (C1W2); the only taxa that did not persist were the polychaetes *Nicomache* sp. and polynoids. Ten additional taxa that had not settled in the cool habitat also appeared on the blocks transplanted to warm conditions. In contrast, fewer than half of the taxa (8 of 20) that settled in warm habitat (W1) were still found on the transplants into the cool environment (W1C2), and only two additional taxa settled on

these transplants. Just one species, the protist *Abyssotherma pacifica* Brönnimann, Van Dover and Whittaker, colonized the end-interval blocks in cool habitat (C2). This is surprising because other blocks in this habitat type, from the C1 and C1C2 treatments, supported many more taxa (11 each), and the community of species settling in this habitat is typically more diverse, even after short intervals (e.g., Micheli et al. 2002). Temperatures recorded at the bases of the C2 blocks on deployment and recovery were no different from the ambient deep-sea temperature (1.8°C). We suspect that the environment around the C2 blocks was not typical of the suspension-feeder zone, but instead was characteristic

of a more peripheral region where vent fluids are undetectable and *A. pacifica* is the only vent-endemic inhabitant.

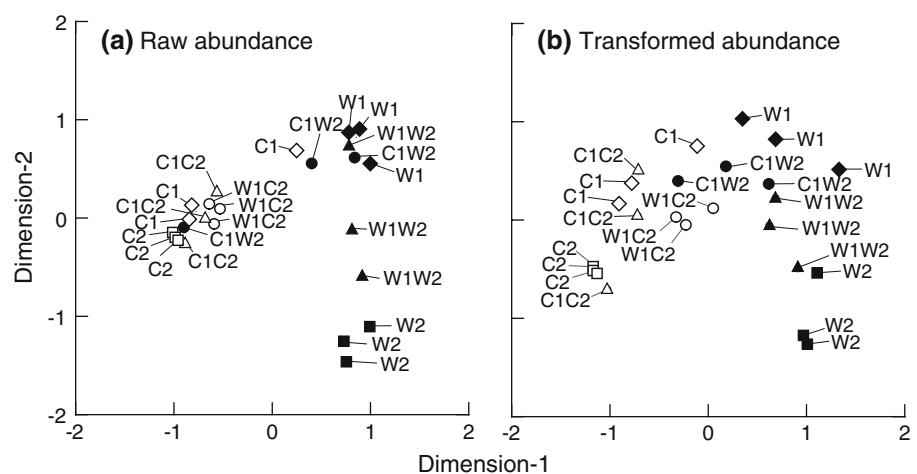
Species composition on the blocks recovered from the warm habitat differed qualitatively from those recovered from the cool habitat, as indicated by their separation along the first dimension of the MDS plot (Fig. 2a, b), which reflects their relatively low pairwise correlations. Faunal assemblages on transplanted blocks (C1W2 and W1C2) differed from corresponding end-interval blocks (W2 and C2), causing them to separate along the second dimension. This separation was greater (reflecting lower pairwise correlations) in treatments recovered from warm habitat than cool when raw abundances were analyzed (Fig. 2a). The asymmetry in the pattern was less distinct when transformed abundances were used (Fig. 2b), suggesting that abundant species contributed to the pattern more than rare ones. The difference between transplant and end-interval faunas suggests that transplanted blocks retained a past imprint from the prior residents, particularly when conditions changed from cool to warm.

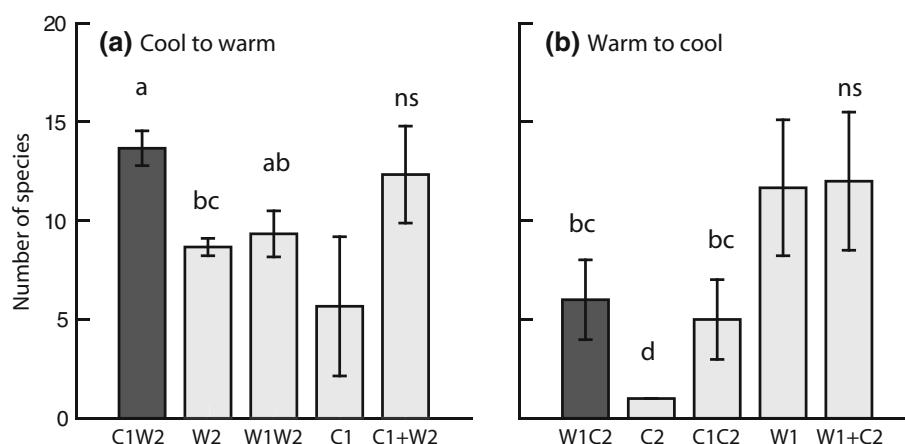
The average number of taxa was greater on the transplanted blocks than on end-interval blocks in both the cool-to-warm and warm-to-cool transplant directions (Fig. 3). The two-way ANOVA indicated that effects of history and recovery environment were significant ( $P < 0.05$ ), but not their interaction (Table 2), indicating that a legacy effect on species richness occurred in both transplant directions. Post-hoc Tukey contrasts, in fact, showed a significant difference between transplant and end-interval treatments in both transplant directions (Fig. 3). The transplant control did not differ from the transplant or end-interval in the cool-to-warm direction, and differed only from the end-interval in the warm-to-cool direction. A subsequent one-way ANOVA showed no difference between the transplant and summed start- and end-interval averages, suggesting that neither inhibition nor facilitation of colonization of new species by residents had occurred.

A two-way MANOVA on log-transformed abundances of the common taxa revealed significant effects of recovery environment, history, and their interaction (Table 3). This result suggests that, at least for some taxa, legacy effects depended on the direction of transplant. Five taxa were selected for subsequent univariate analyses, based on a SIMPER analysis that indicated they were responsible for most of the variation in community composition evident in the MDS plots (Fig. 2). Those five were vestimentiferan tubeworms, the polychaetes *Amphisamytha galapagensis* Zottoli and *Laminatubus alvini* Ten Hove and Zibrowius, and the protists *Metafolliculina* sp. and *Abyssotherma pacifica*. For all but the vestimentiferans, abundances of these taxa on the transplanted blocks were generally greater than on the end-interval ones (Fig. 4). Average vestimentiferan abundance was lower on the transplanted blocks than end-interval ones in the cool-to-warm transplant. Five individual vestimentiferans survived the warm-to-cool transplant, but none was found on any of the other blocks recovered from the cool habitat (C1, C2, or C1C2).

Univariate two-way ANOVAs showed a significant interaction of history and recovery environment for vestimentiferans, *A. galapagensis* and *A. pacifica*, and a significant effect of transplant history, independent of recovery environment, for *L. alvini* and *Metafolliculina* sp. (Table 4). For *A. galapagensis*, the post-hoc Tukey contrasts revealed a significant difference between transplant and end-interval treatments in the warm-to-cool direction, but not the reverse direction (Fig. 4). The control also was significantly different from the transplant in the warm-to-cool direction. A subsequent one-way ANOVA indicated that the summed start- and end-interval abundances were significantly greater than transplant abundances in the warm-to-cool transplant, suggesting that inhibition might have occurred for this species. For *Metafolliculina* sp., post-hoc tests showed significant differences between transplant and end-interval abundances in both transplant directions.

**Fig. 2** Linear multidimensional scaling analysis (MDS) of (a) raw abundances, and (b) fourth-root transformed abundances for treatments: transplant (C1W2 and W1C2, circles), end-interval (W2 and C2, squares), initial interval (C1 and W1, diamonds) and transplant control (W1W2 and C1C2, triangles). Filled symbols designate blocks recovered from warm habitat, unfilled indicate blocks recovered from cool habitat. Kruskal Stress: 0.090 (a) and 0.104 (b)





**Fig. 3** Number of species (mean  $\pm$  SE,  $n = 3$ ) on treatments from (a) cool-to-warm, and (b) warm-to-cool transplant experiments: transplant (C1W2 and W1C2, dark gray bars for emphasis), end interval (W2 and C2), transplant control (W1W2 and C1C2), start interval (C1 and W1) and summed start- and end-interval (C1 + W2 and W1 + C2). Bars sharing letters were not significantly different in post-hoc Tukey

contrasts of transplant, end-interval and control treatments based on two-way ANOVA (Table 2). Subsequent one-way ANOVA ( $df = 1$ ) detected no significant difference (ns) between transplant and summed-interval values for cool-to-warm ( $F = 0.46$ ,  $P = 0.54$ ) or warm-to-cool ( $F = 3.86$ ,  $P = 0.12$ ) transplant direction

**Table 2** Two-way analysis of variance (ANOVA) of total number of taxa in the transplant experiments, with Recovery environment (warm or cool) and History (transplant, control, or second interval) as fixed factors

| Source           | SS     | df | MS     | F     | P      |
|------------------|--------|----|--------|-------|--------|
| Recovery         | 193.39 | 1  | 143.39 | 64.46 | <0.001 |
| History          | 75.11  | 2  | 37.56  | 12.52 | 0.001  |
| Recovery*History | 11.11  | 2  | 5.56   | 1.85  | 0.199  |
| Error            | 36     | 12 | 3      |       |        |

**Table 3** Two-way multivariate analysis of variance (MANOVA) on all common taxa (those with 10 or more individuals total in experiment)

| Source           | Wilks' $\lambda$ | F      | df    | P      |
|------------------|------------------|--------|-------|--------|
| Recovery         | 0.0014           | 1305.4 | 11, 2 | <0.001 |
| History          | 0.0016           | 35.7   | 22, 4 | 0.002  |
| Recovery*History | 0.0003           | 9.8    | 22, 4 | 0.019  |

Fixed factors are Recovery environment (warm or cool) and transplant History (transplant, control, or second interval)

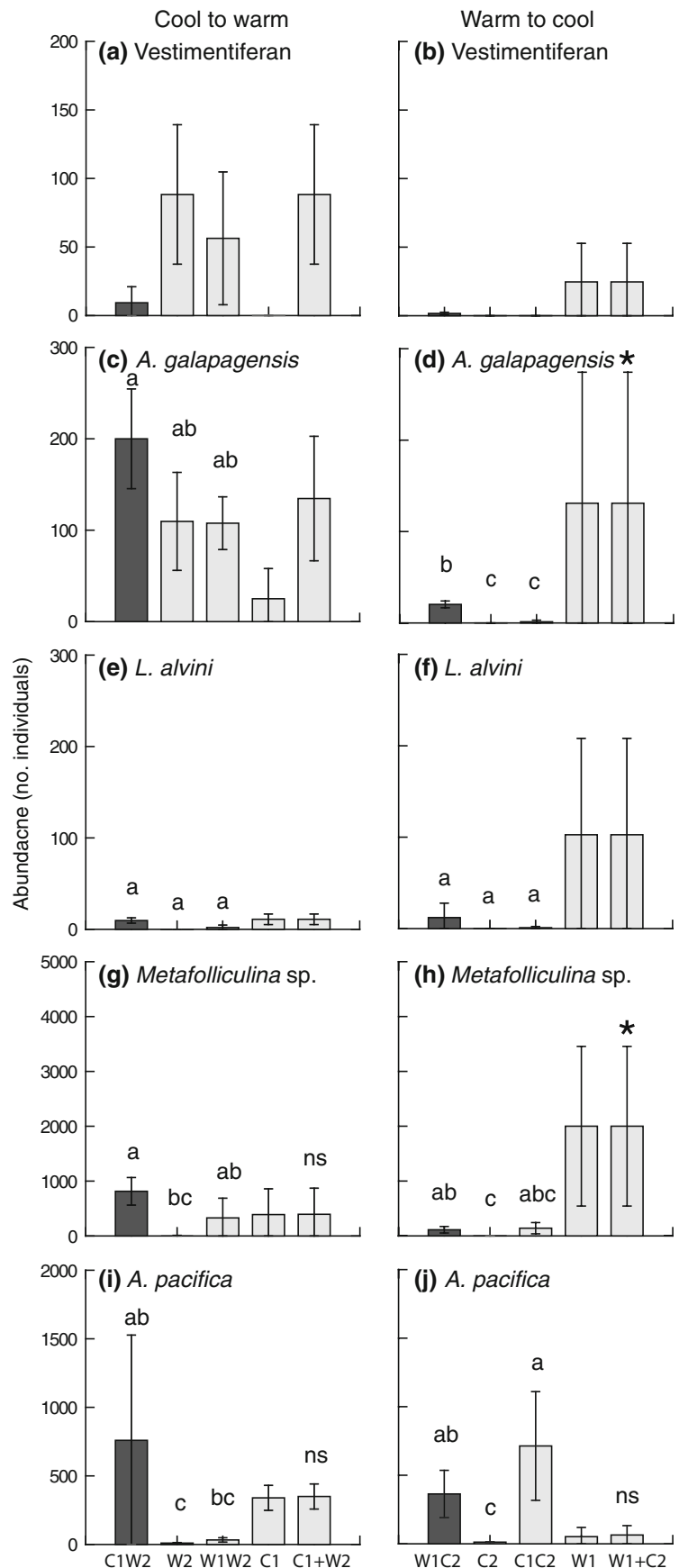
Abundances on the controls were not different from those on transplant or end-interval treatments. A subsequent one-way ANOVA indicated that the summed start- and end-interval abundances were significantly greater than transplant abundances in the warm-to-cool transplant, but not in the reverse direction. For *A. pacifica*, post-hoc tests showed significant differences between transplant and end-interval treatments in both transplant directions. The control abundances also differed from the end-interval abundances. The subsequent one-way ANOVA showed no significant difference between the summed start- and end-interval treatments and the transplants.

## Discussion

Our results indicate that abrupt environmental change at deep-sea vents does not necessarily result in elimination of existing fauna and rapid replacement by the fauna typical of the new physico-chemical environment. Instead, an imprint of the past community may persist for many months after the disturbance. Thus, succession following disturbance and resulting community structure in this deep-sea environment may be influenced not only by local environmental conditions and recruit availability, but also by the community history and legacy of early residents. Such legacy effects contribute to increasing the variability of the successional process and resulting communities. When vent fluid flux increased rapidly, raising temperatures from near ambient (cool) to 4°C or more above ambient (warm), the resulting community had greater species numbers and different species abundances than a community arising de novo in the warm environment. Most of the species starting in the cool habitat appeared to survive the environmental change, and many new species colonized after temperatures warmed. In contrast, the community developing after a rapid cooling of the environment retained a less distinct imprint from the original residents. Most species that had colonized the blocks when located in the warm habitat appeared not to survive the environmental change. Of the species that did survive, all but three were also typical colonists of cool habitat (Table 1), so the fauna developing after transplantation was similar to faunas originating in cool habitat. Thus, the past imprint was more distinct when vent fluid flux increased than when it decreased.

An asymmetry in the past imprint effect also is seen in overall community composition and relative contributions

**Fig. 4** Abundance (mean  $\pm$  SE,  $n = 3$ ) of five individual taxa on treatments in cool-to-warm and warm-to-cool transplant experiments. **a, b** Vestimentiferan; **c, d** *Amphisamytha galapagensis*; **e, f** *Laminatubus alvini*; **g, h** *Metafolliculina* sp.; **i, j** *Abyssosherma pacifica*. These taxa were identified by SIMPER analysis as responsible for most of variation in MDS. Treatment abbreviations as in Fig. 3. Bars sharing letters were not significantly different in post-hoc Tukey contrasts of transplant, end-interval and control treatments for two-way ANOVA (Table 4; Tukey contrast done only when effect of history was significant). Subsequent one-way ANOVA ( $df = 1$ ) compared transplant and summed-interval values ( $*P < 0.05$ , ns = no significance) for cases in which a significant past imprint was detected: *Metafolliculina* sp. ( $F = 2.42$ ,  $P = 0.19$ ) and *A. pacifica* ( $F < 0.001$ ,  $P = 0.99$ ) in cool-to-warm direction; and *A. galapagensis* ( $F = 12.06$ ,  $P = 0.026$ ), *Metafolliculina* sp. ( $F = 18.49$ ,  $P = 0.013$ ) and *A. pacifica* ( $F = 6.49$ ,  $P = 0.063$ ) in warm-to-cool direction



**Table 4** Two-way analyses of variance (ANOVA) on the five taxa responsible for most of the variance in multidimensional scaling analysis (MDS)

| Factor taxon                        | SS     | df | MS     | F       | P      |
|-------------------------------------|--------|----|--------|---------|--------|
| <b>Recovery</b>                     |        |    |        |         |        |
| Vestimentiferans                    | 32.879 | 1  | 32.879 | 31.218  | <0.001 |
| Error                               | 12.638 | 12 | 1.053  |         |        |
| <i>Amphisamytha galapagensis</i>    | 58.54  | 1  | 58.54  | 179.662 | <0.001 |
| Error                               | 3.91   | 12 | 0.326  |         |        |
| <i>Laminatubus alvini</i>           | 0.86   | 1  | 0.86   | 0.811   | 0.386  |
| Error                               | 12.721 | 12 | 1.06   |         |        |
| <i>Metafolliculina</i> sp.          | 9.109  | 1  | 9.109  | 3.439   | 0.088  |
| Error                               | 31.783 | 12 | 2.649  |         |        |
| <i>Abyssotherma pacifica</i>        | 5.134  | 1  | 5.134  | 6.365   | 0.027  |
| Error                               | 9.678  | 12 | 0.807  |         |        |
| <b>History</b>                      |        |    |        |         |        |
| Vestimentiferans                    | 2.858  | 2  | 1.429  | 1.357   | 0.294  |
| Error                               | 12.638 | 12 | 1.053  |         |        |
| <i>Amphisamytha galapagensis</i>    | 12.325 | 2  | 6.162  | 18.913  | <0.001 |
| Error                               | 3.91   | 12 | 0.326  |         |        |
| <i>Laminatubus alvini</i>           | 9.785  | 2  | 4.892  | 4.615   | 0.033  |
| Error                               | 12.721 | 12 | 1.06   |         |        |
| <i>Metafolliculina</i> sp.          | 85.027 | 2  | 42.513 | 16.052  | <0.001 |
| Error                               | 31.783 | 12 | 2.649  |         |        |
| <i>Abyssotherma pacifica</i>        | 35.643 | 2  | 17.822 | 22.097  | <0.001 |
| Error                               | 9.678  | 12 | 0.807  |         |        |
| <b>Recovery*History interaction</b> |        |    |        |         |        |
| Vestimentiferans                    | 12.115 | 2  | 6.057  | 5.752   | 0.018  |
| Error                               | 12.638 | 12 | 1.053  |         |        |
| <i>Amphisamytha galapagensis</i>    | 4.483  | 2  | 2.241  | 6.879   | 0.010  |
| Error                               | 3.91   | 12 | 0.326  |         |        |
| <i>Laminatubus alvini</i>           | 1.09   | 2  | 0.545  | 0.514   | 0.611  |
| Error                               | 12.721 | 12 | 1.06   |         |        |
| <i>Metafolliculina</i> sp.          | 1.001  | 2  | 0.5    | 0.189   | 0.830  |
| Error                               | 31.783 | 12 | 2.649  |         |        |
| <i>Abyssotherma pacifica</i>        | 8.306  | 2  | 4.153  | 5.149   | 0.024  |
| Error                               | 9.678  | 12 | 0.807  |         |        |

Fixed factors are Recovery environment (warm or cool) and History (transplant, control, or second interval)

of different species. Multivariate ordinations (MDS) show a greater difference between transplanted and end-interval faunas in the cool-to-warm transplant direction than in the reverse. The MANOVA of individual species provides parametric support for this asymmetry in the form of the significant interactions between the history and transplant direction. Given this asymmetry, we might have expected the two-way ANOVA of number of species to also have an interaction effect, with a significant difference between

transplanted and end-interval values in blocks recovered from the warm, but not cool, habitat. Such an interaction was not detected, but it may have been masked by the misplacement of end-interval cool (C2) blocks into peripheral habitat instead of environment characteristic of the suspension-feeder zone. If those blocks had been located as we intended, they would likely have developed faunas similar to others recovered from cool habitat (e.g., C1 and C1C2), with species numbers more similar to the W1C2 transplants. That result would have further decreased or eliminated a past imprint in the warm-to-cool transplant.

Asymmetry in the degree of past imprint effects can help indicate which processes (e.g., primary production, extreme environmental conditions such as high temperatures or toxic chemicals, or species interactions) limit distributions of vent species. A past imprint in the warming treatment (cool-to-warm transplant) indicates that more 'extreme' thermal and chemical conditions do not limit the distributions of at least some species typical of cool habitat. This observation, however, raises the question of why these species are not typically found in the established communities in warm conditions. We suggest they may be excluded by species that grow more quickly, are more effective at using the enhanced productivity, or disturb or prey upon (Micheli et al. 2002) their propagules. On a longer time scale, it is possible that species interactions would eliminate these 'cool' species or their longevity would be exceeded and, without replacement by new recruits, cause the transitional community to gradually resemble the warm community. Our results suggest that physico-chemical conditions in vent fluids reaching 30°C do not limit distributions of several vent species typical of the suspension-feeder zone, although higher temperature fluids (50°C and above) most certainly do (Lee 2003).

The less distinct past imprint in the cooling treatment (warm-to-cool transplant) suggests that most species typical of established 'warm' faunas may be unable to survive in a habitat with more dilute reduced chemicals and lower productivity. In particular, invertebrate species with endosymbionts are expected to be limited to warmer habitats (Childress and Fisher 1992). In general, species living in the range of environmental conditions that we investigated were apparently not limited in their distribution by high temperature or toxic chemicals, but were instead limited by primary production (in the cool habitat) and possibly competitive or predator-prey interactions (in the warm habitat).

The most widely studied and broadly informative research on causes of distributional limits along environmental gradients comes from the rocky intertidal habitat. Living higher on the shore exposes the marine organisms to more extreme temperatures, ultraviolet light levels, and desiccation risk during longer periods out of water. Locations lower on the shore experience more stable environmental conditions, yet competition for limited attachment

space and risk of predation increase. Connell (1972, 1975) reviewed available experimental evidence to propose that physical stress generally limits upwards distributions of rocky shore species, while biological interactions limit their penetration downwards. Underwood and Denley (1984) noted that the elevation in the intertidal zone confounds two important gradients: the physical stress increase with elevation plus an additional gradient of reduction in productivity because of decreased feeding times at higher elevations. Wethey (1984) conducted experiments with barnacles that demonstrated that shading allowed barnacle survival higher on shore, implying that feeding time and productivity limitations failed to explain, and that physiological stress could explain, the higher distributional limit. As on the intertidal shore, changing proximity to intense fluid flux from deep-sea vents confounds two gradients, the one in physical environmental stress and the other in intrinsic productivity; however, in the vents system the two gradients are parallel rather than opposing. Proximity to more intense fluid flux implies more physical stress of higher temperature and elevated metals and sulfide concentrations but at the same time greater potential biological productivity and food availability. Our transplant experiments under this dual gradient reveal that in the vents system productivity enhancement appears to outweigh potential physiological stress in setting limits to distributions of vent invertebrates. Consequently, this new insight should serve to restore interest in teasing out the role of productivity variation in setting species distribution patterns along environmental gradients, where previously only physico-chemical factors have achieved much consideration.

The simplest explanation for the past imprint in these transplant experiments is survival of at least some initial residents after transplantation, and successful recruitment of some new individuals. This mechanism is consistent with the observed persistence of most ‘cool’ and some ‘warm’ species after transplantation, and the addition of at least a few new species in both transplant directions (Table 1). It is also supported by the lack of a significant difference in the number of species between transplanted blocks and the summed start- and end-interval blocks (Fig. 3). Analyses of abundance of individual species indicate tolerance of new recruits by initial residents in populations of *Metafolliculina* sp. in the cool-to-warm transplant, and in populations of *A. pacifica* in both transplant directions (Fig. 4). Two species, *A. galapagensis* and *Metafolliculina* sp., show evidence for mortality or inhibition in the warm-to-cool transplant, as indicated by greater abundances on summed intervals than on transplants. These results should be interpreted cautiously because the absence of these species on the C2 blocks may have been due to misplacement of the blocks. An increase in abundance of these species on properly located C2 blocks might have

eliminated the observed past imprint in the warm-to-cool transplant. For any of these inferences of survival and tolerance, we are unable to reject alternative more complicated scenarios, such as mortality of initial residents followed by facilitation of new recruits or early facilitation followed by competition. Our experimental design cannot detect combinations of positive and negative interactions, which deserve more study in the future.

The observation of live vestimentiferans on the warm-to-cool transplant blocks was unexpected, given that they are not found in cool habitats as adults (Tunnicliffe et al. 1998) or as new recruits (Mullineaux et al. 2003). We assume that these individuals survived transplantation rather than settling afterward because no new vestimentiferan recruits were found in any of the other treatments recovered from cool habitat. The possibility that they survived for 11 months in cool habitat is very interesting and puzzling because they depend on chemoautotrophic endosymbionts for nutrition. We hypothesize that vestimentiferans can use stored energy reserves for survival in the short term, but that they eventually perish when the reserves run out.

Although our experimental design should not result in a past imprint being detected when none exists, mortality during transplantation could result in failure to detect a past imprint when one might have occurred. Analysis of the transplant control blocks showed that for *L. alvini*, mortality may have occurred during transplantation, given that abundances on the controls were not significantly different from end-interval treatments (Fig. 4). It is also possible that the low number of replicates in our design and relatively high variation among replicates hampered our ability to detect significant differences in this species. If we had included an undisturbed control in our experimental design, and had used separate disturbance and translocation treatments instead of a single transplant-control that incorporated both effects (as recommended by Chapman 1986 and others), we would be better informed about what specific process caused mortality in transplanted *L. alvini*. Lack of those treatments, however, does not alter our interpretation of past imprints that were detected in other species and in overall species richness.

The results of our study show that patterns of succession in vent communities can be predicted when venting decreases. For these situations, it seems likely that the invertebrate community will transition quickly to the suite of species typically found in the cooler environment. When the venting increases, however, it is much more difficult to predict the resulting faunal changes. The individual replicate communities on our cool-to-warm transplant blocks were highly variable in species composition, ranging from those with mostly ‘warm’ species to those dominated by ‘cool’ species (Fig. 2). Thus, it appears that a decrease in vent fluid flux channels successional transition toward a predictable community composition

(canalized succession; Berlow 1997), whereas after an increase in fluid flux, initial conditions are more important and may result in variable trajectories in community succession. Since warm habitat is conspicuously patchy on small scales (e.g., Le Bris et al. 2006), an increase in vent fluid flux may result in a mosaic of different species assemblages, reflecting that environmental patchiness.

Many natural disturbances do not completely eliminate existing communities (as reviewed in Sousa 2001; Platt and Connell 2003). Instead, some individuals can survive and influence the following colonization and establishment processes, thereby decreasing the predictability of successional change after disturbance. Here we show that even the dramatic, sudden, and persisting shifts in environmental conditions at Pacific vent communities can result in a biological legacy of past residents. Vent species, even those with distinct habitat affinities, can survive rapid warming and, to a lesser degree cooling, on time scales of months to a year. These survivors influence species composition in the transitional community through their persistence and may also interact with potential new colonists to influence the path of future succession. Our manipulation of the vent environment produced a disturbance in a local site but did not eliminate species from the surrounding environs. This resulted in a situation where post-disturbance colonization should be determined by life-history characteristics of remnant species at the site and of other species that might invade from outside (Platt and Connell 2003). We know the dispersive and competitive abilities of a few vent species: the vestimentiferan tubeworm *Tevnia jerichonana* is an early colonist, whereas the larger, faster-growing tubeworm *Riftia pachyptila* and the mussel *Bathymodiolus thermophilus* typically arrive later (Hessler et al. 1988; Lutz et al. 1994; Shank et al. 1998). These late species did not survive a decrease in venting (with the possible exception of a few tubeworm individuals that were too small to identify to species), nor did they recolonize in the following 11 months, leaving them with no influence on directional replacement of species during that time. When exposed to an increase in venting, the mussel (and possibly the tubeworm *R. pachyptila*) did recolonize within 11 months, and may have accelerated or bypassed the typical successional sequence by excluding the pioneer *T. jerichonana*.

The recovery of vent communities after a disturbance parallels some, but not all, aspects of vegetation recovery after terrestrial volcanic eruptions. The 1980 eruption of Mt. St. Helens (Washington State, USA) created extensive barren areas where initial plant growth was mainly from remnant vegetative parts of surviving species (del Moral 1983). Recolonization by new seedlings was surprisingly slow despite the proximity of seed sources in lightly disturbed areas nearby (Wood and del Moral 1987), and occurred predominantly near established plants that

ameliorated the harsh conditions. The remnant individuals contributed to recovery by facilitating other species, including highly dispersive ones that could not survive in the barren areas on their own. At vents, remnant individuals contributed to community diversity after a disturbance, but predominantly in the warming scenario, where resources became readily available. Their contribution was much less apparent in the cooling scenario. Unlike the remnant volcano plants, remnant vent invertebrates did not appear to ameliorate conditions in the resource-poor, and presumably less hospitable, environment created by reduced vent fluid flow. Differences like these in the interactions between remnants and new colonists result in a variety of recovery patterns after non-catastrophic disturbances from other agents such as fires (Platt 1999; Keeton and Franklin 2005) and hurricanes (Connell et al. 1997).

In deep-sea vent environments, and possibly more generally in other marine and terrestrial environments, the history of environmental phase shifts may be a key contributor to the observed patterns and temporal trajectories in community composition. Our results suggest that an environmental transition that increases primary production is more likely to produce a legacy effect than a transition that decreases production, although the generality of this prediction and its applicability to other ecosystems needs to be tested. A better understanding of the conditions and mechanisms underlying these historical effects is needed to anticipate biological responses to anthropogenic and natural environmental change. The pattern we observed at vents may provide useful predictions of how natural communities may be expected to change under environmental shifts that occur as a consequence of climate change.

**Acknowledgments** We thank the Captain and crew of the R/V Atlantis, and Alvin submersible group for support of at-sea operations. C. Fisher was Chief Scientist on two cruises and contributed to discussions of experimental design and methods. S. Mills sorted samples and provided identifications. We thank participants of the three cruises for their assistance: E. Berntson, H. Hunt, G. Johnson, S. Kim, A. Metaxas, G. Sancho, S. Schafer, S. Simmons, and R. Scheltema. The manuscript has benefited from comments by D. Adams (née Poehls), H. Fuchs, L. Gulmann, R. Jennings, S. Mills and C. Strasser, and from insightful critiques by P. Petraitis, A. J. Underwood and an anonymous reviewer (any remaining statistical errors are ours). N. Markus was supported by the Christopher Frantz Fund and by the NSF's REU program. The research was supported by NSF grants OCE-969105 and OCE-9712233 to L.M., OCE-9712809 to C.H.P. and OCE-9712808 to C. Fisher. The experiments were conducted on the high seas, and subsequent sample shipping and processing complied with the current laws of the countries in which they were performed.

## References

- Arnett A, Gotelli N (1999) Geographic variation in life-history traits of the ant lion, *Myrmeleon immaculatus*: evolutionary implications of Bergmann's rule. *Evolution* 53:1180–1188

- Berlow E (1997) From canalization to contingency: historical effects in a successional rocky intertidal community. *Ecol Monogr* 67:435–460
- Butterfield D et al (1997) Seafloor eruptions and evolution of hydrothermal fluid chemistry. *Philos Trans R Soc A* 355:369–386
- Chapman MG (1986) Assessment of some controls in experimental transplants of intertidal gastropods. *J Exp Mar Biol Ecol* 103:181–201
- Childress JJ, Fisher CR (1992) The biology of hydrothermal vent animals: physiology, biochemistry, and autotrophic symbioses. *Oceanogr Mar Biol* 30:61–104
- Clements FE (1928) *Plant succession and indicators*. Wilson, New York
- Connell JH (1972) Community interactions on marine rocky intertidal shores. *Annu Rev Ecol Syst* 3:169–192
- Connell JH (1975) Some mechanisms producing structure in natural communities: a model and some evidence from field experiments. In: Cody ML, Diamond JM (eds) *Ecology and evolution of communities*. Belknap, Cambridge, pp 460–490
- Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *Am Nat* 111:1119–1144
- Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. *Ecol Monogr* 67:461–488
- D'Antonio CM, Hughes RF, Vitousek PM (2001) Factors influencing dynamics of invasive C4 grasses in a Hawaiian woodland: role of resource competition and priority effects. *Ecology* 82:89–104
- del Moral R (1983) Initial recovery of subalpine vegetation on Mount St. Helens, Washington. *Am Midl Nat* 109:72–80
- Drury WH, Nisbet ICT (1973) Succession. *J Arnold Arbor* 54:331–368
- Fornari DJ, Embley RW (1995) Tectonic and volcanic controls on hydrothermal processes at the mid-ocean ridge: an overview based on near-bottom and submersible studies. In: Humphris SE, Zierenberg RA, Mullineaux LS, Thomson RE (eds) *Seafloor hydrothermal systems: physical, chemical, biological, and geological interactions*, vol Geophysical Monograph 91. American Geophysical Union, Washington, DC, pp 1–46
- Forrester GE, Fredericks BI, Gerdeman D, Evans B, Steele MA, Zayed K, Schweitzer LE, Suffet IH, Vance RR, Ambrose RF (2003) Growth of estuarine fish is associated with the combined concentration of sediment contaminants and shows no adaptation or acclimation to past conditions. *Mar Environ Res* 56:423–442
- Franklin JF, Frenzen P, Swanson FJ (1988) Re-creation of ecosystems at Mt. St. Helens: contrasts in artificial and natural approaches. In: Cairns J Jr (ed) *Rehabilitating damaged ecosystems*, vol II. CRC, Boca Raton, pp 1–37
- Haymon RM, Fornari DJ, Edwards MH, Carbotte S, Wright W, MacDonald KC (1991) Hydrothermal vent distribution along the East Pacific Rise Crest (9°09'–54'N) and its relationship to magmatic and tectonic processes on fast-spreading mid-ocean ridges. *Earth Planet Sci Lett* 104:513–534
- Haymon RM, Fornari DJ, von Damm KL, Lilley MD, Perfit MR, Edmond JM, Shanks WC, Lutz RA, Grebmeier JM, Carbotte S, Wright D, McLaughlin E, Smith M, Beedle N, Olson E (1993) Volcanic eruption of the mid-ocean ridge along the East Pacific Rise crest at 9°45'–52'N: direct submersible observations of seafloor phenomena associated with an eruption event in April, 1991. *Earth Planet Sci Lett* 119:85–101
- Hessler RR, Smithey WM, Keller CH (1985) Spatial and temporal variation of giant clams, tubeworms and mussels at deep-sea hydrothermal vents. *Bull Biol Soc Wash* 6:411–428
- Hessler RR, Smithey WM, Boudrias MA, Keller CH, Lutz RA, Childress JJ (1988) Temporal change in megafauna at the Rose Garden hydrothermal vent (Galápagos Rift; eastern tropical Pacific). *Deep Sea Res* 35:1681–1709
- Hunt HL, Metaxas A, Jennings RM, Halanych K, Mullineaux LS (2004) Testing biological control of colonization by vestimentiferan tubeworms at deep-sea hydrothermal vents (East Pacific Rise, 9°50'N). *Deep Sea Res I* 51:225–234
- Huston M, Smith T (1987) Plant succession: life history and competition. *Am Nat* 130:168–198
- Jollivet D (1996) Specific and genetic diversity at deep-sea hydrothermal vents: an overview. *Biodivers Conserv* 5:1619–1653
- Karl DM (1995) *The microbiology of deep sea hydrothermal vents*. CRC, New York
- Keeton WS, Franklin JF (2005) Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? *Ecol Monogr* 75:103–118
- Le Bris N, Govenar B, Le Gall C, Fisher C (2006) Variability of physico-chemical conditions in 9°50'N EPR diffuse flow vent habitats. *Mar Chem* 98:167–182
- Lee RW (2003) Thermal tolerances of deep-sea hydrothermal vent animals from the Northeast Pacific. *Biol Bull* 205:98–101
- Lenihan HS, Mills SW, Mullineaux LS, Peterson CH, Fisher CR, Micheli F (2008) Biotic interactions at hydrothermal vents: recruitment inhibition by the mussel *Bathymodiolus thermophilus*. *Deep Sea Res* 55:1707–1717
- Lubchenco J (1980) Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology* 61:333–344
- Lutz RA, Shank TM, Fornari DJ, Haymon RM, Lilley MD, Von Damm K, Desbruyères D (1994) Rapid growth at deep-sea vents. *Nature* 371:663–664
- McCook LJ (1994) Understanding ecological community succession: causal models and theories, a review. *Vegetatio* 110:115–147
- Micheli F, Peterson CH, Mullineaux LS, Fisher C, Mills SW, Sancho G, Johnson GA, Lenihan HS (2002) Predation structures communities at deep-sea hydrothermal vents. *Ecol Monogr* 72:338–365
- Mills SW, Mullineaux LS, Tyler PA (2007) Habitat associations in gastropod species at East Pacific Rise hydrothermal vents (9°50'N). *Biol Bull* 212:185–194
- Mullineaux LS, Peterson CH, Micheli F, Mills SW (2003) Successional mechanism varies along a gradient in hydrothermal fluid flux at deep-sea vents. *Ecol Monogr* 73:523–542
- Paine RT (1977) Controlled manipulations in the marine intertidal zone and their contributions to ecological theory. In: Goulden CE (ed) *The changing scenes in natural sciences*. Academy of Natural Sciences, Philadelphia, pp 245–270
- Platt WJ (1999) Southeastern pine savannas. In: Anderson RC, Fralish JS, Baskin JM (eds) *Savannas, barrens, and rock outcrop plant communities of North America*. Cambridge University Press, Cambridge, pp 23–51
- Platt WJ, Connell JH (2003) Natural disturbances and directional replacement of species. *Ecol Monogr* 73:507–522
- Sarrazin J, Juniper SK, Massoth G, Legendre P (1999) Physical and chemical factors influencing species distributions on hydrothermal sulfide edifices of the Juan de Fuca Ridge, northeast Pacific. *Mar Ecol Prog Ser* 190:89–112
- Schoen DJ, Stewart SC, Lechowicz MJ, Bell G (1986) Partitioning the transplant site effect in reciprocal transplant experiments with *Impatiens capensis* and *Impatiens pallida*. *Oecologia* 70:149–154
- Shank TM, Fornari DJ, von Damm KL, Lilley MD, Haymon RM, Lutz RA (1998) Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9°50'N, East Pacific Rise). *Deep Sea Res II* 45:465–515
- Sousa W (2001) Natural disturbance and the dynamics of marine benthic communities. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine Community Ecology*. Sinauer Associates, Sunderland, pp 85–130
- Tolstoy M, Cowen JP, Baker ET, Fornari DJ, Rubin KH, Shank TM, Waldhauser F, Bohnenstiehl DR, Forsyth DW, Holmes RC, Love B, Perfit MR, Weekly RT, Soule SA, Glazer B (2006) A sea-floor

- spreading event captured by seismometers. *Science* 314:1920–1922
- Tunnicliffe V, McArthur AG, McHugh D (1998) A biogeographical perspective of the deep-sea hydrothermal vent fauna. *Adv Mar Biol* 34:355–442
- Underwood AJ, Denley EJ (1984) Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong DR, Simberloff D, Abele LG, Thistle AB (eds) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, Princeton, pp 151–180
- von Damm KL (2000) Chemistry of hydrothermal vent fluids from 9°–10°N, East Pacific Rise: ‘‘Time zero’’, the immediate post-eruptive period. *J Geophys Res Solid Earth* 105:11203–11222
- Wetley DS (1984) Sun and shade mediate competition in the barnacles *Chthamalus* and *Semibalanus*: a field experiment. *Biol Bull* 167:176–185
- Wood DM, del Moral R (1987) Mechanisms of early primary succession in subalpine habitats on Mount St. Helens. *Ecology* 68:780–790