

INVITED REVIEW

Genetic diversity and connectivity of deep-sea hydrothermal vent metapopulations

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Abstract

Deep-sea hydrothermal vents provide ephemeral habitats for animal communities that depend on chemosynthetic primary production. Sporadic volcanic and tectonic events destroy local vent fields and create new ones. Ongoing dispersal and cycles of extirpation and colonization affect the levels and distribution of genetic diversity in vent metapopulations. Several species exhibit evidence for stepping-stone dispersal along relatively linear, oceanic, ridge axes. Other species exhibit very high rates of gene flow, although natural barriers associated with variation in depth, deep-ocean currents, and lateral offsets of ridge axes often subdivide populations. Various degrees of impedance to dispersal across such boundaries are products of species-specific life histories and behaviours. Though unrelated to the size of a species range, levels of genetic diversity appear to correspond with the number of active vent localities that a species occupies within its range. Pioneer species that rapidly colonize nascent vents tend to be less subdivided and more diverse genetically than species that are slow to establish colonies at vents. Understanding the diversity and connectivity of vent metapopulations provides essential information for designing deep-sea preserves in regions that are under consideration for submarine mining of precious metals.

Keywords: hydrothermal vent, metapopulations, stepping-stone dispersal

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'There are many questions to be answered about these animal communities. One concern is how they locate and colonize new vents. It is clear that an individual vent area has a finite lifetime. We discovered several dead vent areas along the axial ridge, recognizable by the abundant dead clam shells that were slowly dissolving away...' (Corliss *et al.* 1979, p. 1079).

Introduction

The scientists who discovered deep-sea hydrothermal vents along the Galápagos Rift (GAR) were astonished to find dense animal communities composed of metre-long tubeworms, giant clams and mussels, crabs and anemones, a variety of fish and thick mats of filamentous bacteria (Fig. 1). Such high biological productivity was anomalous in the absence of sunlight and photosynthesis; so, they hypothesized that hydrogen sulphide in the vent effluents supported chemolithoautotrophic

bacteria that fix organic carbon and serve as primary producers for these lush communities (Corliss *et al.* 1979). These pioneers also recognized the ephemeral nature of vent habitats and the significance of dispersal for vent animals (above quote). Now, we know that vents are distributed worldwide along the global mid-ocean ridge system, on volcanic seamounts, and in back-arc spreading centres (Fig. 2A). Dead and senescent patches, characterized by remnant bivalve shells or degraded worm tubes, are common sights at many vent fields (Fig. 1B, E). Nascent vent fields have also been observed, providing scientists with opportunities to document the colonization and growth of these communities (Tunnicliffe *et al.* 1997; Shank *et al.* 1998a). This inherent instability is expected to produce nonequilibrium conditions that affect the composition and diversity of species in vent communities (Juniper & Tunnicliffe 1997) and also the distribution of genetic diversity in vent metapopulations (Vrijenhoek 1997).

Vent effluents start as cold seawater that percolates through faults in the crust and is heated in the

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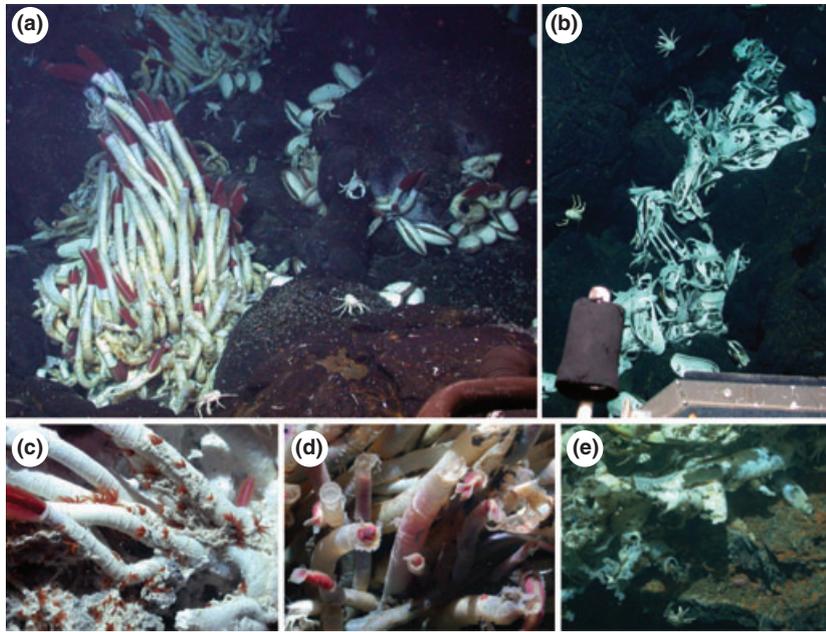


Fig. 1 Life and death at Hanging Gardens hydrothermal vents, 21°N latitude on the East Pacific Rise. (a) Healthy *Riftia pachyptila* tubeworms and *Calyptogena magna* clams living in diffuse hydrothermal effluents between pillow basalts. Numerous *Bythograea thermydron* crabs and *Munidopsis subsquamosa* squat lobsters are visible against the basalts. (b). An adjacent patch of dissolving *C. magna* shells at a dead vent. (c) Healthy *R. pachyptila* tubeworms in 20 °C vent water. Bacterial mats cover bases of the tubes and numerous *Alvinella pompejana* palm worms grow on the tubes. (d) Senescent tubeworms in a 2 °C patch. The red gill-like obturacula are abraded because of predation. (e) Decaying worm tubes in a dead patch. Rusty-brown deposits reveal elevated iron (Fe^{III}) associated with declining gaseous sulphides.

lithosphere, where it extracts metals, minerals, and reduced volcanic gases. Hydrogen sulphide concentrations are greatest at nascent high-temperature vents, and they tend to decline with time, until a vent no longer supports chemosynthetic organisms (Luther *et al.* 2001). Focused vents commonly develop mineralized chimneys that emit water as hot as 400 °C. Diffuse vents emit cooler water through cracks between rocks or channels in sulphide-laden sediments. Vent species tend to segregate among discrete habitat patches defined by different temperatures, fluid flux and chemical regimes (Sarrazin *et al.* 1999; Luther *et al.* 2001). At eastern Pacific vents, the polychaete worm *Alvinella pompejana* lives on chimney walls and occupies hot sulphidic waters, whereas the siboglinid (formerly Vestimentifera) tubeworm *Riftia pachyptila* occurs in warm diffuse flows at the flanks of chimneys (Fig. 1a). *Bathymodiolus* mussels congregate in mounds at the base of chimneys and in surrounding diffuse vents. Vesicomyid clams also exploit cooler diffuse vents (Fig. 1a). These large invertebrates are foundation species that alter the flow of vent fluids and create structural habitat for many small gastropod limpets, polychaete annelids, and swimming lysianassid amphipods. Most vents also host populations of brachyuran crabs, mudiid squat lobsters, and various scavengers, grazers, filter- and suspension-feeding animals. This remarkable enrichment of biomass around vents attenuates rapidly, however, giving way to a background of taxonomically diverse but sparse bathyal organisms. In this regard, vents are analogous to 'oases' in relatively barren submarine 'deserts' (Lutz 1984).

Because individual vent fields tend to be ephemeral, vent-restricted species share many of the characteristics of terrestrial 'weedy species' (Baker 1965) — i.e. requiring well-developed dispersal capabilities, rapid growth rates, and early reproduction. Depending on their individual characteristics, codistributed vent species will be affected differently by metapopulation processes and dispersal barriers. Life history and behavioural traits, therefore, play significant roles in determining their genetic diversity and geographical structure. Herein, I review our current understanding of metapopulation processes and regional geology that affect the distribution of genetic diversity in vent species. Previous substantive reviews of this subject were prepared when our knowledge was based mostly on allozyme polymorphisms that were analysed with traditional population genetic methods (Jollivet 1996; Vrijenhoek 1997). Now, a second decade of studies has examined vent animals with additional molecular markers and with phylogeographic and coalescent methods. It is time to assess how our scientific inferences have progressed and what lies on the horizon for studies of vent metapopulations. A good start in this direction is provided by a recent review of efforts to model demographic and dispersal processes affecting vent communities (Shea *et al.* 2009). Before considering these theoretical and empirical studies, it will be necessary to consider some physical (geology, chemistry, and hydrography), historical (geography, vicariance, range expansions, etc.), and biological factors (life histories, behaviours, demography, and symbioses) that are expected to affect the connectivity and diversity of vent species.

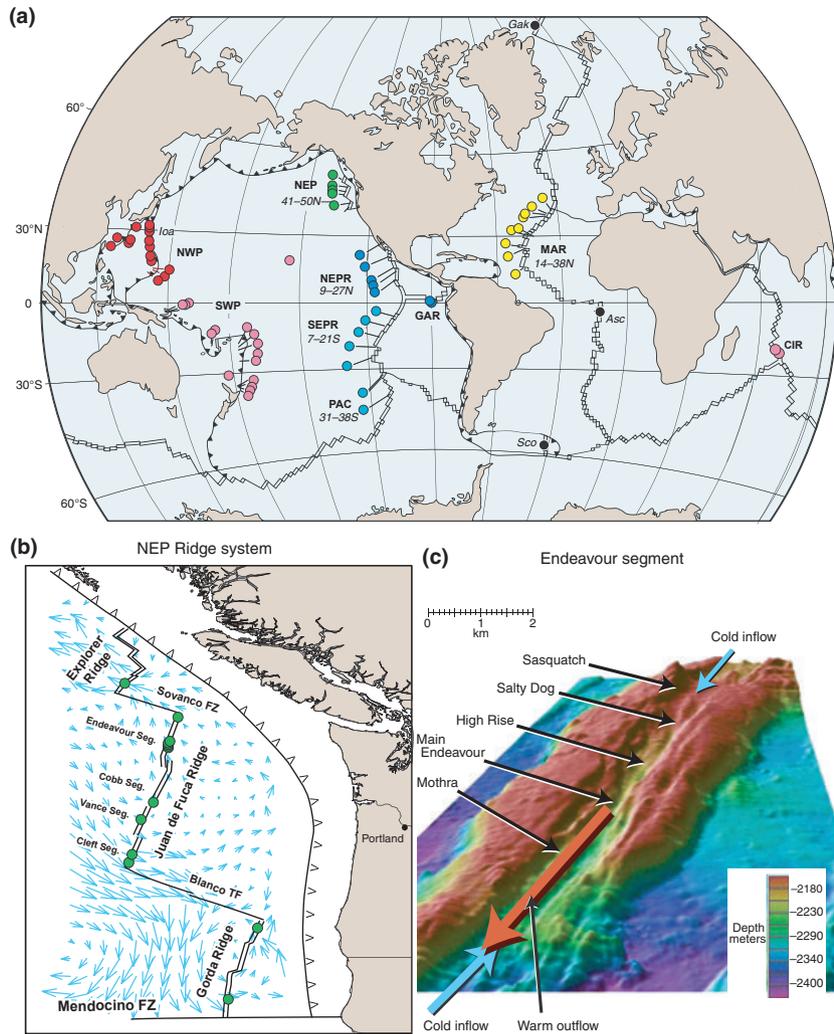


Fig. 2 Hierarchical geography of vents fields. (a) Worldwide distribution of deep-sea hydrothermal vents known to support chemosynthetic communities. Spreading centres are indicated with double lines, and subduction zones are indicated with directional arrowheads. Colours represent major biogeographic provinces: green, northeast Pacific (NEP) ridge system; dark blue, northern East Pacific Rise (NEPR) + Galápagos Rift (GAR); lighter blue, southern East Pacific Rise (SEPR) and Pacific-Antarctic Ridge (PAC); red, northwest Pacific (NWP); pink, southwest Pacific (SWP) + central Indian Ridge (CIR). Black dots indicate several recently discovered deep-sea vents: *Gak*, Gakkel Ridge; *Asc*, Ascension Ridge; *Sco*, Scotia Ridge. Modified from Van Dover *et al.* (2002) and updated with information from Bachraty *et al.* (2009). (b) The northeast Pacific ridge system is composed of the Explorer, Juan de Fuca, and Gorda ridge axes. Large lateral offsets separate the three axes. Blue arrows indicating current vectors at 2500 m depth are based on geostrophic circulation models (modified from Fig. 1 in Young *et al.* 2008). Green dots represent discrete NEP vent fields. (c) A northward view of vent fields along a 10-km portion of the Endeavour segment. Image is centred at the Main Endeavour vent field (47° 57' N, 129° 06' W, 2196 m depth) with 3× vertical exaggeration. Current patterns driven by tidal forces and hydrothermal activity are indicated (from Thomson *et al.* 2003).

Biogeography of vents

Insufficient sampling and limited integration of phylogenetic information have hampered development of a robust historical biogeography for vent faunas. Because of their remoteness and foul weather, ridge systems in the southern Atlantic, Antarctic, and Arctic regions are mostly unexplored (Fig. 2a). Phylogenetic relationships with similar faunas from cold seeps and sites of organic deposition have not been fully integrated with vent bi-

ogeographies (Tunnicliffe *et al.* 1998). For example, families of vesicomyid clams, mytilid mussels, and siboglinid tubeworms that dominate vents worldwide probably diversified first in seeps or other chemosynthetic environments and subsequently invaded vents multiple times (Peek *et al.* 1997; Baco *et al.* 1999; Distel *et al.* 2000; McMullin *et al.* 2003; Jones *et al.* 2006). Furthermore, taxonomic uncertainties resulting from phenotypic plasticity and species crypticism have resulted in poor estimates of faunal diversity and overlap among

geographical provinces; nonetheless, molecular systematic studies have begun to unravel these complexities (reviewed in Vrijenhoek 2009).

Modern faunas can be partitioned into a number of provinces (Fig. 2a). Fauna inhabiting northeastern Pacific (NEP) ridge axes have been isolated from cognate fauna on the northern East Pacific Rise (NEPR) for 20–30 million years (Tunnicliffe *et al.* 1998). The NEP and NEPR axes presently do not share vent-restricted species, but several sister-species pairs of annelids were split by this vicariant event (Chevaldonné *et al.* 2002). The GAR hosts a subset of the more diverse NEPR fauna. The NEPR and southern East Pacific Rise (SEPR) share

many of the same species, but a dispersal filter across the equator impedes dispersal of a number of vent species. South of the Easter and Juan Fernandez microplates (Fig. 3), the SEPR connects with the Pacific-Antarctic (PAC) Ridge, which in turn connects with fragmented spreading centres in southwest Pacific (SWP). Vent fields along the central Indian Ridge (CIR) share many genera with the SWP fauna (Van Dover *et al.* 2001). Bachraty *et al.* (2009) found that the mid-Atlantic Ridge (MAR) fauna is most similar to the NEPR fauna, suggesting connections that may have existed before closure of deep-water connections across the modern Isthmus of Panama region. Although eastern and western Pacific vent faunas

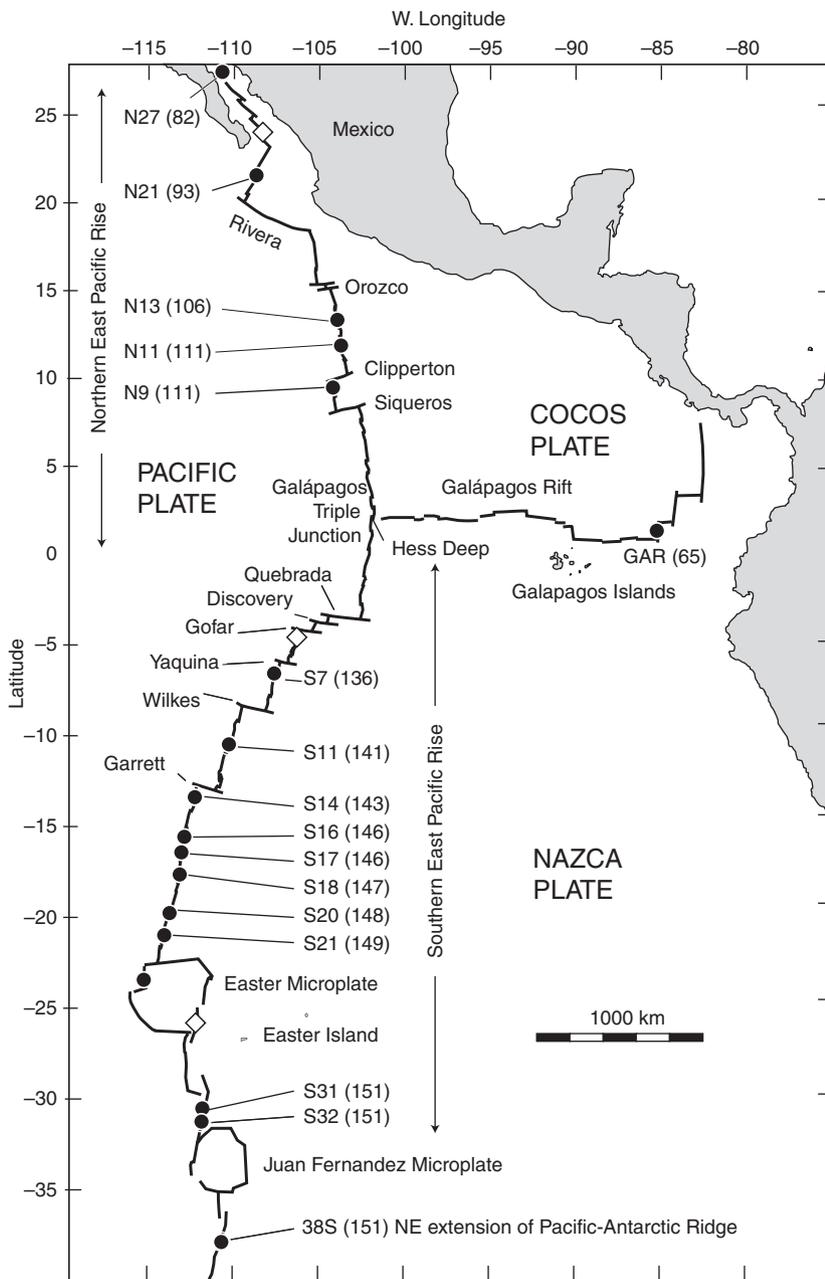


Fig. 3 Known hydrothermal vent areas along the East Pacific Rise (EPR) and Galápagos Rift (GAR). Seafloor spreading rates (mm/year) following the locality names were estimated with the Nuvel-1A model implemented in the Seafloor Spreading Rates Calculator (http://ofgs.ori.u-tokyo.ac.jp/~okino/platecalc_new.html). Closed circles represent vent areas that have been sampled for one or more of the taxa involved in genetic studies (Table 1). Open diamonds represent areas that were explored, but active vents were not found or animals were not sampled for genetic studies. Lines perpendicular to the main axes indicate fracture zones (e.g. Rivera, Quebrada). Modified from Audzijonyte & Vrijenhoek (2010).

are mostly distinct, trans-Pacific connections exist for several vesicomyid clam species (Kojima *et al.* 2004). These opportunistic clams are not vent-restricted, however, and may move via stepping-stone connections through unexplored north Pacific cold seeps and possibly sunken whale carcasses.

Deep-sea biogeographers have long been interested in ocean currents because the larvae of many marine animals are hydrologically advected (Table 1). Deep-ocean currents are driven by tides, winds, and earth's rotation and constrained by the geomorphology of ocean basins (Van Dover *et al.* 2002). For example, the Antarctic

Table 1 Biological characteristics and dispersal rates of hydrothermal vent species that have been studied genetically

Species	Axes/areas	Adult		Larvae		<i>Nm</i> ^e	Markers ^f	References ^g
		Mob. ^a	Nutr. ^b	Mob. ^c	Nutr. ^d			
Polychaeta								
<i>Riftia pachyptila</i>	NEPR/SEPR/GAR	S	S	N	L	H	1–5	1–5
<i>Tevnia jerichonana</i>	NEPR/SEPR	S	S	N	L	V	1, 2	3
<i>Oasisia jerichonana</i> complex	NEPR/SEPR	S	S	N	L	nd	1, 2	3, 6
<i>Ridgeia piscesae</i>	EXP/JDF/GOR	S	S	N	L	M	1, 2	6–8
<i>Alvinella pompejana</i>	NEPR/SEPR	V	G	N, D	L	V	1, 2	3, 9–10
<i>A. caudata</i>	NEPR/SEPR	V	G		L	H	1	9
<i>Paralvinella grasslei</i>	NEPR/GAR	V	G			M	1	3, 9
<i>Branchiopolynoe symmytilida</i>	NEPR/SEPR/GAR	V	C		L	V	1	3, 10
<i>Hesiolyra bergi</i>	NEPR/SEPR	M	P			V	2	10
Bivalvia								
<i>Calyptogena magnifica</i>	NEPR/SEPR/GAR	S	S	S	L	H	1–3	11–12
<i>Bathymodiolus thermophilus</i>	NEPR/SEPR/GAR	S	S	S	P	H–V	1, 2	10, 13–15
<i>B. aff. thermophilus</i>	PAR	S	S	S	P	nd	1, 2	15
<i>B. azoricus</i>	MAR	S	S	S	P	V	1, 2	16–18
<i>B. puteoserpentis</i>	MAR	S	S	S	P	V	1, 2	16–18
<i>B. brevior</i> complex	SWP/CIR	S	S	S	P	V	2	19
Gastropoda								
<i>Eulepetopsis vitrea</i>	NEPR/SEPR/GAR	V	G	S	L	L	1, 2	10, 20
<i>Lepetodrilus elevatus</i> s.s.	NEPR	V	G	S	L	M	1, 2	10, 20
<i>L. aff. elevatus</i>	SEPR	V	G	S	L	M	1, 2	10, 20
<i>L. galriftensis</i>	NEPR/SEPR	V	G	S	L	M	1, 2	10
<i>L. ovalis</i>	NEPR/SEPR	V	G	S	L	nd	2	10
<i>L. pustulosus</i>	NEPR	V	G	S	L	M	1	20
<i>L. fucensis</i>	EXP/JDF	V	G, S	S	L	H	1, 3	21
<i>L. gordensis</i>	GOR	V	G	S	L	H	1, 3	21
<i>Alviniconcha hessleri</i> complex	SWP/CIR	V	S	B	L	nd	2	22
<i>Ifremeria nautilei</i>	SWP	V	S	B	L	nd	2, 5	22–24
Amphipoda								
<i>Ventiella sulfuris</i>	NEPR/GAR	M		B	L	M	1	25
Decapoda								
<i>Rimicaris exoculata</i>	MAR	M	S, G	P	P	V	1, 2	26–28

^aAdult mobility: S, sessile or sedentary; V, limited vagility; M, highly mobile.

^bAdult nutrition: S, nutritional endosymbionts; F, filter/suspension feeding; C, commensal of mussels; G, bacterial grazing; P, predator.

^cLarval mobility: S, free-swimming; N, nonswimming; D, demersal; P, pelagic zone; B, brooding. Information distilled from Tyler & Young 1999; Desbruyères *et al.* 2006.

^dLarval nutrition: L, lecithotrophic; P, planktotrophic; B, brooding (from Tyler & Young 1999).

^eMean rate of gene flow (*Nm*) along ridge axes: (L) low, $Nm \leq 1$; (M) moderate, $1 < Nm \leq 5$; (H) high, $5 < Nm \leq 25$; (V) very high, $Nm > 25$; nd, not determined.

^fGenetic markers: (1) allozymes; (2) mtDNA; (3) nuclear DNA; (4) AFLPs; (5) DNA microsatellites.

^gReferences: (1) Bucklin 1988; (2) Black *et al.* 1994; (3) Hurtado *et al.* 2004; (4) Shank & Halanych 2007; (5) Fusaro *et al.* 2008; (6) Black *et al.* 1997; (7) Southward *et al.* 1996; (8) Young *et al.* 2008; (9) Jollivet *et al.* 1995; (10) Plouviez *et al.* 2009; (11) Hurtado *et al.* 2003; (12) Karl *et al.* 1996; (13) Grassle 1985; (14) Craddock *et al.* 1995; (15) Won *et al.* 2003a; (16) Maas *et al.* 1999; (17) O'Mullan *et al.* 2001; (18) Won *et al.* 2003b; (19) Kyuno *et al.* 2009; (20) Craddock *et al.* 1997; (21) Johnson *et al.* 2006; (22) Kojima *et al.* 2000; (23) Suzuki *et al.* 2006; (24) Thaler *et al.* 2010; (25) France *et al.* 1992; (26) Creasey *et al.* 1996; (27) Shank *et al.* 1998a,b; Teixeira *et al.* 2010.

Circumpolar Current spans the southern oceans in a swift easterly flow. Yet modern circulation has limited predictive power for historical biogeography, because continental barriers shifted dramatically during the Mesozoic and Cenozoic. The Antarctic Circumpolar Current is only about 20 MY old, since the Bransfield Strait opened between Antarctica and South America. Conversely, Cenozoic closures severed a Tethys Sea connection between the Indian and Atlantic oceans and a trans-Panamanian connection between the western Atlantic and eastern Pacific oceans. Thermohaline circulation drives a conveyor system that oxygenates deep Atlantic waters, but this conveyor shut down several times during the late Cretaceous and early Cenozoic, leading to hypoxic conditions that may help to explain the young and derived vent fauna of the MAR (Little & Vrijenhoek 2003).

Extrinsic factors affecting connectivity and genetic diversity

The genetic diversity and geographical structure of vent species is affected by a number of physical processes including ridge geomorphology, oceanic currents, and the temporal stability of vents. Relatively linear ridge axes are frequently interrupted by lateral offsets, caused by transform faults (TF) and fracture zones (FZ). For example, the Blanco TF, a 450-km-long offset, separates the Blanco and Juan de Fuca (JDF) axes of the NEP system (Fig. 2b). Bathymetry also varies along ridge axes. Mid-Atlantic vents vary between 850 and 3650 m in depth. The EPR is fairly uniform in depth (2400–2800 m), except for the Gulf of California, which is heavily sedimented, and the Hess Deep, a 6000-m depression that intersects the NEPR and SEPR axes at the Galápagos Triple Junction (Fig. 3). This region at the equator presents a boundary that impedes the dispersal of a number of vent species.

Spreading rates and the stability of vents

The temporal stability and spatial distribution of vents is linked to tectonic spreading rates, which in turn are products of magma supplies and the magnitudes of volcanism and faulting along ridge axes (Juniper & Tunnicliffe 1997; MacDonald 1998; Van Dover 2000). Spreading rates vary greatly among ridge systems (Table 2). Slow-spreading axes like the MAR have distantly spaced vent fields (clusters of vents) that are relatively stable. Deep faulting creates fissures that support the circulation of vent fluids for hundreds of years (Fornari & Embley 1995). The MAR axis spans a broad range of depths and numerous TFs that laterally displace its spreading segments. These characteristics were predicted to favour geographical subdivision and possibly speciation (Van Dover 2000). In contrast, the fast-spreading EPR is relatively linear with numerous closely spaced fields (Fig. 3) set upon shallow faults that support ephemeral vents. During the past 30 years of vent studies, scientists have documented magmatic eruptions that obliterated known vent fields, extirpated local communities, and also created new vents (Tunnicliffe *et al.* 1997; Shank *et al.* 1998a,b). Vents along the fast-spreading SEPR axis tend to persist for a few decades or less. My colleagues and I have observed recent lava flows populated by the remnant tubes of *Tevnia jerichonana* tubeworms and the shells of dead *Bathymodiulus* mussels (Hey *et al.* 2006). We found that recently dead vent fields were more common than living vent fields along a superfast-spreading region (31–38°S latitude), where the Pacific-Antarctic Ridge (PAR) joins the SEPR. A few active vents explored during our 1999 expedition were dead or senescent when we visited them again during 2005. This rapid tempo of extirpation and recolonization sets the pace for metapopulation processes that affect genetic diversity

Table 2 Comparison of fast- and slow-spreading ridge systems

Characteristic	EPR	NEP	MAR
Spreading rate (mm/year)	Fast (85–150)	Medium (50–80)	Slow (20–40)
Habitat longevity	Several decades or less	Several decades or more	100s to 1000s of years
Appearance of new vents	Frequent	Less frequent	Rare
Distance between vent fields (km)	Short (~100)	Short (100–200)	Long (100s to 1000s)
Depth range (m)	Monotonous (2000–2830)	Variable (1500–3300)	Highly variable (850–3650)
Axial walls	Absent to low	Medium	High
Transform offsets (km)	≤240	≤450	≤952
Transform relief	Low	High	Very high
Dominant taxa	Siboglinid tubeworms, bathymodiolin mussels, vesicomid clams, provannid snails, lepetodrilid limpets bythograeid crabs	Siboglinid tubeworms, vesicomid clams, provannid snails, lepetodrilid limpets	Alvinocarid shrimp, bathymodiolin mussels

within and among colonies of vent-restricted species (Vrijenhoek 1997).

Hydrology

Oceanographers estimate modern currents directly with stationary current meters and mobile drifters and indirectly with geostrophic circulation models (Reid 1997) and geochemical tracers. (Lupton 1998). Circulation along the MAR axis is constrained by very high walls that flank wide axial valleys (Thurnherr *et al.* 2008). Deep circulation along the NEP system is deflected southward by high relief of the Blanco TF (Fig. 2B). At a smaller scale, high walls and rising hydrothermal plumes along the JDF axis drive inflows of cold bottom water (Fig. 2C) that may help to retain vent larvae near their natal sites (Thomson *et al.* 2003). Tidally driven axial currents have been measured along portions of the NEPR, but larvae that rise above the axial walls are likely to be advected away from vents (Marsh *et al.* 2001). Sporadic megaplumes can also drive buoyant larvae above the axial walls and act as vehicles for long-distance dispersal (Mullineaux *et al.* 1991). Breaches in these walls and intersection by TFs permit cross-axis currents to intrude and drive passively dispersing larvae off axis (Mullineaux *et al.* 2002). Larval retention may be most problematic along magmatically inflated segments of the fast-spreading SEPR, which have low to nonexistent axial walls. Strong cross-axis currents in this region are hypothesized to impede retention and disrupt along-axis dispersal of vent species with planktotrophic larvae (Won *et al.* 2003a; Hurtado *et al.* 2004).

Intrinsic factors affecting genetic connectivity

Potential and realized dispersal

The adults of many vent species are sessile or relatively immobile; so dispersal is mediated through larvae or mobile juveniles (Table 1). Planktotrophic larvae feed in the water column, whereas lecithotrophic larvae persist mostly on yolk reserves. Larval durations are prolonged in some lecithotrophic species by the production of large eggs or arrested development. Demersal larvae spend their lives on or very near the bottom, whereas other larvae migrate vertically to feed in the pelagic zone. Some actively swim and others are passively advected by currents. Knowing larval durations and advection rates in the relevant water layers allows oceanographers to predict the dispersal potential of marine species. Yet inferences from larval biology alone have limited predictive power with respect to realized dispersal as evidenced in the studies of genetical population structure (Tyler & Young 2003; Weersing & Toonen 2009).

Estimates of gene flow (Nm) have been obtained now for nearly 30 vent species (Table 1). The estimates reported here are mean rates along contiguous ridge segments. They do not include reduced rates across geomorphological or hydrological barriers, which are discussed in the following sections. Because Nm estimates are only approximate at best, I categorize them as low ($Nm \leq 1$), moderate ($1 < Nm \leq 5$), high, ($5 < Nm \leq 25$), and very high ($Nm > 25$). The categories roughly follow criteria developed in models for assessing population differentiation and connectivity (Waples & Gaggiotti 2006; Audzijonyte & Vrijenhoek 2010). The reported values for Nm are averages of published values or estimates derived from gene frequencies and F_{ST} values (references in Table 1). For example, the mussel *Bathymodiolus thermophilus* produces tiny eggs ($\sim 50 \mu\text{m}$) and free-swimming planktotrophic larvae that are expected to have long-distance dispersal potential (Lutz *et al.* 1979), and it exhibits very high rates of gene flow along contiguous portions of the NEPR and GAR. Rates are slower along the SEPR where it encounters strong cross-axis currents. The codistributed clam *Calyptogena magnifica* produces larger eggs and lecithotrophic larvae that are expected to have lower dispersal potential (Lutz *et al.* 1984); yet it also exhibits high rates of gene flow across the NEPR and GAR axes. Several codistributed limpet species produce lecithotrophic larvae that are expected to have similarly limited dispersal potentials (Lutz *et al.* 1986), but rates of gene flow along the NEPR and GAR axes varied from low to high among these species. Clearly, behavioural and other aspects of their individual life histories must affect realized rates of dispersal.

Inferences about dispersal potential are improved when information on larval energetics and development times is coupled with detailed knowledge about deep-sea currents. Marsh *et al.* (2001) reported that *Riftia pachyptila* produces relatively small ovate eggs ($\sim 100 \mu\text{m}$) and nonfeeding larvae with duration of about 38 days. They estimated that near-bottom currents along the NEPR axis should result in mean dispersal distances of 100–200 km. These inferences are consistent with previous estimates of gene flow and stepping-stone dispersal (SSD) in *Riftia pachyptila* (Black *et al.* 1994). Pradillon *et al.* (2001) reported that codistributed *Alvinella pompejana* worms produce larger eggs ($\sim 180 \mu\text{m}$) and lecithotrophic larvae that arrest development in cold 2°C bottom waters. Development ensues when the larvae experience elevated temperatures. Prolonged larval duration (PLD) is expected to produce high dispersal potential, and indeed, *A. pompejana* has among the highest rates of gene flow reported to date for species living along the NEPR and SEPR axes. Curiously, however, dispersal appears to be completely impeded across the equator. The scaleworm *B. seepensis*

produces even larger eggs (~400 µm) that are expected to contribute to PLD (Jollivet *et al.* 1998). It exhibits very high rates of gene flow both within and between the NEPR and SEPR axes. These expectations of PLD fail to explain the presence of isolation in *A. pompejana* vs. its absence in *B. seepensis*. Other behavioural differences must be involved. Species with free-swimming adults also exhibit dramatic life history differences that affect dispersal. The Atlantic shrimp *Rimicaris exoculata* produces very large lecithotrophic eggs and planktotrophic larvae that feed in the photic zone before settling as juveniles (Dixon & Dixon 1996). This species exhibits extraordinarily high rates of gene flow along the MAR (Teixeira *et al.* 2010). In contrast, the eastern Pacific amphipod *Ventiella sulfuris* broods its young and exhibits moderate rates of gene flow along the NEPR axis and possible isolation between the NEPR and GAR axes (France *et al.* 1992). Additional information about larval durations and behaviours along with more detailed knowledge of deep-sea currents may resolve many of the discrepancies between inferences about realized and potential dispersal. These will be hard-won victories, however, because deep-sea biologists work in difficult and remote environments with species that mostly cannot be reared in culture. The rapid progress made in the studies of gene flow and population structure should help to define the most informative targets for these difficult studies.

Symbiosis

Reliance on obligate chemosynthetic symbioses constrains many vent species to living in environmental patches that emit hydrothermal effluents (Table 1). *Riftia pachyptila* uses a feathery plume (the obturaculum) to absorb dissolved sulphides from vent water. These reduced compounds and respiratory gases are then delivered to a specialized organ (the trophosome) that houses sulphur-oxidizing (thiotrophic) endosymbionts. *Calyptogena magnifica* clams protrude a highly vascularized foot into basaltic fissures and absorb sulphides that are delivered to thiotrophs housed in the gills. Various bathymodiolin mussel species are capable of absorbing sulphides or methane through gills that house thiotrophic or methanotrophic bacteria and in some cases both types of endosymbionts.

The means that vent animals use to acquire symbionts have profound ecological and evolutionary consequences (reviewed in Vrijenhoek 2010). Vesicomid clams transmit their thiotrophic endosymbionts vertically through eggs, which results in cytoplasmic cotransmission with host mitochondria and clonality of the symbionts within a host lineage. Host mitochondrial and symbiont genes exhibit gametic phase disequilib-

rium in *C. magnifica* populations (Hurtado *et al.* 2003). Fifty to 60 million years of vertical cotransmission in vesicomids is manifested in cospeciation between the host species and their symbiont lineages (Peek *et al.* 1998b). The bacterial lineages hosted by *Vesicomya okutanii* and *C. magnifica* clams have lost many of the genes required for metabolism and reproduction in the ambient environment along with nearly half of their DNA (Kuwahara *et al.* 2007; Newton *et al.* 2008). These endosymbionts are evolutionarily enslaved, requiring many host proteins to conduct essential aspects of DNA replication and central metabolism. Vertical transmission provides a host with 'symbiont assurance' because dispersing larvae already possess bacterial symbionts when they colonize new vent habitats.

In contrast, species that lack vertical transmission may risk failing to acquire a symbiont when colonizing new vents, but those that succeed might compensate for this risk by obtaining 'locally optimal' strains (Won *et al.* 2003c). For example, *Riftia pachyptila* is first infected by bacteria from the environment in which the symbiont-free worm larvae settle (Nussbaumer *et al.* 2006). Environmental acquisition typically results in infection by multiple strains of the endosymbiont (Vrijenhoek *et al.* 2007). Cospeciation does not exist in these siboglinid tubeworms (McMullin *et al.* 2003). Robidart *et al.* (2008) found that genome size and functionality of the *R. pachyptila* endosymbiont are similar to those of free-living thiotrophs, which suggests that the bacteria maintain a fully functional environmental phase. Their analysis of genic content suggests that these thiotrophic symbionts also are capable of heterotrophic metabolism. Despite the risk of failure, environmental acquisition is more common than vertical transmission in vent taxa. Another possible benefit of horizontal transmission is that larvae would not carry a metabolic burden of heterotrophy by endosymbionts as the larvae disperse through intermediary environments that lack reduced gases.

Transmission modes affect symbiont demographics. Strictly vertical transmission dramatically reduces the bacterial effective population size (N_e) because of repeated bottlenecks during the delivery of symbionts to the eggs or embryos (Peek *et al.* 1998a; Risper & Moran 2000). Predominantly clonal inheritance in bacteria also acts to increase the risk of mutational decay because of random fixation of slightly deleterious mutations (Muller 1964; Ohta 1987). As expected, vertically transmitted symbionts associated mostly with vesicomid clams exhibit significantly faster nucleotide substitution rates than their free-living or horizontally transmitted counterparts, and they accumulate potentially deleterious mutations (Peek *et al.* 1998a), which parallels the pattern reported for vertically transmitted *Buchnera* endosymbionts of aphids (Moran 1996).

Strictly vertical cytoplasmic inheritance also results in effective coupling of symbiont genes with host mitochondrial genes (Hurtado *et al.* 2003). Consequently, a selective sweep involving one of these genomes should result in fixation of hitchhiking mutations in the cotransmitted genome (Hurst & Jiggins 2005). These matters warrant further investigation, especially in the light of a recent report that symbiont transmission might not be strictly vertical in at least one vesicomymid species (Stewart *et al.* 2008).

Models of population structure and connectivity among southeast Pacific vents

Prior to 1999, most studies of gene flow and population structure involved species from the EPR and GAR

(Fig. 3). The first allozyme studies, which included *Bathymodiolus thermophilus* and *Riftia pachyptila* (Grassle 1985; Bucklin 1988), revealed sufficient polymorphism to warrant more extensive sampling efforts. During 1990, my colleagues and I undertook a month-long expedition with the R/V *Atlantis* and deep-sea research submarine DSR *Alvin* to sample the NEPR/GAR vent fields known to us at the time. Initially, a subset of eastern Pacific species was examined mostly for allozymes (Fig. 4). These data were sufficient to reveal several patterns of population structure (Box 1 and Vrijenhoek 1997). Subsequent expeditions obtained samples from the SEPR. With 14 species, broader geographical sampling, and applications of more polymorphic molecular markers, we found further evidence for some of these patterns and identified new patterns.

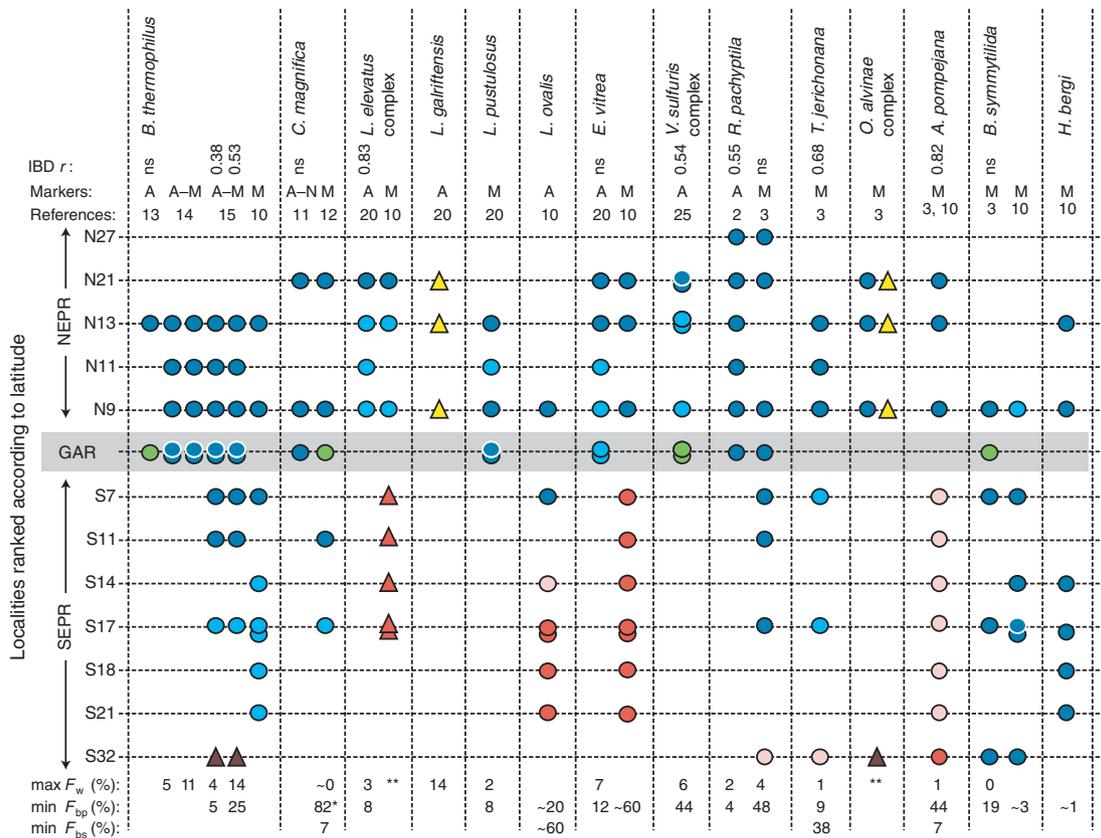


Fig. 4 Patterns of differentiation in vent species from the northern (NEPR) and southern (SEPR) East Pacific Rise and Galápagos Rift (GAR, grey box). Figure is modified and updated from Audzijonyte & Vrijenhoek (2010), who estimated the correlations (IBD *r*) between genetic and geographical distances from original genetic data, where possible; *ns* denotes a nonsignificant correlation. Genetic markers are (A) allozymes; (M) mtDNA; and (N) nuclear DNAs. Numbered references are listed in footnote 'g' of Table 1. Green dots denote significantly divergent GAR samples. Blue vs. red dots indicate major partitions along the EPR (shades of blue and red indicate subpopulations within each partition). Triangles indicate putative cryptic species. Listed below each column are maximum values for differentiation within subpopulations (max F_w , expressed as percentage of total diversity) and minimum values for differentiation between partitions (min F_{bp}) and subpopulations within partitions (min F_{bs}). Estimates obtained from reverence 10 (Plouviez *et al.* 2009) are approximate. *Owing to unique haplotype fixed in GAR sample. **Differentiation not estimated because of mixed sampling across morphologically cryptic species (see text).

Box 1. Population structure and sampling sufficiency in vent animals

The following, nonexclusive, categories of population structure were reported for eastern Pacific vent species. Categories 1–3 are repeated from Vrijenhoek (1997). Further examples for categories 2–5 are discussed in the accompanying text.

Island-model population structure (Wright 1931). Under this model, populations that have achieved equilibrium between gene flow and genetic drift are expected to show no correlation between estimates of gene flow (Nm) and geographical distance (Slatkin 1993). Initially, we determined that NEPR/GAR samples of *Bathymodiolus thermophilus* mussels fit expectations for island model population structure (Craddock *et al.* 1995); however, subsequent analyses that included SEPR samples and mtDNA sequences indicated that a stepping-stone model provides a better fit across this species' 6000-km range (Won *et al.* 2003a). Our initial studies of *Calyptogena magnifica* clams, *Lepetodrilus pustulosus* limpets, and *Eulepetopsis vitrea* limpets from NEPR/GAR samples also did not reject an island model (Karl *et al.* 1996; Craddock *et al.* 1997), but an insufficient numbers of geographical samples or polymorphic genetic markers limited the statistical power needed to refute the model (Audzijonyte & Vrijenhoek 2010). Subsequent studies involving more comprehensive geographical sampling and more variable genetic markers (e.g. mtDNA) have revealed that an unstructured island model may not be suitable for any vent species distributed across a broad geographical range.

Stepping-stone dispersal (Kimura & Weiss 1964). A one-dimensional stepping-stone model provides a reasonable expectation for dispersal along nearly linear ridge systems like the EPR (Audzijonyte & Vrijenhoek 2010). At equilibrium, this model is expected to produce a positive correlation between genetic differentiation and geographical distance, which resembles the pattern also resulting from isolation by distance (IBD) in continuously distributed populations (Wright 1943; Slatkin & Barton 1989; Rousset 1997). Although researchers commonly

identify this pattern as IBD, this correlation can result from nonequilibrium processes such as clinal selection, vicariance with secondary contact, or recent range expansions (Slatkin 1993).

Hierarchical subdivision (Wright 1951). Genetic differentiation is structured according to nested geographical partitions, and it is exemplified by hierarchical F -statistics. This category is not exclusive of the previous categories because population structure might fit an island model or stepping-stone model within a lower-level partition and a different model at a higher level. For example, populations of the vent amphipod *Ventiella sulfuris* and polychaete *Paralvinella grasslei* exhibit very low levels of allozyme differentiation along the NEPR axis (<3% of the total genetic variance) and much greater differentiation between NEPR and GAR populations (France *et al.* 1992; Jollivet *et al.* 1995). Higher-level subdivision is often associated with physical boundaries.

Variable dispersal filters (Hurtado *et al.* 2004). Physical boundaries differentially impede the movement of codistributed vent species. Effects can range from complete isolation and speciation (vicariance) to lesser degrees of impedance, depending on the distinctive life histories and behaviours of individual species. As discussed in the accompanying text, the EPR, NEP, MAR, and SWP systems all exhibit geomorphological and hydrological features that create variable dispersal filters.

Vicariance involves geographical splitting of a taxon into isolated allopatric populations and potentially into distinct species (Cracraft 1982). For example, the NEP ridge axes and NEPR were once connected through the Farallon Ridge, which was subducted beneath the North American Plate 20–30 million years ago (Atwater 1989). The modern NEP and NEPR axes share several sister-species pairs of polychaete annelids and gastropod limpets (Chevaldonné *et al.* 2002; Johnson *et al.* 2008). Within the NEP system, vicariance associated with orogeny of the Blanco TF appears to be responsible for the isolation of limpet species inhabiting the JDF and Gorda (GOR) ridge axes (Johnson *et al.* 2006).

Isolation by distance

Geographical differentiation in species with limited dispersal potential is expected to reveal a signature that is consistent SSD or IBD (Slatkin & Barton 1989). Consequently, measures of interpopulational differentiation, like F_{ST} , should decline with increasing distances between vent localities. Nonetheless, this signature of IBD was not observed in many initial allozyme surveys of NEPR/GAR species. Instead, hierarchical patterns of geographical subdivision were attributed to species-specific dispersal modes, topographical discontinuities of the ridge axes, nonequilibrium metapopulation scenarios, and cryptic species (reviewed in Jollivet 1996; Vrijenhoek 1997). Recently, Audzijonyte & Vrijenhoek (2010) tested these inferences by generating expectations based on computer simulations of a one-dimensional stepping-stone model with varying levels of gene flow between adjacent colonies ($Nm = 1, 5, \text{ and } 25$). We conducted forward-based simulations with EASYPOP (Balloux 2001) to represent allozyme differentiation and conducted coalescent simulations with SIMCOAL2 (Laval & Excoffier 2004) to represent differentiation in mitochondrial DNA sequences. Considering the results of these simulations, we concluded that previous failures to detect evidence for IBD in most vent species could be explained by low statistical power from sampling too few colonies, or to examination of an insufficient number of polymorphic gene loci, or both (Fig. 4).

Geographical subdivision and sampling gaps

Audzijonyte & Vrijenhoek (2010) also evaluated whether previous inferences about geographical subdivision of eastern Pacific vent organisms were statistically robust when compared to an alternative hypothesis of SSD that included gaps in the sampling scheme. The simulations showed that sampling gaps, if large enough, are capable of generating significantly inflated pairwise F_{ST} 's (examples in Plouviez *et al.* 2009); nonetheless, many of the earlier inferences about geographical barriers to dispersal at eastern Pacific vents were supported. With the present expanded sampling scale that spanned about 7000 km, none of EPR species exhibited a population structure that was consistent with island-model population structure. Patterns of subdivision are illustrated for 14 nominal species (Fig. 4). Six species fit expectations for IBD, and others exhibit evidence for significant subdivision across the following boundaries.

The Galápagos (GAR) boundary. The GAR joins the EPR axis at the Galápagos Triple Junction (Fig. 3). GAR

vents are displaced about 2000 km east of the EPR axis, and they host a subset of EPR fauna (Desbruyères *et al.* 2006). Three species exhibit evidence for limited connectivity with EPR populations (Fig. 4). Allozyme frequencies in the amphipod *Ventiella sulfuris* differ substantially from those of NEPR populations (France *et al.* 1992). *Calyptogena magnifica* clams and *Branchiopolynoe symmytilida* scale worms from the GAR exhibit mitochondrial haplotypes that are rare or absent in EPR samples (Hurtado *et al.* 2003, 2004). Despite an earlier report that allozyme frequencies differed in *Bathymodiolus thermophilus* mussels from GAR (Grassle 1985), subsequent researchers found no evidence for allozyme or mtDNA differentiation between GAR and NEPR populations (Craddock *et al.* 1995; Won *et al.* 2003a; Plouviez *et al.* 2009).

The Equatorial (EQ) boundary. Hurtado *et al.* (2004) first identified the EQ region of the EPR as a variable dispersal filter because *Alvinella pompejana* appeared to be completely isolated across this boundary, *Tevnia jerichonana* experienced significant impedance to dispersal, and *Branchiopolynoe symmytilida* showed no impedance along the EPR. More recently, Plouviez *et al.* (2009) hypothesized that subdivision of *A. pompejana* and several other species coincided with a (~1.3 Ma) vicariance event that separated the NEPR and SEPR axes. Assuming past isolation, they used mitochondrial genealogies to estimate similar coalescence times for *Bathymodiolus thermophilus* mussels and the limpets, *Lepetodrilus ovalis* and *Eulepetopsis vitrea*. Yet Won *et al.* (2003a) had previously reported that *B. thermophilus* mussels exhibit high rates of gene flow ($Nm \geq 5$) within the NEPR and SEPR axes and minimal impedance between them. Based on computer simulations, (Audzijonyte & Vrijenhoek 2010) found that the reported low levels of differentiation across the EQ boundary ($F_{ST} \approx 0.03$) are expected for SSD with one or more sampling gaps. The sampled vent fields flanking the equator (N9 and S7) are 1650 km apart. Intermediate vents exist in the Hess Deep region (T. Shank 2009, personal communication), and the mussels also occur at GAR vents (Won *et al.* 2003a). Plouviez *et al.* (2009) further hypothesized that an older vicariance event (~11.3 Ma) isolated *L. elevatus* limpets across the equator, but they did not consider contrary evidence. Their 'NEPR and SEPR' mitochondrial lineages are sympatric along the NEPR axis and correspond to the cryptic species *Lepetodrilus elevatus* sensu stricto and *Lepetodrilus galrifensis* (Craddock *et al.* 1997; Johnson *et al.* 2008). Nonetheless, nonequilibrium processes including vicariance with secondary contact, frequent local extinctions and recolonization events, and range expansions can generate patterns of differentiation that resemble the product of SSD (Slatkin 1993)

and greatly complicate inferences about the demographic histories of vent organisms (Shea *et al.* 2009).

The Easter microplate (EM) boundary. Several species exhibit evidence for vicariance across the EM region of the SEPR. *Bathymodiolus* mussels from north and south of the Microplate differ genetically and may represent distinct species (Won *et al.* 2003a). The mitochondrial genealogies for northern and southern mussels are reciprocally monophyletic and may have split coincidentally with orogeny of the EM 4–5 million years ago (Naar & Hey 1991). Also, sister-species pairs of bythograeid crabs are separated across this boundary (Guinot *et al.* 2002; Guinot & Hurtado 2003). As with the EQ boundary, the EM region presents a variable dispersal filter for other species (Hurtado *et al.* 2004). Mitochondrial haplotype frequencies for *Riftia pachyptila* and *Tevnia jerichonana* shift significantly across this boundary, but not substantially for *Alvinella pompejana*, and not at all for *Branchiopolynoe symmytilida*. This superfast-spreading region of the SEPR axis is bathymetrically inflated; so, lateral walls do not protect its axial valleys from strong cross-axis currents. It is notable that mussels and crabs with free-swimming planktotrophic larvae are isolated across this region, but annelids with lecithotrophic larvae are slightly or not at all impeded across this boundary.

Cryptic species

During the course of our population genetic surveys, we uncovered several cryptic species complexes (reviewed in Vrijenhoek 2009). The *Lepetodrilus elevatus* species complex comprises three independent evolutionary lineages that cannot be distinguished morphologically (Craddock *et al.* 1997; Johnson *et al.* 2008; cf. Plouviez *et al.* 2009). *Lepetodrilus elevatus* s.s. and *L. galriftensis* co-occur at NEPR localities (Fig. 4), and a highly divergence allopatric lineage from the SEPR also deserves recognition as a distinct species (S. Johnson 2010, personal communication). Similarly, the *Oasisia alvinae* species complex includes three independent evolutionary lineages (Hurtado *et al.* 2004). Two distinct lineages are sympatric along the NEPR axis, although their frequencies shift north and south of the Rivera FZ, and an allopatric third lineage occurs south of the EM (Fig. 4).

Subdivision in other ridge systems

The Northeast Pacific

The NEP vents are hierarchically ordered (Fig. 2B–C). The NEP system is composed of the Explorer (EXP), Juan de Fuca (JDF), and GOR ridge axes, which are

separated by the Sovanco FZ and the Blanco TF. Each axis, like the JDF, is composed of several spreading segments (Endeavour, Cobb, etc.) that are separated by small offsets. Individual segments, like Endeavour (Fig. 2C), may contain multiple vent fields separated by tens of kilometres. Depths of the vents range from 1500 m on Axial Seamount to 3300 m in the North Escanaba Trough. This complex geomorphology creates opportunities for subdivision and speciation. For example, the 450-km-long Blanco TF is associated with vicariance of the limpets *Lepetodrilus fucensis* and *L. gordensis* (Johnson *et al.* 2006). Mitochondrial and nuclear gene genealogies suggest that the two species split about 9–11 Ma ago, roughly concordant with orogeny of the Blanco TF.

As previously noted, a geographical filter that is manifested as vicariance for one taxon may be manifested as restricted dispersal for another. The tubeworm *Ridgeia piscesae* exhibits limited unidirectional gene flow across the Blanco TF (Young *et al.* 2008). The proportion of genetic variance among axes ($\phi_{CT} = 0.378$, because of divergence of the GOR populations) is very large relative to differentiation within the EXP, JDF, and GOR axes ($\phi_{CS} = 0.041$). Analysis with the isolation-with-migration (IM) model (as developed by Nielsen & Wakeley 2001; Hey & Nielsen 2004) identified southward dispersal across the Blanco TF that is about 20 times greater than the reverse direction. These unidirectional vectors of dispersal are consistent with the strong southeasterly currents that move across this region (Fig. 2B).

Knowles *et al.* (2005) sampled the polychaete *Paralvinella pandorae* from five vents along the JDF axis. They hypothesized that its lecithotrophic larvae might have limited dispersal potential and predicted IBD along the 500-km sampled range. Their analysis of *mtCOI* revealed limited variation and no evidence for IBD. As previously demonstrated for EPR species, additional polymorphic loci and more population samples from a broader range are often needed to adequately test the IBD hypothesis (Audzijonyte & Vrijenhoek 2010).

The Mid-Atlantic Ridge

The slow-spreading MAR also exhibits great depth variation, high flanking walls, wide axial troughs, broad lateral offsets, and cross-axis currents that are predicted to favour increased subdivision and possibly speciation (Table 2). Researchers have examined this hypothesis in two taxa that dominate MAR vents.

Dense swarms of *Rimicaris exoculata* shrimp occur at most MAR vents. Grey individuals with a dorsal photoreceptor shaped like an angel-wing dominate microhabitat patches emitting hot effluents and smaller

orange shrimp with an oval photoreceptor dominate the cooler patches. Although taxonomists initially assigned the morphotypes to distinct genera and species, genetic studies revealed that the orange shrimp are juveniles of *R. exoculata* (Creasey *et al.* 1996; Shank *et al.* 1999). Teixeira *et al.* (2010) recently examined mitochondrial variation in *R. exoculata* and found very little differentiation among hydrothermal fields spanning 36° N to 4° S, about 9500 km of the MAR axis. Based on a very shallow, star-like, mitochondrial genealogy, the authors suggested that *R. exoculata* may have recently expanded into this region of the MAR. Closely related and possibly conspecific populations occur at Indian Ocean vents (Van Dover *et al.* 2002). However, a recent selective sweep involving the MAR populations also is possible. Testing these hypotheses will require independent nuclear markers.

Population genetic studies of MAR mussels led to the first report of a mid-ocean hybrid zone. *Bathymodiolus azoricus* occurs at the shallower (850–2251 m) northern localities, and *B. puteoserpentis* occurs at the deeper (3080–3650 m) southern localities (Maas *et al.* 1999). Examination of DNA sequences from seven nuclear loci and a mitochondrial locus suggest that these closely related species may have split <1 million years ago (Faure *et al.* 2009). They mix and hybridize at an intermediate latitude (O'Mullan *et al.* 2001), where a significant excess of nonrecombinant cytonuclear genotypes suggests that backcrossing is relatively limited (Won *et al.* 2003b). *B. azoricus* and *B. puteoserpentis* also host distinct strains of thiotrophic endosymbionts that they acquire from the local environment (Won *et al.* 2003c). Mixed symbiont infections occur in the hybrid zone, but the symbionts do not appear to 'leak' across the depth boundary that separates the host species.

The Indo-Pacific region

Western Pacific and Indian Ocean vent animals have received the least attention from population geneticists. Efforts have focused mostly on biogeography, species descriptions, and molecular taxonomy. The Kermadec Arc and the Manus, Lau, and North Fiji back-arc basins host a diverse vent fauna dominated by bathymodiolin mussels, provannid gastropods, siboglinid tubeworms, alvinocarid shrimp, and bythograeid crabs (Desbruyères *et al.* 2006). Recently explored vents along the CIR host many of the same genera (Van Dover *et al.* 2001); consequently, the CIR fauna clusters with the southwest Pacific Province (SWP) (Bachraty *et al.* 2009). In contrast, vents in the northwest Pacific Province (NWP) are dominated by genera of vesicomid clams and bathymodiolin mussels that also occur at cold seeps located off Japan (Kojima *et al.* 1995, 1996). Several genera of

siboglinid tubeworms occur at western Pacific vents. They appear to comprise independent radiations into vent habitats from ancestors that lived at hydrocarbon seeps (McMullin *et al.* 2003).

Taxonomists designated four species of mussels from this region: *Bathymodiolus brevior* Cosel *et al.* (1994) from the Lau Basin; *B. elongatus* Cosel *et al.* (1994) from the N. Fiji Basin; *B. septemdiarium* Hashimoto & Okutani (1994) from Suiyo and Mokuyo Seamounts south of Japan; and *B. marisindicus* Hashimoto (2001) from the central Indian Ridge. Yet several genetic studies reveal no evidence that these mussels are distinct evolutionary lineages (Van Dover *et al.* 2001; Iwasaki *et al.* 2006; Jones *et al.* 2006). Kyuno *et al.* (2009) examined mtDNA sequences in representative samples of the nominal species. They estimated very high rates of gene flow ($Nm \approx 30$) between western Pacific samples of *B. septemdiarium* and *B. brevior* taken 5000 km apart and moderate rates of gene flow ($Nm \approx 1.5$) between the western Pacific samples and Indian Ocean samples of *B. marisindicus* taken ~10 000 km apart. Using an IM analysis, the authors estimated that the Indian Ocean population was larger and older; so, they hypothesized that it recently expanded into the western Pacific. We have completed a multigene analysis of these Indo-Pacific mussels, and our results are consistent with this hypothesis (R. Vrijenhoek, P. Hoos and W. Jones, unpublished data). These mussels should be considered conspecific, with *B. brevior* as the senior synonym. Present-day opportunities to disperse via currents between the Indian Ocean and western Pacific are limited through the Indonesian region. Wallace's line marks a well-known boundary for marine and terrestrial faunas (Barber *et al.* 2000). Dispersal may have occurred through vents along the southern Indian Ridge and Kermadec Arc, but these regions remain mostly unexplored. Other vent animals from the Indo-Pacific should be studied in a similar ways to establish connectivity throughout a region that will soon be exploited for submarine mining of polymetallic sulphides.

Demographic processes and diversity

Demographic instability resulting from local extinction and recolonization events is expected to reduce the genetic diversity in a widely distributed species (Wright 1940; Slatkin 1977). The degree to which instability retards or augments differentiation among colonies depends on several factors, such as the number of founding colonists, the degree to which colonists derive from mixed sources (island model vs. propagule pool), and on rates of gene flow among the extant colonies (Wade & McCauley 1988). As long as gene flow exists ($Nm > 0$), the number of extant colonies (k) will affect

the overall effective size of a metapopulation and hence its capacity to retain genetic diversity (Maruyama & Kimura 1980). Consequently, genetic diversity should covary with k , the number of colonies that supply migrants. Species that maintain numerous closely spaced colonies (high site occupancy) should have a greater probability of colonizing a nascent vent in that region than species with fewer and more distantly spaced colonies. Considering the Maruyama–Kimura effect, species with high site occupancy should retain more genetic diversity than species with low occupancy.

A relationship between allozyme diversity and site occupancy was previously reported for eastern Pacific vent species (Vrijenhoek 1997). Site occupancy was estimated as the proportion of NEPR/GAR vents sampled during our 1990 expeditions that supported colonies of a particular vent species. Examination of published population genetic studies revealed that mean heterozygosity per locus increased with the site occupancy of these species ($R^2 = 0.50$; Fig. 5a). The mean proportion of polymorphic loci per population shows an even stronger correlation ($R^2 = 0.63$; Fig. 4 in Vrijenhoek 1997). This relationship is not a product of increasing the number of samples, because mean heterozygosity per sample should not be correlated with the number of samples; however, total genic diversity for a metapopulation should increase with the number of samples because it also includes the variance among colonies.

Because subsequent genetic studies turned their attention to mitochondrial DNA, I have plotted mean haplotypic diversity (h) per population against the proportion of vent areas at which I have sampled or observed each species along the NEPR/SEPR/GAR axes. Haplotypic diversity (h) was estimated from published reports (Table 1). At this broad geographical scale, h also increases with site occupancy of these species ($R^2 = 0.54$; Fig. 5b). *Alvinella pompejana* and *Branchiopolyno symmitilida* have high genic diversities and correspondingly high site occupancies, whereas *Calyptogena magnifica* has low diversity and occupancy. *Bathymodiolus thermophilus* has higher site occupancy along the SEPR than the NEPR/GAR, and its mitochondrial diversity is correspondingly higher in the south, increasing the overall average. Conversely, the *Riftia pachyptila* tube-worms have low occupancy along the SEPR and correspondingly lower mitochondrial diversity overall.

Evolutionary and ecological constraints might affect these relationships. Species with high site occupancy are among the pioneers to establish colonies at nascent vents (Vrijenhoek *et al.* 1998). On average, the pioneer species (black markers in Fig. 5) have higher allozyme heterozygosity than the late-arriving species (open markers), but this dichotomy does not appear to hold

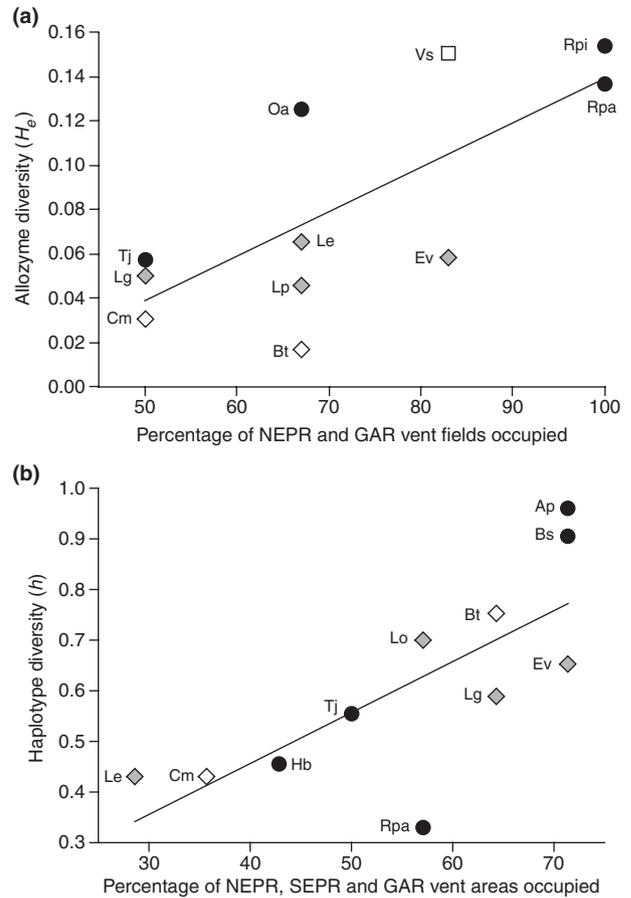


Fig. 5 Relationship between genic diversity and occupancy (%) as defined in the text. (a) Allozymes—mean heterozygosity (H_{exp}) vs. occupancy of eastern Pacific vent fields. (b) Mitochondrial DNA—mean haplotypic diversity (h) vs. occupancy of sampled eastern Pacific areas identified in Fig. 4. Note, Y-axes of graphs (a) and (b) are at different scales. Symbols: (◆) gastropod limpets; (◇) bivalve mollusks; (●) polychaete annelids; (□) amphipod crustacean. Species abbreviations: (Ap) *Alvinella pompejana*; (Bs) *Branchiopolyno symmitilida*; (Bt) *Bathymodiolus thermophilus*; (Cm) *Calyptogena magnifica*; (Ev) *Eulepetopsis vitrea*; (Hb) *Hesiolyra bergi*; (Le) *Lepetodrilus elevatus* s.s.; (Lg) *Lepetodrilus galriftensis*; (Lo) *Lepetodrilus ovalis*; (Lp) *Lepetodrilus pustulosus*; (Oa) *Oasisia alvinae*; (Rpa) *Riftia pachyptila*; (Rpi) *Ridgeia piscesae*; (Tj) *Tevnia jerichonana*; (Vs) *Ventiella sulfuris*.

for mitochondrial diversity. Similarly, annelids tend to have higher allozyme heterozygosity than the mollusks, but again this difference also does not apply to mtDNA. It is surprising that a relationship exists at all for mtDNA, because some researchers do not consider it a sensitive indicator of neutral genic diversity and effective population size (Bazin *et al.* 2006), but different opinions exist on this matter (Mulligan *et al.* 2006). The reported diversity measures are not very sensitive to recent demographic events, because they are mostly products of evenness rather than the richness of alleles, but these are the terms I could extract

from published studies without completely reanalysing original sequences that were not always accessible. While these apparent relationships between genetic diversity and site occupancy are intriguing, they warrant further investigation as other unsuspected factors may be involved. Nuclear DNA sequences should also be investigated to assess the consistency of these patterns.

Shallow star-like genealogical networks are apparent in the mtDNA studies of vent organisms (Won *et al.* 2003a; Hurtado *et al.* 2004; Kyuno *et al.* 2009; Plouviez *et al.* 2009; Teixeira *et al.* 2010). These studies reported significant values for Tajima's (1989) D , Fu's (1997) F_s , or mismatch distributions (Harpending 1994), which are commonly interpreted as indicators of recent population growth or expansions (Kuhner 2009). Demographic instability because of regional extinction events and colonization of re-activated ridge segments are hypothesized to create such patterns (Hurtado *et al.* 2004; Plouviez *et al.* 2009). For example, the tempo of extinction-recolonization events is expected to be greatest along the SEPR axis, which has superfast-spreading rates (Fig. 3). If demographic instability contributes to smaller population sizes, genetic diversity should be lower in SEPR populations, but the evidence is inconsistent. The expected patterns occur for nuclear and mitochondrial DNA sequences in *R. pachyptila* tubeworms (K. Coykendall 2010, personal communication) and *L. pustulosus* limpets (S. Johnson 2010, personal communication), but the opposite relationship is seen in published studies of *A. pompejana*, *C. magnifica*, and *B. thermophilus*. The southward declines in mitochondrial diversity might be products of re-invasions from the North following vicariance and regional extinction events and *vice versa* in other species (e.g. Plouviez *et al.* 2009). Shea *et al.* (2009) provide an excellent review of demographic and ecological processes that are expected to result in nonequilibrium population and community dynamics. Further empirical studies with multiple independent gene markers will be needed to address these hypotheses.

Cognate environments

Soon after the discovery of hydrothermal vents, similar chemosynthetic communities were found at cold-water hydrocarbon seeps off the West Florida Escarpment (Paull *et al.* 1984). Now we know that seeps occur worldwide along continental margins and that the associated animals show strong ecological and evolutionary connections with those found at hydrothermal vents (reviewed by Sibuet & Olu 1998). Chemosynthetic communities also occur in deep anoxic basins such as fjords and at sites of organic enrichment such as decomposing

wood and sunken whale carcasses (Smith & Baco 2003). The spatial distributions and temporal stabilities of these communities differ greatly, however. Cold seeps occur mostly along continental margins, and they are believed to produce a steadier supply of reduced gases than vents, providing relatively stable habitats. Sunken animal carcasses are distributed mostly along the migratory paths or feeding and breeding grounds of large cetaceans. Whale-falls persist for several decades in the deep anoxic basins off southern California, but they degrade more rapidly in the deep oxic waters off Monterey, CA (Braby *et al.* 2007). If seeps are more stable on average than vents and whale-falls, the associated taxa should retain greater genetic diversity than vent and whale-fall taxa. Very few population genetic studies have been undertaken with seep and whale-fall taxa, so comparative data are limited. Two bone-eating siboglinid worms, *Osedax rubiplumus* and *O. roseus*, found on whale-falls off Monterey, CA, have mitochondrial diversities that are as great or greater than those found in eastern Pacific vent tubeworms (Rouse *et al.* 2008; Vrijenhoek *et al.* 2008b). The two boneworm species are very widespread, also occurring off the Japan coast (F. Pradillon 2010, personal communication), and they can grow on other sunken mammalian bones (Jones *et al.* 2008; Vrijenhoek *et al.* 2008a,b). Although sunken bones provide small and ephemeral habitats, they might serve as stepping stones that connect chemosynthetic habitats along the eastern and western North Pacific margins. These matters are the subjects of ongoing studies.

Phylogenetic analyses reveal historical interchanges among chemosynthetic environments. Various bathymodiolin mussel species, for example, exploit wood, whale-fall, seep or vent habitats, though controversy surrounds the order in which these habitats might have been invaded (Distel *et al.* 2000; Jones *et al.* 2006). Siboglinid tubeworms and vesicomid clams are found at vents, seeps, and sites of organic deposition. Seep lineages are the most diverse phylogenetically, and they occupy basal nodes in their respective phylogenies. In contrast, other vent taxa like alvinocarid shrimp and bythograeid crabs have only been reported from vents. Present phylogenetic evidence for both taxa suggests relatively recent (Cenozoic) 'explosive' evolution of these taxa (Shank *et al.* 1999; L. Hurtado 2010, personal communication).

It is hypothesized that whale-falls might provide stepping stones that connect distantly spaced vent and seep habitats (Smith *et al.* 1989). For example, the seep tubeworm, *Escarpia spicata*, has also been found living near sedimented hydrothermal vents and at a whale-fall (Feldman *et al.* 1998). Several species of vesicomid clams that are primarily seep-restricted have been

reported from sedimented vent localities and whale-falls (Baco *et al.* 1999). International efforts to resolve the systematic relationships of vesicomyid clams and conduct phylogeographic studies are presently underway (A. Audzijonyte 2010, personal communication). These studies should help to test the 'whale-falls as stepping-stones' hypothesis. Similar international efforts should be directed at the siboglinid worms and several gastropod taxa.

The past, present, and future of vents

Excitement surrounding discoveries of putative 'relict species' at the Galápagos hydrothermal vents led several researchers to hypothesize that chemosynthetic environments have provided refugia from the global mass extinction events that decimated biotic diversity in the photic zone at the end of the Paleozoic and Mesozoic eras (McLean 1985; Newman 1985; McArthur & Tunnicliffe 1998). Evidence from fossilized vent and seep deposits for Silurian monoplacophorans and Devonian 'vestmentiferan' tubeworms and 'vesicomyid' clams fed excitement regarding the 'living fossils' hypothesis, but these identifications have been disputed (reviewed in Little & Vrijenhoek 2003; Campbell 2006; also Amano & Kiel 2007; Kiel & Dando 2009). Deep-sea hydrothermal vents are not eternally stable refugia, immune to forces that have affected Earth's surface. Vent animals are all aerobic, obtaining nutrition by eating microbes or hosting them as symbionts, or as suspension feeders, predators, and scavengers. Vent microbes and their invertebrate hosts live in narrow zones defined by an interface between oxic and anoxic waters (Stewart *et al.* 2005). The delivery of reduced gases in anoxic vent effluents is ephemeral, and hydrodynamic circulation that delivers oxic waters to ocean depths also changes over time. For example, the development of anoxic ocean basins during the Cretaceous (~90 Ma) and early Cenozoic (~56 Ma) is associated with extinctions of many deep-sea taxa (Jacobs & Lindberg 1998). Vent animals living at narrow oxic-anoxic interfaces would be especially vulnerable to such events. Perhaps these catastrophic climate changes in Earth's history help to explain why phylogenetic analyses have revealed relatively recent origins for most of the dominant vent and seep taxa (Little & Vrijenhoek 2003). Fossil evidence suggests that related faunas from hydrocarbon seeps may be somewhat older (Kiel & Little 2006); nonetheless, fossil vent and hydrocarbon seep deposits reveal dramatic changes in community composition through geologic time (Little & Vrijenhoek 2003; Campbell 2006). Present-day accumulations of greenhouse gases and global warming, though small compared to catastrophic events during the Cretaceous and

early Cenozoic, may nevertheless threaten deep-ocean circulation regionally and thereby affect the viability of vents and other chemosynthetic environments.

Mining poses a more immediate threat to vent communities. Nautilus Minerals, Inc. has secured leases from the Papua New Guinea government to explore for high-grade copper, gold, zinc, and silver in massive sulphide deposits of the Manus Basin vents (<http://www.nautilusminerals.com/s/Projects-Solwara.asp>).

The animals living on these hydrothermal mounds will surely be disturbed, but it is not known whether these anthropogenic disruptions will have more substantive impacts than the submarine volcanic events that regularly disturb this region. The Nautilus Solwara Project appears to be heavily invested in developing an implementation plan based on ecologically sound 'best practices' for sustainable recovery of minerals, and they have funded genetic studies aimed at assessing the potentially unique nature of the Manus Basin fauna (e.g. Thaler *et al.* 2010). Studies are now underway to assess genetic relationships and gene flow between the Manus basin fauna and the Lau and North Fiji back-arc basins (A. Thaler 2010, personal communication).

Scientific exploration and sampling of vents with human-occupied and robotic submersibles also poses threats. Submarine vehicles could carry hitchhiking animals, microbes, and potentially diseases between vents (Van Dover *et al.* 2007). Clearly, it is wrong to think of deep-sea vents as eternally stable habitats that are protected from surficial catastrophes and anthropogenic disturbances. The same anthropogenic factors that have impacted terrestrial islands (exploitation, habitat destruction, invasive species, and diseases) will probably affect deep-sea hydrothermal vents. Two nations have created Marine Protected Areas (MPAs) for vents. Lucky Strike and Menez Gwen vent fields on the MAR were designated the first deep-sea MPAs by the Azores government in June 2002. Canada designated the Endeavour Segment a marine MPA in March 2003. Other vent fields that lie in national waters may eventually gain similar status, but protection of vents that lie outside of exclusive economic zones will require international cooperation. With their mineral wealth and recent advances in submarine mining technologies, protecting these deep-sea environments and their fauna will be a daunting task. It is hoped that rapidly accumulating genetic data on species boundaries, connectivity, and diversity will help to design these preserves.

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