

# Processes and Interactions in Macrofaunal Assemblages at Hydrothermal Vents: A Modeling Perspective

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Our understanding of the biological assemblages at hydrothermal vents is growing rapidly, in part facilitated by the coupling of experimental and observational methods with theoretical modeling efforts. We review theoretical approaches in four main areas, and link them to empirical studies of the biology of hydrothermal vent systems. First, we describe models of dispersal of vent organisms within and among vent sites. These models fall broadly into two categories: those based on larval biology and currents that predict dispersal capabilities from a source, and those using genetic data to address historical genetic links between populations. Then we discuss models for individual and population growth at a location, and give examples from work in a biologically similar deep-sea environment: cold seeps. Third, we address how these two aspects can be integrated using models that couple dispersal and demography. Last, we summarize existing modeling approaches for community succession in other types of habitats, and outline the conceptual models and the sorts of data that currently exist for hydrothermal vent communities. Throughout, we also examine the use of models in improving experimental design.

## 1. INTRODUCTION

The geological setting of hydrothermal vents presents the biological assemblages that inhabit them with several important challenges. First, the physical and chemical charac-

teristics of vent habitats limit their accessibility to relatively few specifically adapted species, and often limit them to a particular type of microhabitat. Second, these habitats can be geologically unstable on annual to decadal timescales and chemically unstable on subannual scales. Individual habitats are subject to destruction by paving, chimney collapse or cessation of hydrothermal flow, as well as other less extreme forms of disturbance such as changes in the chemistry, temperature, or flow paths of the local source of vent fluid. Third, vent sites can be separated by hundreds to thousands of kilometers of habitat that is inhospitable to vent organisms. The difficulties faced by organisms in this extreme, unstable, and patchy habitat are also faced by the researchers attempting to understand their dispersal, establishment, population growth, and the biological communities that result. Observational and experimental studies that would be relatively simple in terrestrial or even shallow-water marine systems are logistically challenging or even impossible in these extreme deep sea habitats. The use of models as a tool to augment empirical efforts has a strong appeal.

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Although modeling of the physical and chemical environment at deep-sea hydrothermal vents is relatively advanced, modeling of biological systems in these locations is in its initial stages. In part, this is the result of a lack of sufficient biological information for many types of models. Although it can be argued that models are difficult, if not impossible, to formulate without adequate biological information, models can, in fact, significantly advance our understanding of these deep-sea systems. For example, by developing alternative models based on our best understanding of the systems, and using insights from other marine systems, it may be possible to assess the likelihood that certain mechanisms and processes explain observed patterns. Where alternative models differ in predictions, we may be able to design studies to assess which model is more plausible. In addition, models can be used to develop or refine the experimental methods used to assess such alternatives. Once a mechanistic understanding is reached, models can also be used to identify important parameters on which to focus more detailed empirical efforts.

The dynamics of deep-sea hydrothermal vent populations and communities are driven by a combination of local population growth and community development within a suitable patch, and the dispersal of organisms between patches. The existence of the patches themselves in the generally nutrient-limited deep sea is a result of microbial primary productivity. Within a patch, spatial and temporal differences in the macrobiological biological communities are tightly tied to chemical and thermal properties of diffuse vent effluent. Models addressing chemical transformations that occur in hot vent fluid and sulfide structures, and the microbial populations that contribute to these transformations, are discussed elsewhere in this volume [Huber and Holden, this volume; McCollom, this volume; Schrenk et al., this volume]. In this paper, we discuss models that focus on four main aspects of the macrobiological communities of these systems. For these models, microbial chemoautotrophic primary production is tied to vent chemistry, although details of chemical transformations that determine the properties of diffuse vent fluid are not considered. First, we discuss models of dispersal, both in general and specifically between suitable habitat patches, including the resultant genetics of the postsettlement population. These spatial aspects have been receiving increased experimental and theoretical attention in recent years, and there is a rich literature on similar processes in terrestrial and shallow marine systems. Second, we consider models of population growth and of energy flow and allocation within individuals at a location, which are only now becoming possible because of our increased understanding of the basic biology of some key vent species. Third, we present a suite of increasingly complex models that incor-

porate both the regional and local processes affecting populations at a variety of spatial and temporal scales. Increasingly complex models that link demography and dispersal are being developed in terrestrial systems [see, e.g., Neubert and Caswell, 2000; Easterling et al., 2000; Jongejans et al., 2008; Skarpaas and Shea, 2007], and clearly many of these can be usefully applied to address vent population and community dynamics. Several ecological studies and long-term observations over the past 15 years have described patterns of community change over time and have begun to explore potential factors that regulate these patterns. In the fourth section, we provide an overview of observations and experiments, and of conceptual models for community succession at hydrothermal vents. Throughout this work, we also address ways in which models can be used to assist in directing research, or in designing empirical studies.

## 2. MODELS OF DISPERSAL

Because of the patchy and ephemeral nature of vents and the high endemism of vent biota, successful colonization of newly formed vent sites can usually only be achieved by long-distance larval dispersal. Dispersal is defined as the movement of diaspores away from their source (sensu Nathan [2001]). A diaspore is the unit of dispersal and may be a whole organism (at any life stage) or part of an organism (e.g., a piece of a modular organism). Because most vent organisms disperse during their larval stage (either through evolutionary constraints or because adults are sessile), we will focus on these early life-history dispersal stages. However, we note that adults of some groups (e.g., fish, crabs, shrimp) are quite motile and may also have limited dispersal potential.

There are three main sequential components to dispersal, which relate to the source of the diaspores, the movement of the diaspores, and the cessation of movement at a destination [Isard and Gage, 2001]. Most vent larvae are effectively free-drifting because they are very small, with relatively little ability to propel themselves over significant distances by swimming. Successful movement between suitable hydrothermal vent habitat patches is a complex process, and depends on interactions between physical flows, particularly deep-sea currents, hydrothermal plume dynamics, and diaspore biology (e.g., larval physiology, buoyancy, and life span), as well as on the availability of suitable habitat once the larvae are ready to settle. The two main approaches that have been used to better understand the mechanisms of animal dispersal between vent sites arise from focusing on either the movement of all diaspores away from a source (be they successful or not), or on successful movement between a source and a particular destination.

## 2.1 Models of Movement From a Source

In models that focus on the movement process, combination of estimates of biological parameters (such as larval abundance, larval development/survival times, fecundity, recruit to adult ratio) and of point estimates of hydrodynamics (used to constrain current speeds and directions) are used to predict the physical displacement of larvae from the time of release until the end of competence (the last stage in larval development before settlement). This estimated displacement is independent of the availability of habitat suitable for settlement at that time; many diaspores disperse without ever reaching suitable habitat and thus are lost. In non-vent marine ecosystems, larval mortality during the dispersal phase of life history can be as high as 90% [Rumrill, 1990]. For the tubeworm *Riftia pachyptila*, Marsh *et al.* [2001] estimated that 61% of larvae would be lost during dispersal through advection off the spreading axis to unsuitable habitats. Even for tubeworm larvae that are retained within the axis, suitable habitat is limited to areas with direct exposure to venting fluid, and consequently only a small percentage of those larvae will successfully settle and colonize.

Different conceptual models of larval dispersal potential have been proposed for spatial scales ranging from between vents within a vent field (10 m–1 km scale), to between vent fields (1–100 km scale) to between ridge segments (100–1000 km scales). At the smallest scale, larval abundance in the water column within a vent field has been measured in a handful of studies on the East Pacific Rise (EPR) and the Juan de Fuca Ridge (JdFR). At all locations, larvae of vent species were more abundant within 5 m of the bottom than at heights >20 m above the bottom [Mullineaux *et al.*, 1995; Kim and Mullineaux, 1998; Metaxas, 2004; Mullineaux *et al.*, 2005]. Abundance may [Mullineaux *et al.*, 2005] or may not [Kim and Mullineaux, 1998; Metaxas, 2004] decrease with distance from the vents up to ~10 km, and the observed pattern has been attributed to hydrodynamics [Metaxas, 2004]. These studies suggest that larval dispersal of many vent species likely occurs near bottom, where the mean direction of advective currents is typically along the axial valley [Mullineaux and France, 1995; Marsh *et al.*, 2001; Thompson *et al.*, 2003].

The intermediate spatial scale (10–100 km) appears to provide a realistic range for along-axis larval dispersal potential within one larval cohort/generation, at least for tubeworms and alvinellid polychaetes. Based on the energy reserves of the egg and the energy requirements for respiration, larvae of the tubeworm *R. pachyptila* can potentially survive in the water column for 38 d [Marsh *et al.*, 2001]. Based on models that used simulated releases of batches of tubeworm larvae from a vent at 9°50'N on the EPR and point measures of cur-

rents collected for the area, Marsh *et al.* [2001] suggested that tubeworm larvae can disperse approximately 90 km along axis within 20 days after release.

In addition to modeling actual dispersal, related models can be used to design optimal strategies for sampling propagules or recruits. For example, in cases where the number of logistically possible sampling stations may be limited, the location of such samples will be critical in providing the most relevant information. Models have been used to address such issues for plant seeds dispersing by wind [Skarpaas *et al.*, 2005; Bullock *et al.*, 2006]. Using a simulation model, a range of possible seed-trap arrangements was tested against a range of plausible dispersal kernels, for scenarios of isotropic and anisotropic diaspore dispersal [Skarpaas *et al.*, 2005]. The trapping designs that consistently recaptured the underlying “true” dispersal kernel distributions were the ones most likely to return useful information on dispersal patterns. Given that some commonly used spatial sampling arrangements performed very poorly in these simulations, assessment of the effectiveness of different sampling designs before sample collection will enable more productive use of limited resources and submersible time.

Using alvinellid polychaetes as an example organism, Chevaldonné *et al.* [1997] utilized a propagule flux model (PFM) to define the range of potential dispersal among all known vent fields between 14°N and 7°N on the EPR. The PFM calculates the number of migrants ( $N_m$ ) that are potentially exchanged in one generation between two randomly chosen populations.  $N_m$  depends on the number of eggs produced per generation in the source population (i.e., produced propagules) and the probability that a dispersing propagule will encounter an active vent while still alive, and it has to equal at least 1 to prevent genetic drift and speciation between populations. Not surprisingly,  $N_m$  decreased logarithmically with increasing duration of dispersal, and fell below 1 after 8 days. Based on the current regime, this duration corresponds to a traveled distance of 8–40 km. Given the spatial separation of known vent fields in this area, the range of potential dispersal is short and only possible within, but not between, sectors [Chevaldonné *et al.*, 1997].

An alternative conceptual model proposed that mesoscale flows, generated by the buoyant plume, can influence larval dispersal on 100 km scales [Mullineaux and France, 1995]. Mesoscale vortices can form in the plume, which are eventually shed downstream. The model proposed that if larvae become entrained and concentrated in the plume, they can be transported in patches in the shed vortex. Kim *et al.* [1994] used a passive tracer to confirm that plume models can be used to estimate larval flux by entrainment. Kim *et al.* [1994] estimate that 100–1000 larvae are entrained per hour and their models suggest that larval concentration in

the spreading plume is 2 orders of magnitude lower than near the bottom.

Given the low probability of larval dispersal between active vent fields suggested by existing models, most larvae within a vent field must be produced locally to sustain populations on ecological time scales [Metaxas, 2004; Van Dover and Lutz, 2004]. Metaxas [2004] measured larval supply at Axial Volcano on the JdFR, using passive larval collectors, and found little spatial variability among vents. She proposed that a homogeneous larval pool existed within the entire vent field, which is formed in large part by retention of locally produced larvae whose dispersal is constrained by local near-bottom hydrodynamics.

### 2.2 Models of Movement Between a Source and a Destination

Models that focus on the links between a source and a destination are only concerned with realized dispersal (i.e., dispersal that also includes successful establishment). Studies utilizing genetic data focus on documenting genetic relationships within and between populations along a ridge axis to examine realized dispersal. Mutations in DNA sequences contain historical information about the demography of species and can be used to test demographic hypotheses. The spatial scale of larval movement determines the genetic structure of populations because adults of most vent invertebrates are sessile or have limited dispersal capabilities.

There is considerable interest in using genetic data to infer population connectivity in the shallow water marine environment. Initially, the lack of obvious physical barriers in the ocean led to the parsimonious expectation of broad larval dispersal and genetically well-mixed populations. In fact, self-recruitment and high local retention of larvae is the rule rather than the exception in many shallow water marine species [Swearer *et al.*, 2002; Jones *et al.*, 2005]. Distinct genetic subpopulations have been documented empirically for many marine species (e.g., reef fish [Taylor and Hellberg, 2003]; Atlantic cod [Pogson *et al.*, 2001]; corals [Baums *et al.*, 2005]; and barnacles [Sotka *et al.*, 2004]) and likely arise from critical breaks in larval movement due to current patterns at the time of dispersal, even in species with relatively long larval duration. Models suggest that larval behavior may in part explain local retention [Kingsford *et al.*, 2002]. Biophysical models have been used to constrain the spatial extent of ecologically relevant larval dispersal [James *et al.*, 2002; Cowen *et al.*, 2006] and confirm that the interaction of currents and larval biology can lead to such genetically rich patterns.

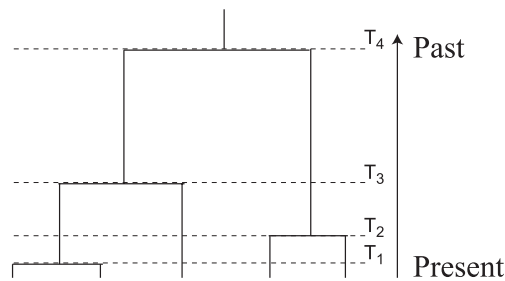
The relationship between physical and geological processes (e.g., ocean circulation and birth/death of vents), ge-

netic diversity within vent populations, genetic divergence between populations, and total metapopulation diversity is complex. Nevertheless, population geneticists have made considerable progress toward developing genetic models that incorporate population structure and the dynamics of extinction/recolonization processes. Substantial progress also has been made in the development of statistical methodologies to estimate parameters, test hypotheses, and determine model adequacy under structured population models [Beerli and Felsenstein, 2001; Nielsen and Wakeley, 2001; Hey and Nielsen, 2004; Young *et al.*, 2008]. The development of coalescent theory over the last 20 years has contributed immensely to this progress [Hudson, 1990; Rosenberg and Nordborg, 2002].

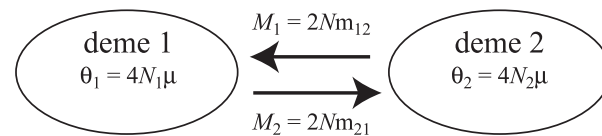
Coalescent theory focuses on modeling samples of DNA sequences rather than entire populations. Just as the birth and death of species is a branching process, the birth and death of individuals in a population is a branching process. Thus, the relationships among individuals in a sample can be represented by a genealogy composed of the branching order of individuals and ancestors, as well as the times that they first share a common ancestor (Figure 1a). Coalescent theory predicts the structure of sample genealogies under various demographic scenarios, where a species' demography might include population number and sizes, dispersal rates, and extinction/recolonization rates. The particular configuration of mutations in DNA sequences is the result of mutations that randomly accumulate along this genealogy. Therefore, coalescent theory links DNA sequence data to model parameters of interest through the stochastic ancestral and mutation processes. Using this theory, we can extract historical information about demography from genetic data.

Genetic models generally operate on a time scale of  $N$  generations, where  $N$  is the total number of individuals in a population. Because many factors (e.g., rapid population fluctuations or a high variance in reproductive success) affect the time scale, geneticists refer to  $N$  as an effective population size. In many cases, this time scale might be millions of years [e.g., Johnson *et al.*, 2006]. Coalescent-based genetic estimates of dispersal are averages over thousands to millions of generations, unlike the ecological models previously discussed that generally focus on dispersal over one or a few generations. In addition to the vastly different temporal scales of the direct and indirect approaches, genetic homogeneity of populations is achieved if populations exchange as few as tens of migrants per generation [Wright, 1931]. Therefore, although population connectivity in the ecological sense can be quite low, populations may appear genetically homogenous [e.g., Becker *et al.*, 2007]. In addition, species with strongly leptokurtic dispersal kernels (i.e., with a probability distribution of dispersal distances that has

## Q2 A) Genealogy



## B) Demographic parameters



**Figure 1.** (a) Genealogy composed of branching order and times of ancestor events ( $T_n$ ). Coalescent theory models genealogies as a reverse-time Markov death process on the number of ancestors in the sample. The waiting times are exponentially distributed and depend on the demographic parameters of the model. DNA sequence mutations are then scattered on the genealogy in proportion to the branch lengths. See *Hudson* [1990] for a detailed treatment of coalescent theory. (b) Demographic parameters in a simple two-deme genetic model.

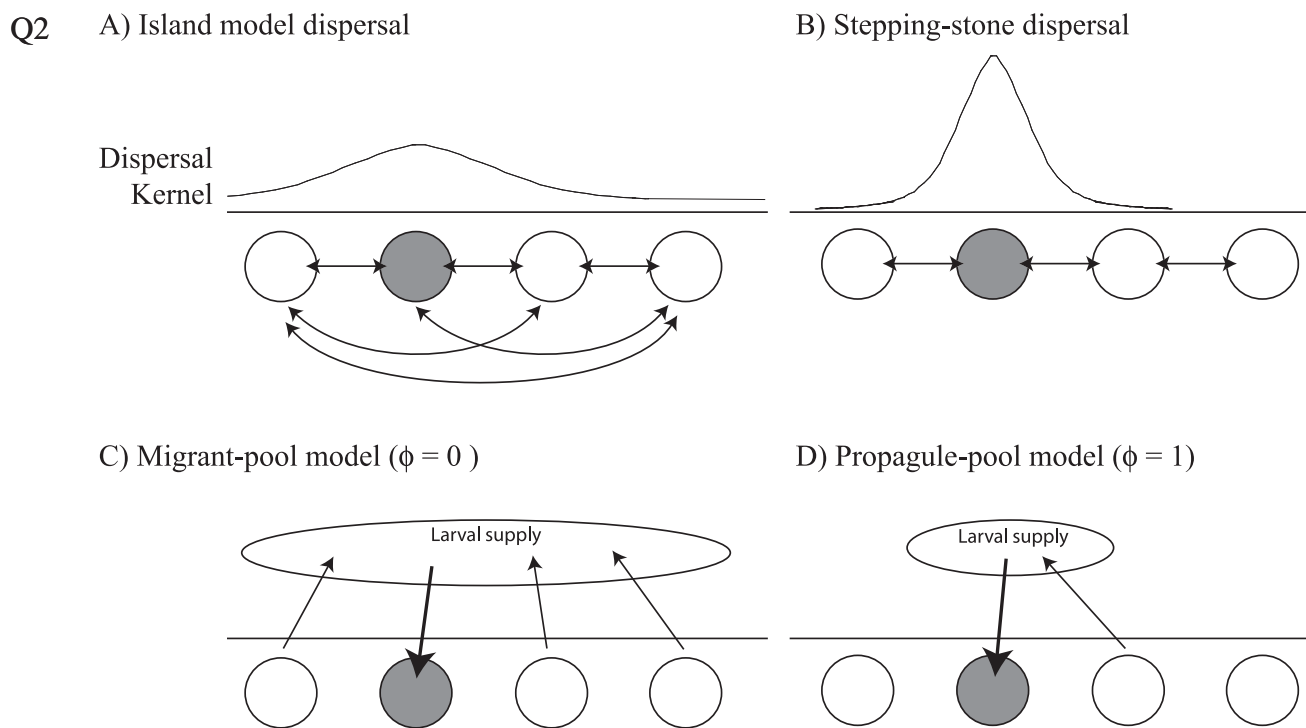
fatter tails and narrower peaks than the normally distributed equivalent, as in Figure 2a) will generally exhibit genetic differentiation indicative of high dispersal, even if average dispersal distances are considerably lower [Kinlan and Gaines, 2003]. Genetic- and invasion-based estimates of dispersal distances for marine taxa often substantially exceed direct estimates of dispersal distances [Kinlan and Gaines, 2003]. Genetic estimates can also be influenced by infrequent or sporadic dispersal events due to the small amount of genetic exchange necessary to homogenize populations [Slatkin, 1987]. For these reasons, ecological and genetic estimates of dispersal offer complimentary information about dispersal processes.

Models of genetic variation in structured populations (i.e., nonrandomly mating) have been extensively studied [Donnelly and Tavaré, 1995]. A structured population consists of a number of demes of size  $N$ , where a deme is a local, randomly mating population.  $N$  is estimated from genetic data, which cannot distinguish the effect of mutation rate from that of population size on levels of genetic diversity. Therefore, the population size of deme  $i$  is represented by the composite parameter,  $\theta_i = 4N_i\mu$ , where  $\mu$  is the per-gene per-generation mutation rate. The number of immigrants entering deme  $i$  is  $M_i = 2Nm_{ij}$ , where  $m_{ij}$  is the proportion of immigrants in deme  $i$  arriving from deme  $j$  in each generation (Figure 1b). We can compare population sizes among demes by comparing estimates of  $\theta_p$ , because we assume that the mutation rate is the same among populations. Alternately, we can use prior estimates of mutation rates to determine the absolute sizes of populations. To measure dispersal, we are interested in comparing estimates of  $M_i$  among different populations.

One fundamental test of dispersal involves the discrimination between island and stepping-stone models of dis-

persal (Figures 2a and 2b). The island model assumes that immigrants arriving in any deme are drawn from a well-mixed larval pool (i.e.,  $M_i$  is equal for all demes). In other words, immigrants are equally likely to arrive from any of the demes in the metapopulation so that dispersal occurs on about the same spatial scale as the entire metapopulation. Alternatively, migration might only occur between adjacent demes, such that demes act as stepping-stones for migrants (i.e.,  $M_i$  is appreciable only for adjacent demes). In this case, dispersal occurs on a much smaller spatial scale than that of the metapopulation, and a pattern of isolation by distance arises [Wright, 1943]. The stepping-stone model predicts that genetic divergence between populations (measured by  $F_{ST}$ ) will be correlated with geographical distance among populations, whereas the island model predicts no such correlation. The likelihood of rejecting the island model depends on several factors including the spatial distribution of demes comprising the metapopulation, the mutation rate of the genetic loci under consideration, the migration rates among demes, the spatial scale of sampling (i.e., 2–5 times the average dispersal distance of the species), the overall magnitude of genetic divergence relative to sampling error in the study, and critically, whether the metapopulation has reached an equilibrium between gene flow and genetic drift [Slatkin, 1993; Palumbi, 2003].

The island model has been tested in several vent endemic species [Van Dover *et al.*, 2002; Vrijenhoek, 1997]. Some vent species show evidence for stepping-stone dispersal. The genetic population structure of the tubeworm *R. pachyptila* [Black *et al.*, 1994], the amphipod *Ventiella sulfuris* [France *et al.*, 1992], and the mussel *Bathymodiolus thermophilus* (Won *et al.* [2003]; but see Craddock *et al.* [1995]) along the EPR fit the stepping-stone model of dis-



**Figure 2.** Genetic models of dispersal (a and b) and colonization (c and d). (a) The island model assumes that all demes (circles) exchange migrants. The arrows in the figure denote this connectivity. The hypothetical dispersal kernel in the figure depicts the distribution of larvae produced by the gray deme. (b) The stepping-stone model assumes that the only appreciable migration occurs between adjacent demes. The arrows in the figure denote this limited connectivity. The hypothetical dispersal kernel in the figure depicts the distribution of larvae produced by the gray deme. (c) The migrant-pool model assumes that colonists arriving in the gray deme are drawn from the entire metapopulation, similar to the assumption in the island model that immigrants can originate in any deme. (d) The propagule-pool model assumes that colonists arriving in the gray deme are drawn from a single deme in the metapopulation.

persal. However, other vent invertebrates appear to follow the island model, such as the clam *Calymptogena magnifica* [Karl *et al.*, 1996], as well as two species of archaeogastropods [Craddock *et al.*, 1997] on the northern EPR. The horizontal distance represented in these studies far exceeds our current estimates of the dispersal range of a single larva based on the ecological models discussed in the previous section. However, for these species the genetic data suggest that colonization on these scales is either not limited by larval dispersal, or more likely, one or more of the issues discussed above (i.e., statistical power due to sampling or whether the metapopulation has achieved drift-migration equilibrium) affects these species. Extinction and recolonization can also affect the degree of genetic divergence among populations [Slatkin, 1977; Whitlock and McCauley, 1990; Pannell and Charlesworth, 2000]. These processes may well affect estimates of migration rates between

populations as well as alter the likelihood of rejecting the island model of dispersal.

Two fundamental genetic models [Slatkin, 1977] of extinction/recolonization process exist that differ in how populations are colonized, although others have been examined in the literature [Pannell and Charlesworth, 2000; Wakeley, 2004]. These two models assume a constant number of occupied demes in the metapopulation. Under this assumption, a deme is immediately recolonized after an extinction event that occurs with some probability,  $e$ , per generation. The migrant-pool model (Figure 2c), assumes that  $k$  colonists are randomly sampled from the entire metapopulation, whereas in the propagule pool model (Figure 2d), colonists are randomly sampled from a single deme. Whitlock and McCauley [1990] generalized these two models by introducing a parameter,  $\phi$ , describing the probability that two genes in the colonists come from the same deme. Assuming an infinite number

of demes in the metapopulation and island-model migration, they determined that population divergence (measured by  $F_{ST}$ ) will be decreased under recurrent extinction if:

$$k > \frac{2N_m}{1-f} + \frac{1}{2}, \quad (1)$$

where  $\phi = 0$  and  $\phi = 1$  correspond to the migrant- and propagule-pool models, respectively. If larvae from more than a single deme colonize new demes (i.e.,  $\phi > 0$ ) and  $k$  is larger than approximately twice the number of migrants arriving in the deme per generation, then population divergence will be reduced by recurrent extinction. Low population divergence has been observed over broad geographic regions in some vent taxa [Craddock *et al.*, 1995, 1997; Won *et al.*, 2003; Hurtado *et al.*, 2004; Johnson *et al.*, 2006; Young *et al.*, 2008]. The high rate of extinction/recolonization at hydrothermal vents suggests that, if the above conditions apply, we should expect less genetic differentiation among populations of vent taxa than that predicted by restricted migration alone. Consequently, applying models that ignore the effects of extinction and recolonization will overestimate dispersal ability. However, we currently know very little about the ratio of the number of immigrants to the numbers of individuals colonizing new vents, whether colonists arrive from multiple sources, or even the rates of extinction of vent communities.

Genetic studies conducted thus far in hydrothermal vent systems use coalescent models that do not explicitly include extinction/recolonization dynamics, because the statistical methodology to fit these models has not yet been developed. However, results from structured models have been carefully interpreted in light of theoretical results from extinction/recolonization models [e.g., Won *et al.*, 2003; Johnson *et al.*, 2006; Young *et al.*, 2008]. Future work will undoubtedly benefit from the ability of these newer models to distinguish the effects of dispersal from those of extinction/recolonization dynamics [Wakeley and Aliacar, 2001]. Clearly, ecological estimates of dispersal distances, comparisons of recruitment rates in new and established sites, and information on the frequency of habitat turnover in these systems will help clarify the roles of these processes in shaping the distribution of genetic variation in these systems.

Often, bathymetric features, such as the Easter Microplate or transform faults, are associated with significant genetic divergence of vent species, although these features affect species dispersal to varying degrees. In these instances, the application of genetic and ocean circulation models has clarified the nature of these boundaries and helped to point to mechanisms responsible for reduced dispersal or species isolation. *B. thermophilus* populations north and south of the Easter Microplate are genetically isolated from each other

[Won *et al.*, 2003]. Significant cross axis currents produced by the inflated bathymetry of the Easter Microplate were hypothesized to limit dispersal in this mussel species [Won *et al.*, 2003]. In contrast, there is no significant genetic differentiation among populations of either the worm that lives commensally in the mantle cavity of this mussel or among populations of the Pompeii worm *Alvinella pompejana* separated by the Easter Microplate [Hurtado *et al.*, 2004]. The tubeworms, *R. pachyptila* and *Tevnia jerichonana* also seem to traverse the Easter Microplate region more easily than *B. thermophilus*, although significant genetic divergence is observed for these species [Hurtado *et al.*, 2004].

Similar patterns have been observed for some species in the northeast Pacific. A striking example is that of the limpet *Lepetodrilus*, where gene flow was so restricted that speciation has occurred across the Blanco transform fault, resulting in *Lepetodrilus fucensis* occurring to the north and *L. gordensis* to the south of the fault [Johnson *et al.*, 2006]. Although the authors of this study have suggested that major bathymetric barriers can inhibit dispersal, the effect of barriers of similar magnitude is inconsistent, and thus the mechanism of inhibition remains unclear. Recently, deep-ocean circulation was explicitly implicated in the genetic subdivision of the tubeworm *Ridgeia piscesae* across the Blanco transform fault [Young *et al.*, 2008]. These authors proposed that bathymetry and the predominantly southern direction of ocean currents facilitate greater migration (and consequently gene flow) southwards than northwards across the fault (i.e.,  $M_{GOR} > M_{JDF}$ ). Interestingly, the genetic diversity of both the limpets and the tubeworms is higher on the Gorda than the Juan de Fuca Ridge (i.e.,  $\theta_{GOR} > \theta_{JDF}$ ), possibly because populations on the heavily sedimented Gorda Ridge experience fewer extinction events. However, given the complex relationship between demographic parameters and metapopulation effective size, this hypothesis should be tested by multidisciplinary studies.

The application of genetic models to the study of demography in hydrothermal vent systems has significantly increased our understanding of realized dispersal in these organisms. This progress has benefited greatly from the development of statistical methodologies that allow tests of model predictions and even direct tests between simple models in a likelihood or Bayesian framework. Although statistical methodologies have not yet been developed for some of the more complex genetic models, these methods will undoubtedly become commonplace in the near future. Bayesian inference is particularly promising in that genetic data can be coupled with prior information from ecological estimates of the number of colonists ( $k$ ), and the frequency of habitat turnover in these systems ( $e$ ).

### 3. MODELS OF INDIVIDUAL AND POPULATION GROWTH FOR A SINGLE SPECIES

Modeling growth of individuals and populations at a location can be achieved by using a variety of different growth models. This may be particularly informative if applied to keystone species or ecosystem engineers that provide key habitat and alter nutrient flows to improve habitat suitability for additional species. For example, matrix models [Caswell, 2001] have been developed to describe and project the dynamics of a key species at a location. One such study focuses on the numerically dominant limpet *L. fucensis* on the JdFR (Kelly and Metaxas, in preparation). Life history parameters that are incorporated in these population models, such as growth, fecundity, and mortality, are quantified from empirical data collected at vents in Axial Volcano (Kelly and Metaxas, in preparation). The frequent use of matrix models in the terrestrial literature [e.g., Shea *et al.*, 2005] and shallow marine literature [e.g., Crouse *et al.*, 1987] suggests that such applications will likely become more common. Integral projection models, which include continuous demographic variables (such as size of individuals), have also recently been developed [Easterling *et al.*, 2000; Ellner and Rees, 2006].

One extremely promising approach is the use of dynamic energy budget (DEB) models, which model energy flow and allocation within individuals [Kooijman, 1993, 2000]. Originally developed for toxicological studies, they have proven useful over a range of situations (e.g., *Daphnia* growth, insect development; Kooijman [2000]) and at a variety of organizational levels. Excitingly, they allow metabolic processes to be scaled up through individual growth patterns to population and community level dynamics [Nisbet *et al.*, 2000]. These models can be used to improve our understanding of the basic biology of foundation species in vent ecosystems, such as the tubeworms in the Eastern Pacific or the pandemic bathymodiolid mussels. In addition, these models can be used to quantify the role of these species (which also are dominant in terms of biomass) in energy and nutrient cycling, both within the vent ecosystems and in the export potential to the surrounding deep sea.

The laws of thermodynamics apply to all living organisms, and the principle of conservation of energy means that we can model an individual by accounting for all its energetic inputs and outputs. DEB models examine how the energy acquired by an individual is allocated to maintenance, growth and development, and reproduction (Figures 3 and 4). Such models are dynamic, and comprise a series of coupled differential equations linking different processes within the individual, which can be investigated either analytically or numerically. In the models, energy is assimilated

and utilized by the individual. Where there are alternative hypotheses regarding the order of allocation to different requirements, alternative models can be developed. For example, in one plausible scenario (Figure 4a), maintenance demands are met first and then the remaining energy is allocated proportionally to growth or to reproductive processes. In another scenario (based on the  $\kappa$ -rule model of Kooijman [2000]; Figure 4b), a set proportion of energy is allocated to growth and maintenance (with maintenance requirements being met first), while the remaining proportion is allocated to reproductive development or output. In the latter case, energy flux is modeled so that reproduction may continue even when growth has ceased, while in the former case, both processes co-occur. The true state of affairs would be difficult to assess directly, but differences in model predictions (e.g., predicted size at maturity in different energy flow regimes) can then be used to distinguish between such alternatives and hence to improve our mechanistic understanding. Once developed, the DEB models can be integrated across size and age classes and applied to questions of population and community level dynamics, for example, to estimate the primary and net exported productivity of the communities in these deep-sea environments.

This broad type of approach has been used successfully for tubeworm aggregations at cold seeps [Cordes *et al.*, 2003, 2005]. First, the model quantified the levels of sulfide supply necessary to meet the physiological requirements of the aggregations, by incorporating growth, recruitment and metabolic rates, symbiont metabolism, substrate concentrations, diffusion gradients, and kinetics [Cordes *et al.*, 2003]. The models were then used to examine several alternative mechanisms for the production and supply of sulfide to the interstices of the buried posterior portions of worms [Cordes *et al.*, 2005]. Surprisingly, the models indicated that the natural sulfide production in, and fluxes from, the sediment were not sufficient to sustain large tubeworm aggregates to the ages observed at hydrocarbon seeps. However, when sulfate release (sulfate is one end-product of chemoautotrophic sulfide oxidation by the tubeworm symbionts) through the tubeworm's posterior rootlike extensions into hydrocarbon-rich sediments was invoked, sufficient sulfide was produced to allow the model aggregations to persist for centuries. As a result, sulfate release by the tubeworm roots was investigated and has now been confirmed empirically [Dattagupta *et al.*, 2006]. For any model, sensitivity analyses indicate those parameters with the greatest influence on the system, and can direct the collection of data which otherwise may be overlooked. Importantly, sensitivity analyses of these models guided some of the empirical data collection (such as root length), which were subsequently used to better refine the models.

Q2

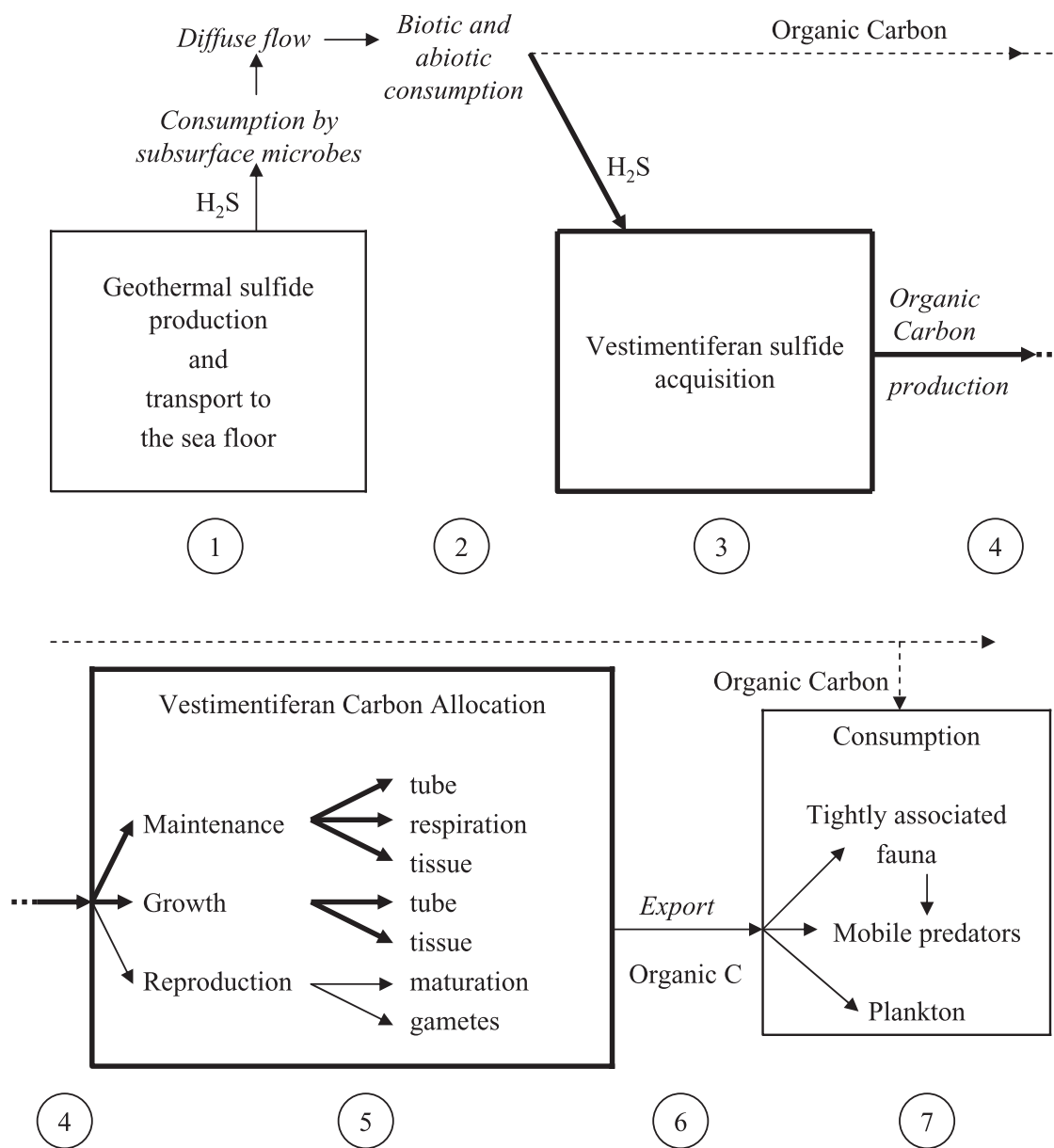


Figure 3. Modeling framework for the study of EPR vestimentiferan communities.

Q2

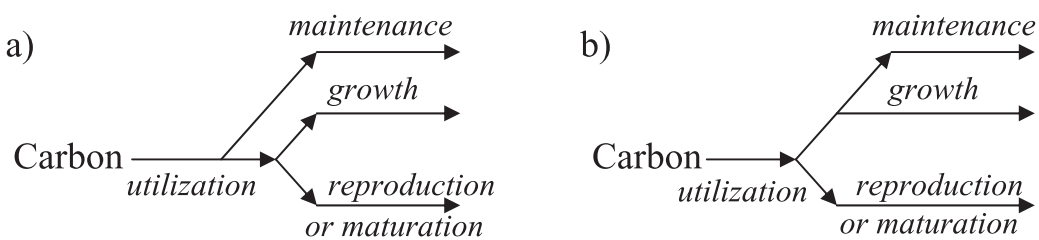


Figure 4. Examples of alternative models for box 5 in Figure 3.

The application of models such as those described above to individuals, populations, and communities at spreading centers would be an obvious and exciting next step. This will require some empirical advances; vent communities exist in a much more spatially and temporally complex environment than seep communities and will require finer scale data collection. However, continuing advances in our ability to survey, monitor, and sample appropriate variables on appropriate scales will enable the next generation of vent models.

#### 4. COUPLED DEMOGRAPHIC AND SPATIAL MODELS

To understand and describe the dynamics of species and communities at landscape scales, models for movement between suitable habitat patches and for growth of individuals, populations, or communities at a location must be combined. There are several axes along which model complexity can be varied: the spectrum from nonspatial, through pseudo-spatial to explicitly spatial models; the shift from single species models, through models with two or a few species, to models that consider whole communities; and the increase in demographic considerations from simple documentation of presence or absence, through models of abundance, to models that include complex demography. Even when considering one species at a time, a fairly complex matrix of possible combinations of levels of detail is possible [e.g., *Jongejans et al.*, 2008]. In the next two sections, we review a few of the most relevant model types, and span these axes, but do not attempt to be exhaustive.

The simplest models that include both demographic and dispersal elements are metapopulation models [*Levins*, 1969; *Hanski*, 1982], commonly used to model the dynamics of patchy terrestrial and marine systems. For a single vent species, the simplest metapopulation models would involve a pseudo-spatial (i.e., space is considered, in that habitat is divided into suitable and unsuitable patches, but exactly where those patches are located is not defined) network of interconnected patches and movement between patches formulated in a relatively simple form. The patches are either occupied by the focal species or not, patches go extinct at a rate determined by geological activity and are colonized at a rate determined by a simple dispersal parameter. Clearly, this approach is highly simplistic, but it incorporates the essential features of local dynamics and between-patch dispersal that underlies more complex models. Patch-occupancy models can be applied where patch states are usually defined by the presence or absence of the species (not its abundance). Documenting species abundances is more complicated, but certainly feasible, and is relatively straightforward for simpler communities. Metapopulation models with specified dis-

persal between patches have also been developed [*Hanski et al.*, 1996]. However, metapopulation models of the underlying variation in the patches themselves are less common [e.g., *Nee and May*, 1992].

A metapopulation model (GENEFLUX) has been used to describe the population dynamics of the alvinellid polychaete *A. pompejana* in the vent fields between 14°N and 7°N on the EPR [*Jollivet et al.*, 1999]. The model incorporated interconnected subroutines of population structure, propagule flux (PFM, as in *Chevaldonné et al.* [1997]), genetic drift, and vent site spatial and temporal dynamics. The goal was to examine the effect of vent instability (extinction and activation, modeled as relocation) on long-term (thousands of generations) population structure of alvinellids. Population genetic structure (allele frequency) was modeled by using a series of juvenile and adult mortality-affected “boxes,” each simulating a single cohort, with multiple adult cohorts contributing to a single migrant pool per generation. Genetic drift was modeled as the probability distribution of the frequency of a particular allele in every set of migrants, given migrant abundance and initial allele frequency. Randomly selected vents were “relocated” (one vent would shut down and another start up) every 40 generations at locations constrained by one of four modes, each representing a different conceptual model for vent site propagation. The model showed that vent “relocation” can affect metapopulation size, migrant fluxes and thus gene flow, allele fixation and genetic drift, and extinction [*Jollivet et al.*, 1999]. The authors concluded that, within hydrothermally active areas on a ridge crest, local populations are strongly interconnected, whereas between sectors recolonization cannot theoretically balance extinction by propagule dispersal, unless spatial redistribution of hydrothermally active zones over time is also considered.

Spatial detail can also be combined with models of a species’ abundance using reaction-diffusion models [*Fisher*, 1937; *Skellam*, 1951; *Shigesada and Kawasaki*, 1997; *Okubo and Levin*, 2001], although analytical versions assume homogeneous space. The number of individuals,  $n$ , at location  $x$  at time  $t$  depends on the growth of an unstructured population with intrinsic growth rate,  $r$ , carrying capacity,  $K$ , and with movement defined by the diffusion coefficient,  $D$ :

$$\frac{\partial n(x, t + 1)}{\partial t} = rn \left(1 - \frac{n}{K}\right) + D \frac{\partial^2 n(x, t)}{\partial x^2} \quad (2)$$

Such models ignore demographic complexity, and require the addition of asymmetry (advection-diffusion models) to model anisotropic movement in currents.

Integrodifference equation models for the spread of structured populations (based on matrix population models) [Neubert and Caswell, 2000; Neubert and Parker, 2004] have recently been developed. These models allow certain life history stages to disperse, while others remain stationary, providing a considerable improvement over demographically unstructured models. This is particularly important in the deep sea, where sessile adults may be long-lived with respect to the dispersive larval stage. In these models, the number of individuals,  $n$ , at location  $x$  at time  $t$  depends on the growth of the population as defined by a population projection matrix  $B_n$  and a dispersal kernel,  $K$ , of movement over space.

$$n(x, t + 1) = \int_{-\infty}^{\infty} [K(x, y) \circ B_n(y)] n(y, t) dy \quad (3)$$

Additional biological and spatial complexity can be incorporated into models, but usually at the cost of reduction in analytical rigor for simulation approaches. Although cellular automata and individual-based models can incorporate great amounts of biological and spatial information, this must be done numerically, and hence they can also be very time-consuming. However, given the interaction of the biological with the chemical and physical environment at vent systems, and their extreme spatial heterogeneity, such complexity is warranted. These models are also heuristically more accessible than extremely complex analytic models. Models of disturbance, in particular, lend themselves well to individual-based modeling approaches [e.g., Roxburgh *et al.*, 2004], where different aspects of disturbance (frequency, extent, duration, timing, and intensity) can be addressed for any number of species.

## 5. MODELS OF COMMUNITY SUCCESSION

Scaling up to multiple species can be computationally challenging. If only species richness is of interest, models based on the theory of island biogeography [MacArthur and Wilson, 1967] are pertinent. Under the assumption that patch persistence is greater than the generation time of the organisms concerned, models of species richness based on patch size and isolation can be developed; smaller, isolated patches are expected to have fewer species. Lower-than-expected species richness would point to recent disturbances.

Metacommunity models shift the focus from a simple description of species richness to explicitly documenting which species are present. An important contribution in this area used a multispecies metapopulation modeling approach to address observed patterns of species diversity at vent sys-

tems [Neubert *et al.*, 2006]. This metacommunity model addressed facilitation-driven succession, where the state is no longer the presence or absence of a single species, but an inventory of all species in a patch. For a single species, two patch types are of interest: occupied or unoccupied. For two species, four patch types are pertinent: empty patches, patches with the first or the second species only, or patches with both. Clearly, as the number of species increases, the number of possible states increases rapidly, and this makes modeling the transitions in diverse community computationally challenging. Neubert *et al.* [2006] approached this problem by using a successional hierarchy to simplify the state space enough to make it tractable.

Matrix models, similar to those used for modeling population growth described above, have also been used to model succession. Whereas in population models the states are ages or life history stages of individuals, in successional models they represent different states of the community, and transitions between them represent probabilities of switching between community types. Most are first-order Markov models and thus assume that only the current state affects the transition probabilities, and that prior history is unimportant. Such models have a relatively long pedigree in terrestrial ecology [Waggoner and Stephens, 1970; Horn, 1975; Usher, 1979; Cooke, 1980; McAuliffe, 1988] and can incorporate the three main conceptual models of succession: facilitation, inhibition, tolerance [Gotelli, 2001], in which late successional species are facilitated by, inhibited by, or indifferent to earlier successional species, respectively. Some of the most detailed and thorough of these models have been developed for shallow marine systems [Tanner *et al.*, 1994, 1996; Wootton, 2001; Hill *et al.*, 2002, 2004]. Models of community succession are still relatively rare for deep-sea systems, and to date have been predominately conceptual. However, because empirical data are relatively abundant and successional processes are critical, the development of relevant successional models is likely to be rapid and productive.

The geological instability of hydrothermal vents on ecological time scales (decades) can cause the complete destruction of the assemblages that occupy them by repaving the substratum with fresh lava flows. Recovery (or reestablishment, depending on the extent of destruction) of the disturbed assemblages depends on: (1) distance to neighboring populations operating as larval sources, (2) successful colonization, and (3) intra- and interspecific interactions. Despite the presumed frequency of occurrence of these events, there have only been three opportunities when both the disturbance (eruption) and the subsequent primary community succession were recorded: at the 9–10°N sector of the EPR in 1991 [Haymon *et al.*, 1993; Shank *et al.*, 1998] and in

2006 [Tolstoy *et al.*, 2006]; ongoing biological studies), and at CoAxial Seamount on the JdFR in 1993 [Embley *et al.*, 1995; Tunnicliffe *et al.*, 1997]. Thus, our measures of primary succession from the onset of colonization of the newly created substrate at these habitats are limited. In contrast, we are rapidly increasing our understanding of processes and regulating factors involved in secondary succession following less destructive changes, such as changes in vent effluent chemistry and small-scale changes in hydrothermal flow patterns.

Repaving events occur at spatial scales of 100s m<sup>2</sup> to <10 km<sup>2</sup>, and well within the range of larval dispersal from neighboring populations [Chevaldonné *et al.*, 1997; Marsh *et al.*, 2001]. In 1991, several newly formed hydrothermal vents were discovered between 9°45'N and 9°52'N on the EPR [Haymon *et al.*, 1993]. The number of colonizing species visible in time-lapse imagery increased incrementally over the recovery period, and was equal to 73% of the regional species pool within 5 years after the eruption [Shank *et al.*, 1998]. Because potential larval sources for colonizers were at distances ranging from 30 to 1450 m [Shank *et al.*, 1998], the successional sequence was most likely not limited by larval availability. At the CoAxial segment of the JdFR, the tubeworm *R. piscosea* and the polychaete *Paralvinella pandorae* had colonized the newly formed Floc Site within 1 year of the eruption and perhaps as early as 7 months after eruption [Tunnicliffe *et al.*, 1997]. The number of mega- and macrofaunal species present 2 years after the eruption was >75% of the regional species pool [Tunnicliffe *et al.*, 1997]. In contrast to 9°50'N, the nearest known extant vents that could have provided a source population were 15–18 km from the eruption site at CoAxial Segment [Tunnicliffe *et al.*, 1997]. These studies suggest that, given the spatial scales of repaving events, larval availability does not limit recolonization of hydrothermal vent habitats, even after complete destruction of the assemblage.

Although sufficient data for quantitative models of colonization and succession are not available for vent communities, robust conceptual models have been developed. Successful colonization during primary and secondary succession depends both on fluid chemistry and local biological interactions. In established communities (i.e., in the absence of a repaving event), rates and patterns of colonization have been measured experimentally at vents in the Galapagos Spreading Center (GSC), EPR, and JdFR by deploying panels or blocks of natural substrate (either slate or basalt), or artificial aggregations of tubeworms over 1- to 5-year periods. Colonization rate is initially (in first month) slow, but increases over several months to a year, leading to spatially variable patterns in abundance among vents [Van Dover *et al.*, 1988; Kelly *et al.*, Spatial and temporal patterns in colo-

nization of deep-sea hydrothermal vent invertebrates on the Juan de Fuca Ridge, NE Pacific, submitted to Marine Ecology Progress Series, 2007, hereinafter referred to as Kelly *et al.*, submitted manuscript, 2007]. This spatial variability can decrease over periods >1 year, as the communities become more similar. Abundance and diversity of colonizers typically decreases with increasing distance from the vents [Van Dover *et al.*, 1988; Govenar and Fisher, 2007; Kelly *et al.*, submitted manuscript, 2007], but colonizers can be found outside the range of adults of the same species [Mullineaux *et al.*, 1998; Govenar and Fisher, 2007]. The physicochemical characteristics of the vent fluid can influence these colonization patterns [Mullineaux *et al.*, 1998], particularly by broadly constraining colonization through physiological tolerance. However, it appears that biological processes play a significant role in fine-tuning these patterns within the imposed bounds [Kelly and Metaxas, 2006; Kelly *et al.*, submitted manuscript, 2007].

Biological processes (both positive and negative interactions) have been shown to influence patterns of colonization exists for 9°50'N on the EPR [Mullineaux *et al.*, 2003], and Axial Volcano and Endeavour on the JdFR (Kelly *et al.*, submitted manuscript, 2007). At the EPR, the fauna at hydrothermal vents show a distinct biological zonation with respect to fluid flux [Hessler *et al.*, 1985]. Mullineaux *et al.* [2003] found that on the periphery of areas of active vent fluid flux (dominated by suspension feeders), positive biological interactions influenced colonization, such as facilitation of sessile colonists by conspecifics [Mullineaux *et al.*, 2003]. In contrast, where diffuse fluid flux was greatest (and tubeworms dominated), negative interactions, such as bulldozing of colonists by mobile species and space limitation by the settlement of sessile species, influenced colonization. At JdFR, although faunal zonation relative to the gradient in fluid flux is not as distinct as at the EPR, particular assemblages are associated with certain physicochemical conditions [Sarrazin *et al.*, 1999]. On the JdFR, both positive (e.g., gregarious settlement for the polychaete *Amphisamytha galapagensis*) and negative (e.g., early recruitment mortality for the numerically dominant gastropod *L. fucensis*) interactions influenced colonization (Kelly *et al.*, manuscript submitted, 2007).

Positive biological interactions during colonization also appear to be important drivers of the patterns of primary succession examined at 9°50'N. After the 1991 eruption, community succession was directed, and associated with changes in fluid chemistry and flow [Shank *et al.*, 1998]. In the first year, dense microbial material was either expelled from the orifices or formed a dense mat on the substratum. *T. jerichonana* had colonized within 12 months, and *R. pachyptila* within 32 months, mostly in areas with existing dense populations of *Tevnia* [Shank *et al.*, 1998]. Mullineaux *et al.* [2000] proposed

a conceptual facilitation model to explain the successional pattern of tubeworms at this site. Using colonization blocks early in the successional sequence (3–4 years after the eruption), they found that *Tevnia* colonized in the absence of other species, but *R. pachyptila* and *O. alvinae* (another tubeworm) did not colonize in the absence of *Tevnia*. However, during a later successional stage in the same area (7–9 years after the eruption), *Riftia* colonized blocks in the absence of *Tevnia* [Hunt *et al.*, 2004]. Hunt *et al.* [2004] proposed that facilitation by *Tevnia* may only be relevant in the early stages of community succession, when the more abundant *Tevnia* may be providing a stronger cue. Such positive interactions have been shown to be critical in terrestrial succession [Chapin *et al.*, 1994], in coastal waters [Harris *et al.*, 1984], and in intertidal communities [e.g., Turner, 1983]. They are highly likely to be key in other vent communities as well.

The conceptual model for succession in established communities of sulfide edifices at the JdFR proposes that the chemical environment is the main driver, and biological processes are only important at certain stages [Sarrazin and Juniper, 1999]. The assemblages that inhabit sulfide edifices are extremely variable on spatial scales of tens of centimeters to meters and in annual temporal scales [Sarrazin *et al.*, 1997; 1999; Govenar *et al.*, 2002]. Each of the five distinct assemblages (I–V) that were described was associated with a particular temperature/fluid flow regime and, accordingly, assigned to a stage in the successional sequence of the community [Sarrazin *et al.*, 1997; 1999]. Observations over a 4-year period indicated that transitions between any pair of assemblages are possible [Sarrazin *et al.*, 1997], and a dynamic succession model has been proposed to describe these transitions [Sarrazin and Juniper, 1999]. Based on their model, most transitions occur as a result of changes in the flow patterns (increases or decreases) and fluid chemistry, but two transitions are biologically facilitated (by the insulation from high temperatures in the fluid by a thermotolerant species, and the increase in space available for colonization arising from tube-worm growth).

## 6. CONCLUSION

A wide variety of models are used in terrestrial and shallow marine systems. Their use in deep-sea hydrothermal vent systems is less common, possibly because a lack of biological information has hampered the development of such models. In this review, we have outlined the state of model development for understanding dispersal, local growth, spatial dynamics, and community succession; in some areas models are fairly detailed and quantitative, in others they are still at the conceptual stage. At the same time, we have tried to indicate where

significant progress can be made with relatively little effort, by drawing on studies from other systems.

One of the major challenges facing biologists is studying this system is its relative inaccessibility. To address this, we have also attempted to outline ways in which theoretical and empirical methods can be coupled to advance the study of vent systems more rapidly, rather than simply continuing to collect empirical information before developing detailed models. For example, we can use models to optimize or refine our experimental and sampling designs. Or, related models may be used to summarize alternative hypotheses, pinpointing where their predictions differ in empirically meaningful ways, and thus help us focus on the studies that would provide most information on poorly understood mechanisms or processes. Some models may even be used to confirm our intuitions, or to make predictions where we have absolutely no intuition. Integrating local demographic and community processes with geophysically and hydrodynamically driven spatial dynamics will be critical in these spatially complex and highly variable environments. As we discover more about these fascinating systems, models offer considerable potential to accelerate our learning.

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