Ecological connectivity in Pacific deep-sea hydrothermal vent metacommunities

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ABSTRACT: Larval dispersal and connectivity between patchy, transient, deep-sea hydrothermal vent communities are important for persistence and recovery from disturbance. We investigated connectivity in vent metacommunities using the taxonomic similarity between larvae and adults to estimate the extent of exchange between communities and determine the relative roles of larval dispersal and environmental limitations (species sorting) in colonization. Connectivity at vent fields in 3 Pacific regions, Pescadero Basin, northern East Pacific Rise (EPR), and southern Mariana Trough, varied substantially and appeared to be driven by different processes. At Pescadero Basin, larval and adult taxa were similar, despite the existence of nearby (within 75 km) vent communities with different species composition, indicating limited larval transport and low connectivity. At EPR, larval and adult taxa differed significantly, despite the proximity of nearby vents with similar benthic composition, indicating substantial larval transport and potentially strong species sorting, but other factors may also explain these results. At the Mariana Trough, the larvae and adults differed significantly, indicating high larval transport but environmental limitations on colonization. We demonstrate that analysis of routinely collected samples and observations provides an informative indicator of metacommunity connectivity and insights into drivers of community assembly.

KEY WORDS: Hydrothermal vent · Connectivity · Larval transport · Larval dispersal · Species sorting · Metacommunity

1. INTRODUCTION

For most marine benthic species, dispersal takes place during a planktonic larval stage. Larval dispersal between habitat patches influences many important processes at the population and community level. These include regional persistence of populations and local and regional population dynamics (Cowen & Sponaugle 2009) as well as community assembly (cf. Weiher et al. 2011). However, the extent to which marine communities are open to larval supply and colonization from distant sources (ecological connectivity) and how this varies between sites

remain important questions (Levin 2006). In patchy marine habitats it can be useful to consider communities within a metacommunity framework (cf. Leibold & Miller 2004) because the extent of connectivity between patches will influence the resilience of the metacommunity to disturbance.

The study of exchange of individuals in marine systems is challenging and often implemented using a population genetics approach focused on individual species (Lowe & Allendorf 2010). However, characterising genetic connectivity of individual species typically provides insights on long (multi-generational) time scales and may reveal little about the overall

connectivity of a community. Some attempts have been made to infer connectivity patterns at the community level by characterising the variation in population genetic structure across many co-distributed species (Selkoe et al. 2014). Although such approaches can provide important information for designing effective marine protected areas (White et al. 2010), they do not provide information on the relative importance of larval dispersal and environmental limitations on colonization as determinants of community assembly.

Deep-sea hydrothermal vents fit very well the ephemeral-patch metacommunity archetype described by Leibold et al. (2004); they comprise assemblages occupying temporary habitat patches that vary in position with time and are distinct from the background habitat matrix. Of the 4 paradigms those authors used to study metacommunities, we adopt the species-sorting framework. Under this paradigm we can characterise larval dispersal between habitat patches in terms of the extent to which the species composition of plankton at the target site is similar to benthos at other sites in the region. The strength of species sorting in each habitat patch is measured by the differentiation in species composition between plankton and the resident benthos. The species composition of benthos in each site is maintained by larval dispersal from other sites and the strength of species sorting, which in combination can lead to differences in the species composition of benthic communities and, therefore, the strength of ecological connectivity (hereafter referred to as connectivity).

Understanding these processes is important for deep-sea hydrothermal vents, which are naturally disturbed, patchy habitats that support abundant faunal communities (Corliss et al. 1979) and may be impacted by deep sea mining in the future (Miller et al. 2018). Evidence from larval physiology and behaviour (Yahagi et al. 2017) and genetics (Teixeira et al. 2012) indicates a potential for long-distance dispersal and high connectivity between vent communities. Long-distance dispersal events are important for the colonisation of disturbed vent sites (Mullineaux et al. 2010), but larval dispersal can be restricted by currents and topographic barriers (Watanabe et al. 2005, Xu et al. 2018). These processes can lead to larval retention near their natal site even if the species has a long planktonic larval duration (Breusing et al. 2016). Larval behaviour can also act to increase larval retention near natal vents, especially in situations where larvae move vertically in sheared currents near the seafloor (Mullineaux et al. 2013). However, the inaccessibility of vent sites means that direct evidence of self-recruitment, for example through larval tagging as used in coastal systems (Jones et al. 2005), is not available.

The extent of connectivity between marine communities is difficult to quantify, but the more-constrained question of whether a community is largely self-recruiting or 'closed' is often simpler to address (Jones et al. 2005). The aim of this study is to explore whether samples routinely collected from hydrothermal vents (larvae, recently settled juveniles, and small adults) can be used to estimate the extent of exchange between communities and determine relative roles of larval dispersal and environmental limitations to colonization. We propose a conceptual framework that uses the similarity in species composition between larvae in the plankton and adults in the benthos at a vent site to assess the relative roles of larval transport (whose geographic extent is set by current-mediated larval transport) and species sorting on community composition (Fig. 1). In this framework, the larval/adult comparisons are most informative when nearby vent fields are dissimilar in species composition to the target vent and become complicated when communities have been disturbed recently. Our general aim of assessing connectivity is like that of many vent population genetics studies (reviewed in Vrijenhoek 2010), but we investigate connectivity at the community level and make a direct connection between connectivity and community assembly processes by documenting the geographic extent of the larval transport. Finally, by comparing the larval supply to the local community, we investigate the process of species sorting that ultimately determines which species are present in the benthos.

We focus on 3 Pacific vent regions that differ in their geological and oceanographic setting, and hence their expected larval dispersal: Pescadero Basin, northern East Pacific Rise (EPR), and southern Mariana Trough. For a target vent field in each of these regions, we locate nearby vent fields and identify the closest one that hosts a distinctly different benthic fauna, based on published species distributions. This information is used to predict the geographic extent of the larval pool and whether it is likely to contain species that are dissimilar to the local benthos. A comparison of species composition of the benthos and plankton at each vent field allows for a test of the relative importance of larval supply and species sorting in driving community assembly in deep thermal vents. The broader goals of this study are to contribute new data on occurrence of vent adults and larvae to global databases and to
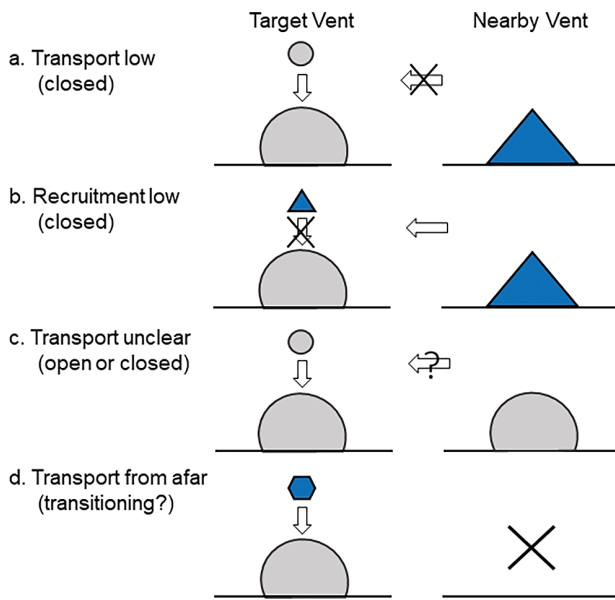
Fig. 1. Connectivity in a vent meta-community. Shape represents species composition of benthos (at seafloor) and larvae (in plankton) at target and nearby vents. Different color indicates different species composition. Horizontal arrows show larval transport to target vent; vertical arrows show species sorting. Scenarios: Benthos and larvae are (a) similar to each other and dissimilar to nearby vent (limited larval transport, closed community); (b) dissimilar (unlimited larval transport, species sorting, closed community); (c) similar at target and nearby vents (possible self-recruitment; larval transport unclear); (d) dissimilar at recently disturbed vent; nearby vent is destroyed (larval transport from remote vents, potential for transition in benthic species)

develop conceptual approaches that extract information on dynamic processes such as dispersal and connectivity from observations that will become increasingly available as part of ocean observing initiatives (Levin et al. 2019).

2. MATERIALS AND METHODS

2.1. Study areas

This study uses existing samples that were collected for other purposes from 3 regions in the Pacific. The vent fields included in this study are Auka in the Pescadero Basin, 9° 50′ N in the northern EPR, and Snail and Pika in the southern Mariana Trough (Fig. 2) as listed in the InterRidge vents database (Beaulieu & Szafrański 2020). Snail and Pika are separated by less than 5 km and for the purposes of this study are considered as a single southern Mariana Trough vent field. Hereafter the study sites are referred to as Pescadero Basin, EPR and Mariana

Trough, respectively. Samples were collected from a number of vents within each field (Table 1); a vent incorporates the area surrounding active venting, usually on the scale of tens of meters. Vent sampling sites at Pescadero Basin were separated by less than 1 km, at the EPR by less than 2 km and in the Mariana Trough by less than 5 km. Larval exchange at this intra-field scale was not addressed in this study, but sampling over multiple vents and vent habitat types was needed to cover the full range of habitat and faunal diversity. At all vent fields, the sample dates for plankton and benthos were matched as closely as possible.

The vent fields differ in their geological setting, which influences their proximity to, and potential connectivity with, other vent fields. The Pescadero Basin is a heavily sedimented spreading centre in the Gulf of California with unusual vent chemistry (Paduan et al. 2018) and a modelled spreading at a rate of 5 cm yr^{-1} (DeMets et al. 2010). The nearest vent field with known community composition is located on the Alarcón Rise, approximately 75 km away (Beaulieu & Szafrański 2020). Vent communities at Alarcón Rise differ in species composition from those in the Pescadero Basin (Goffredi et al. 2017). Other vent fields, not yet listed in the InterRidge database, have been discovered in the Pescadero Basin (Goffredi et al. 2021), but their faunal communities have not yet been fully described, so we consider Pescadero Basin as comprising one vent field (Auka). Pescadero Basin vents are roughly 1300 m deeper than those on the Alarcón Rise (Beaulieu & Szafrański 2020). Based on geographic distance and topographic discontinuity, we expect that larval exchange with Alarcón Rise vent fields to be lower for the Pescadero Basin (Fig. 1a) than for the other fields in our study.

The EPR near 9° 50′ N is a rapidly spreading mid-ocean ridge (10 cm yr^{-1}) with vent field spacing as close as 3.3 km (Baker et al. 2016). Biophysical models incorporating hydrodynamics, pelagic larval duration, and vent field spacing have demonstrated the potential for both larval transport and recruitment along the ridge (Xu et al. 2018). Faunal communities across the northern EPR from 9° to 13° N tend to share similar species composition (Desbruyères et al. 2006), and the vents are similar in chemical characteristics. The nearest vent field known to host substantially different species is Medusa, 77 km away (Klein et al. 2013). For established communities in the 9° 50′ N vent field, larval and ecological connectivity with other vent fields is expected to be relatively high (Fig. 1c) but perhaps not easily distinguished
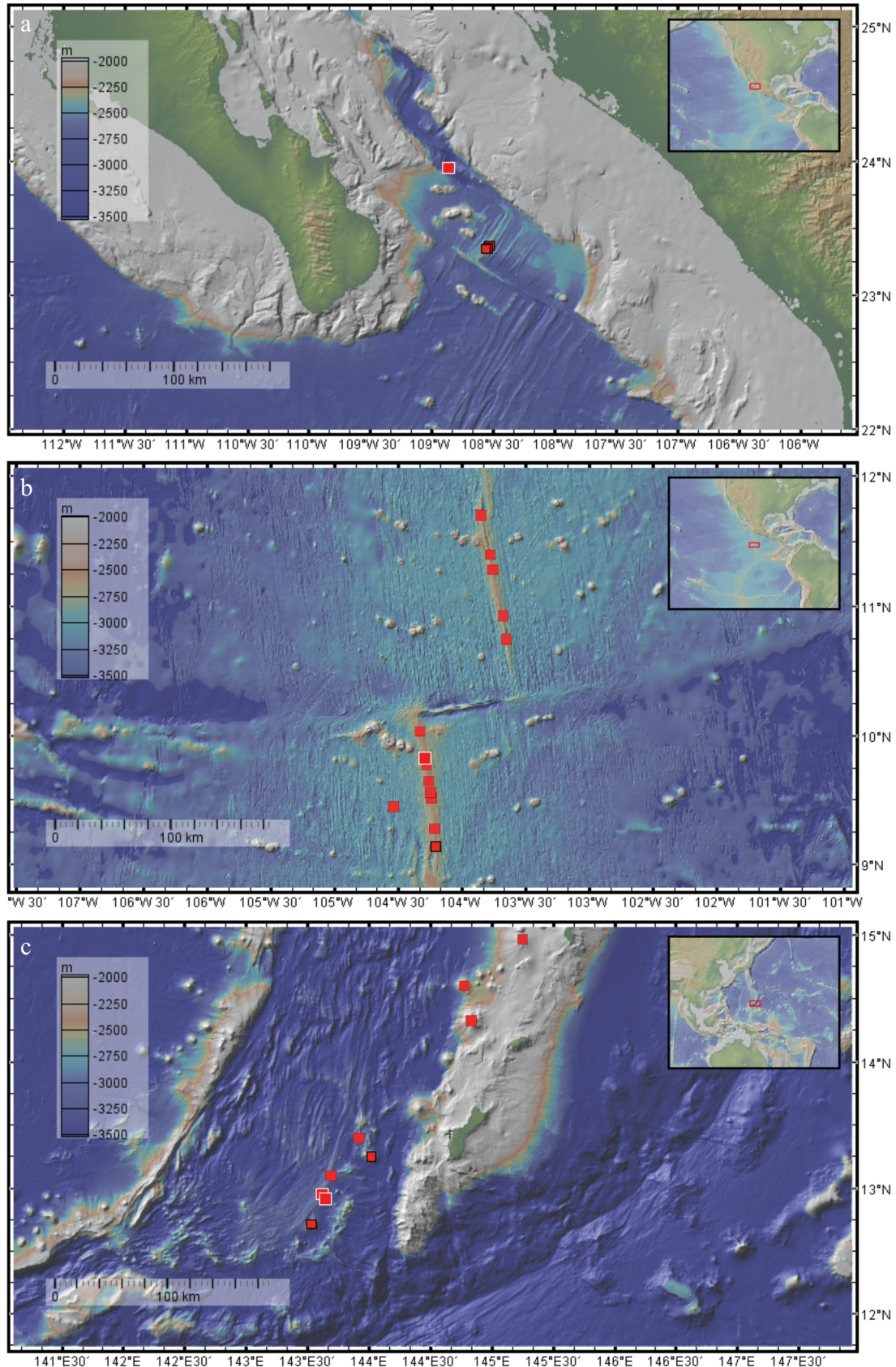
Fig. 2. Vent field locations in the areas surrounding the 3 vent fields in this study: (a) Pescadero Basin (Auka vent field), (b) northern East Pacific Rise (EPR) (9° 50′ N vent field), (c) southern Mariana Trough (Snail/Pika vent field). Target fields shown with white border; nearest faunally dissimilar fields (Alarcón Rise at Pescadero, Medusa vent at EPR, and Seamount X and TOTO Caldera at Mariana) shown with black border. Vent field locations are from the InterRidge vents database (Beaulieu & Szafrański 2020). Maps created in GeoMapApp ver. 3.6.10 (Ryan et al. 2009)

Table 1. Samples in the plankton and benthos at the 3 vent fields. Location and maximum depth of each vent field are from Beaulieu & Szafrański (2020). For the plankton, the individual vent sites are annotated with the number of samples collected (in parentheses; * denotes samples collected away from the vent), the height (m) above bottom (mab), and the kind of collector used. For the benthos, vent sites are annotated with the number of samples in each zone (H: hot; W: warm; C: cool; zones not distinguished for Mariana Trough), and the kind of collector. For the pre-eruption EPR, no benthic samples were available for the precise dates when plankton were sampled, so samples from 17 mo earlier were used

| Vent field | | | Plankton | | | | Benthos | | |
Name	Location	Depth (m)	Date	Vent(s) (no. samples)	Height (mab)	Collector	Date	Vent(s) (no. samples)	Collector
Pescadero Basin	23° 57.40′ N, 108° 51.72′ W	3685	Oct 2017	C (1), Z (3), Matterhorn (3)	1	Slurp	Oct 2017	C (2H,1W), Z (1H,1C), Matterhorn (3H,1W,2C)	Slurp
EPR: pre-eruption	9° 49.80′ N, 104° 17.40′ W	2520	Dec 1998	East Wall (1), X5 (1)	1	Pump	May 1998	East Wall (3H, 3W, 3C)	Block
			May 2000	Biovent (1), Tica (1)					
EPR: post-eruption	9° 49.80′ N, 104° 17.40′ W	2520	Nov 2007	Tica (4)	3–4	Pump	Nov 2007	P-Vent (3H, 3W, 3C)	Sandwich
Mariana Trough	12° 57.20′ N, 143° 37.12′ E (Snail)	2880 (Snail)	Sept 2010	Snail (1, 1*), Archaean (1*), Urashima (1, 1*)	3–4	Pump	Sept 2010	Snail, Pika, Archaean, Urashima	Slurp

from a self-recruiting community, given the similarity of vent community composition along the northern EPR. Eruptive disturbance in this region is frequent (Fornari et al. 2012), so the species composition of individual benthic communities changes over time (Shank et al. 1998), and the region may comprise a mosaic of vent fields in different stages of succession.

At EPR we were able to compare the benthos and plankton at 2 time points when the communities were at different stages in assembly: the first in an established community (pre-eruption) and the second in a community that had been disturbed in a 2006 eruption (post-eruption). Post-eruption communities typically are low-density and low-diversity in early successional stages (e.g. Mullineaux et al. 2012). As local larval production was likely reduced directly after the eruption, and larval immigrants from remote communities prevalent in the plankton (Mullineaux et al. 2010), we expect the plankton and benthos to be less similar in the post-eruption communities (Fig. 1d) than in pre-eruption ones (Fig. 1c).

The southern Mariana Trough is a back-arc basin in the western Pacific, with a spreading rate of roughly 5 cm yr^{-1} (Kato et al. 2003). The Snail/Pika vent field included in this study is within 20 km of other known back-arc basin vents, and within 30 km of vents in the Mariana Arc (Beaulieu & Szafrański 2020). Faunal communities in the southern Mariana Trough have not been extensively documented, al-

though 2 studies report that vents in the Mariana Trough (back-arc basin) have similar community composition that differs from the vent fauna found at Mariana Arc vents (Kojima & Watanabe 2015, Giguère & Tunnicliffe 2021). The nearest vent field known definitively to have different community composition from Snail/Pika is 55 km away at Seamount X (Giguère & Tunnicliffe 2021), although reports of siboglinid tubeworms at TOTO Caldera, 27 km away, suggest it may also differ substantially (Nakagawa et al. 2006). Both Seamount X and TOTO Caldera are located in the Mariana Arc, with TOTO Caldera at similar depth to Snail/Pika. The close proximity of vent fields with both similar and dissimilar community compositions suggests the potential for high larval dispersal but not necessarily high ecological connectivity (Fig. 1b or 1c).

2.2. Sampling

Larvae in the plankton were collected by pumping and filtering seawater over a 63 µm mesh in the vicinity of vent communities (Table 1). All larvae collected were preserved in 95% ethanol. Plankton sampling was done as consistently as possible across the vent fields, but different submergence vehicles and gear were available at each. At Pescadero Basin a suction (slurp) sampler attached to ROV 'Hercules'

was used to sample plankton at ~1 m above bottom. Samples were collected from multiple locations around Matterhorn, Z and C vents. The slurp sampler suctioned seawater for 10 min at a rate of approximately 115 l min^{-1}, filtering a total volume of 1150 l for each sample. At the EPR and Mariana Trough, plankton samples were collected using a McLane WTS-LV50 plankton pump attached to a sub-surface mooring within ~4 m of the bottom, as in Beaulieu et al. (2009). The pump sampled for 24 h at a rate of 30 l min^{-1}, filtering a sample volume of roughly 40 000 l. Where possible, plankton samples were collected near a vent orifice, but due to the limited number of plankton pump samples available from the Mariana Trough, pump samples collected off-site (100–300 m away from the vent) were included in the analysis of that region.

Benthic samples were collected on colonisation surfaces or by seafloor slurp (Table 1), across environmental gradients and their associated faunal zones. The colonisation surfaces had long deployment periods and represented the surrounding benthic community, except for highly mobile species (e.g. fish and large crustaceans). The slurps collected most benthic species effectively, except for those firmly attached to hard substrata (e.g. barnacles and serpulid polychaetes).

For Pescadero Basin, the benthic samples were collected by the slurp on the ROV 'Hercules'. The slurp intake was positioned within a few cm of the seafloor, and the suction operated on decreased power (60%) until the 63 µm filter clogged. Benthic slurp samples were collected at the same locations as the plankton slurps. At each sampling location one sample was collected close to the emerging vent fluid and another collected 50 cm away. At one location an additional sample was collected 75 cm away from the emerging vent fluid due to the bacterial mat zonation present at this site. The mean temperature recorded at each sampling location was used to assign samples to either the hot (>10°C), warm (2–10°C) or cool (<2°C) zone. Each benthic sample was passed through a 38 µm sieve, split into quarters, then preserved in 95% ethanol on board the vessel. One quarter was provided to collaborators, and the other 3 were retained for quantitative analyses.

The colonisation surfaces used for samples at EPR were basalt blocks for pre-eruption and polycarbonate sandwiches for post-eruption time points. Basalt blocks measured roughly 10 cm on a side (Micheli et al. 2002) and were deployed for 37 mo. Sandwiches comprised 6 plates, 10 cm on a side and 0.7 cm thick, separated by 1 cm (Mullineaux et al. 2010), and were deployed for 11 mo. The colonisation surfaces were deployed in 3 different zones: hot (10–30°C), warm (2–10°C) and cool (<2°C), as recorded with a temperature probe. On recovery, the colonisation surfaces were placed into separate compartments and brought up to the surface. The surfaces and any detached individuals retained on a 63 µm sieve were preserved in 80% ethanol.

In the Mariana Trough, the benthos was sampled in 2010 by a slurp attached to the DSV Shinkai 6500, as reported in Beaulieu et al. (2011). Quantitative counts were not available, so a presence–absence list of taxa was constructed for each vent site within the (grouped) Mariana Trough vent field. Identifications for benthic specimens collected during the 2010 cruise were reported in Kojima & Watanabe (2015) and the Japan Agency for Marine-Earth Science and Technology GODAC DARWIN database (JAMSTEC 2019).

2.3. Identification, inclusion, and grouping of taxa

Individual specimens retained on a 63 µm sieve or present on a colonisation surface (including detached individuals >1 mm) were identified morphologically and counted under a dissecting microscope. Identifications were made to the finest taxonomic level possible. From the Pescadero Basin and Mariana Trough, specimens of relatively abundant taxa or morphotypes that lacked defining characteristics were selected for genetic sequencing (details in the Supplement section 'Supplementary sample analyses'; www.int-res.com/articles/suppl/m731p267_supp.pdf). The sequences were compared to those in the GenBank database using a BLAST search (nucleotide BLAST using a megablast search level). In most cases, the results from the BLAST search were insufficient to identify specimens down to species level. Therefore, the genetic results were used primarily as support for the morphological identifications.

The taxa included in analyses were limited to vent-endemic, metazoan species that were likely to be sampled as adults using a slurp or colonization surface (i.e. no highly mobile fish or crustaceans). For groups of taxa in which taxonomic resolution differed between the plankton and benthos, the coarsest grouping was used for both. Taxa with larvae that could not be morphologically identified to a taxonomic rank below class were excluded (details on exclusion and grouping are in the Supplement 'Supplementary sample analyses').

2.4. Comparison of benthic and planktonic taxonomic composition

We used published data for the benthos at EPR (Mullineaux 2020) and Mariana Trough (Kojima & Watanabe 2015, JAMSTEC 2019), and new results from this study for the plankton and benthos at Pescadero Basin, and the plankton at EPR and Mariana Trough. Comparisons between the planktonic and benthic samples were conducted using presence–absence for consistency across all vent fields (counts were not available for the Mariana Trough benthos). A Jaccard dissimilarity matrix was created for the non-metric multidimensional scaling (NMDS) analysis. A permutational analysis of variance (PERMANOVA) was used to test for differences between the plankton and benthic samples as well as differences between zones. PERMANOVA is a non-parametric approach that tests the null hypothesis that there is no difference between the centroids of the groups being tested (Anderson, 2001). All analyses were conducted in R (version 4.0.3) (R Core Team 2020) using the 'vegan' package (version 2.5-6) (Oksanen et al. 2013). To explore the influence of individual prominent species on community patterns, quantitative counts were also compared between benthic and planktonic samples at Pescadero Basin and EPR.

3. RESULTS

In the Pescadero Basin, the taxonomic composition of the planktonic and benthic samples overlapped substantially, with no significant difference detected (Fig. 3a; PERMANOVA, $F_{1,16}$ = 2.17, p = 0.10). All taxa found in the plankton were also found in the benthos (Fig. 4), except for the gastropods *Lepetodrilus* spp. (see Table S2). The benthos showed little differentiation across the 3 temperature zones (Fig. 3a). There was, however, a notable difference between the plankton and benthos in the relative abundance of some of the most numerous taxa (Fig. 3e). Chaetosphaerid polychaetes were abundant in the plankton but rare in the benthos, especially in the hot and warm zones. In contrast, the polychaete *Ophryotrocha* sp. occurred in all samples and dominated the benthos samples except in the cool zone. The neomphalid-like gastropods occurred in most samples and were particularly abundant in the benthic cool zone.

In the pre-eruption EPR, community composition differed significantly between the plankton and benthos (Fig. 3b; PERMANOVA, $F_{1,11}$ = 10.13, p = 0.003). Composition also differed significantly across samples collected in different benthic temperature zones (PERMANOVA, $F_{2,6}$ = 2.99, p = 0.004), demonstrating that it was important to have sampled across environmental gradients. The plankton samples were similar to each other in composition despite having been collected 17 mo apart and at 4 different vent sites (Table 1). Most samples tended to be dominated by a single taxon which differed between the planktonic and benthic samples (Fig. 3f). The gastropods *Lepetodrilus* spp. and *Cyathermia naticoides* were prominent in the plankton, whereas the nectochaete polychaete group dominated most of the benthic samples except in the cool zone where the chaetosphaerid group was prominent. All the taxa found only in the plankton were gastropods (Table S1). Siboglinid tubeworms were found only in the benthic samples, which is not unexpected as siboglinid larvae have never been observed in plankton samples despite being common at vents. The sole bivalve taxon *Bathymodiolus thermophilus* was also found only in the benthos. Despite being relatively abundant in the plankton, only a single individual of *C. naticoides* was found in the benthic samples. The hot and warm zones in the benthos were dominated by the nectochaete group (mostly *Amphisamytha galapagensis*; Table S2). The benthic cool zone displayed higher relative abundance of the chaetosphaerid group (mostly *Laminatubus alvini*) than the other zones (Fig. 3f).

In the post-eruption EPR, patterns in community composition were similar to pre-eruption in that plankton and benthos differed significantly (Fig. 3c; PERMANOVA, $F_{1,11}$ = 5.16, p = 0.004), and benthic zones differed significantly from each other (PERMANOVA, $F_{2,6}$ = 4.67, p = 0.02). The fauna in the benthic warm and cool zones were more similar in composition to each other than to fauna in the hot zone. All plankton and benthic samples were collected on the same cruise at vents within 1 km of each other, so the observed patterns did not appear to be influenced by the sampling design. Similar to the pre-eruption EPR, most of the post-eruption planktonic and benthic samples were dominated by a single abundant taxon. The gastropods *Lepetodrilus* spp. (Fig. 3g) were particularly prominent in the benthic samples in warm and cool zones, whereas *C. naticoides* and siboglinids were abundant in the hot zone. The siboglinids were the only polychaete group not found in both the plankton and the benthos. In contrast to the pre-eruption samples, the nectochaete group or chaetosphaerid group were not
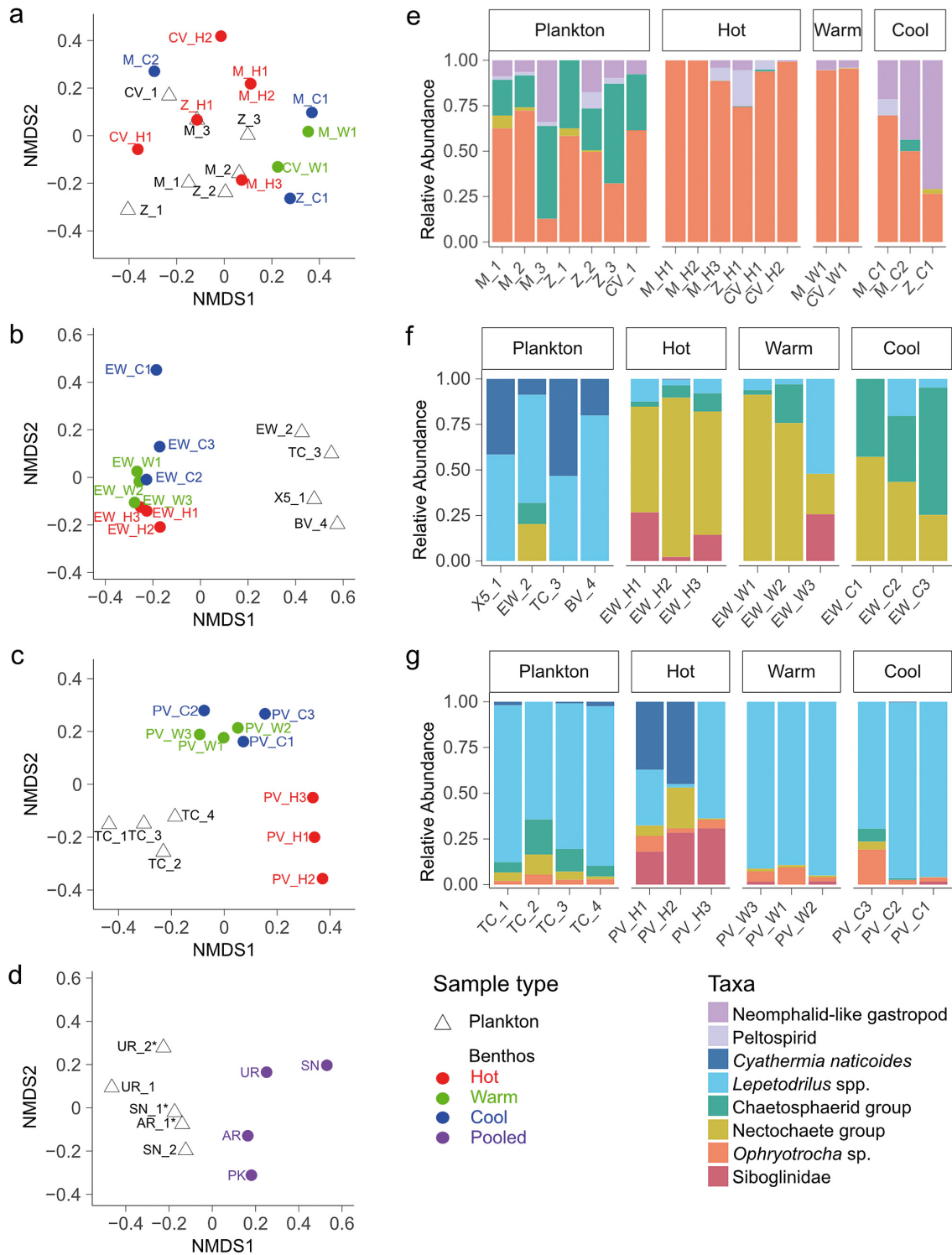
Fig. 3. Community composition and taxon abundance in plankton and benthos of the 3 Pacific sample sites. Community patterns are displayed in a non-metric multi-dimensional scaling analysis (NMDS) using Jaccard dissimilarity matrix calculated from presence/absence data: (a) Pescadero Basin (vents M, Z and CV; stress = 0.11); (b) East Pacific Rise (EPR), pre-eruption (vents EW, X5, BV, and TC; stress = 0.06); (c) EPR, post-eruption (vents PV and TC; stress = 0.07); and (d) Mariana Trough (vents SN, AR, PK, and UR; stress = 0.03). Individual samples are labelled by vent and (for benthos) zone: hot (H, red), warm (W, green), or cool (C, blue). At Mariana Trough, some plankton samples were collected 100–300 m away from the vent orifice (denoted with •); benthic data were pooled across zones (purple). Relative abundances of prominent taxa: (e) Pescadero Basin; (f) EPR pre-eruption; (g) EPR post-eruption. Vent abbreviations correspond to vent names in Table 1: Matterhorn (M), Z and C (CV) at Pescadero Basin, X5, East Wall (EW), Biovent (BV), Tica (TC), and P (PV) at EPR, and Snail (SN), Archaean (AR), Pika (PK) and Urashima (UR) vents at Mariana Trough

prominent in the benthos. As in the pre-eruption state, peltospirids were found only in the plankton and *B. thermophilus* was found primarily in the benthos. One striking pattern in the post-eruption samples was the presence of 5 larval taxa (4 polychaetes and the bivalve *B. thermophilus*; Table S1) that were absent in the pre-eruption plankton, despite being present in the benthos both pre- and post-eruption.

In the Mariana Trough, community composition differed significantly between the plankton and the benthos (Fig. 3d; PERMANOVA, $F_{1,7}$ = 5.08, p-value = 0.01). Composition in plankton samples did not vary substantially between those collected directly at the vents and those 100–300 m away. Similar to the EPR, most taxa found only in the plankton were gastropods (including peltospirids; Table S2). No analysis of abundance was possible for Mariana because the benthic data were available only as presence/absence.

Across the 3 vent fields, the percentage of taxa shared between the plankton and the benthos varied substantially (Fig. 4). The overlap was highest (70%) in the Pescadero Basin and substantially lower (<50%) in the EPR and Mariana Trough, with the lowest value (29%) observed in the pre-eruption EPR. The pre- and post-eruption EPR displayed a similar percentage of taxa found only in the plankton (38 and 35%, respectively), but the percentage found only in the benthos was much higher pre-eruption (32%) than post-eruption (18%).

4. DISCUSSION

This study of 3 Pacific vent fields demonstrates that ecological connectivity, as measured by similarity in species composition of a benthic community and its associated larval supply is consistent with some, but not all, of our expectations derived from geographic or oceanographic isolation. The high similarity in taxonomic composition between larval and adult communities in the Pescadero Basin is distinctly different from patterns in the EPR and Mariana Trough and indicates limited larval transport from nearby vent fields at the time of our study (Fig. 1a). Other nearby vent communities (e.g. Alarcón Rise) differ in faunal composition from our Pescadero samples (Goffredi et al. 2017), but the detection of only 2 non-resident taxa in plankton samples suggests a limited role of species sorting. In contrast, on the EPR, larval composition differed substantially from the local benthic communities, suggesting that transport from nearby vents with different faunal composition was

occurring, but species sorting prevented their colonization (Fig. 1b). This result differs from our expectation for EPR of high connectivity between vent fields of similar community composition (Fig. 1c). In the Mariana Trough, the community composition of larvae in the plankton differed from that of adults in the benthos, but in that region, nearby vents have distinctly different faunal composition. Thus, it appears that larvae are arriving from nearby vents but not colonizing, as at EPR (Fig. 1b). Note that a 'snapshot' observation of dissimilarity in species composition between larvae and benthos at an individual vent field is relevant to connectivity on ecological time scales but does not mean that larval transport cannot occur episodically on longer time scales to maintain genetic connectivity.

At Pescadero Basin vent communities, the limited larval transport from other vent fields is likely driven by oceanographic isolation from the nearest vent field, Alarcón Rise, which is 75 km away and 1300 m shallower. Vents in the Pescadero Basin have unusual vent fluid chemistry due to being located on a heavily sedimented spreading centre (Paduan et al. 2018), and Goffredi et al. (2017) suggest that these environmental conditions may limit species richness through species sorting in the benthos. Our direct observations of larval presence at Pescadero differ from Goffredi et al. (2017), who found DNA only of non-resident larvae in the water column (3 taxa),
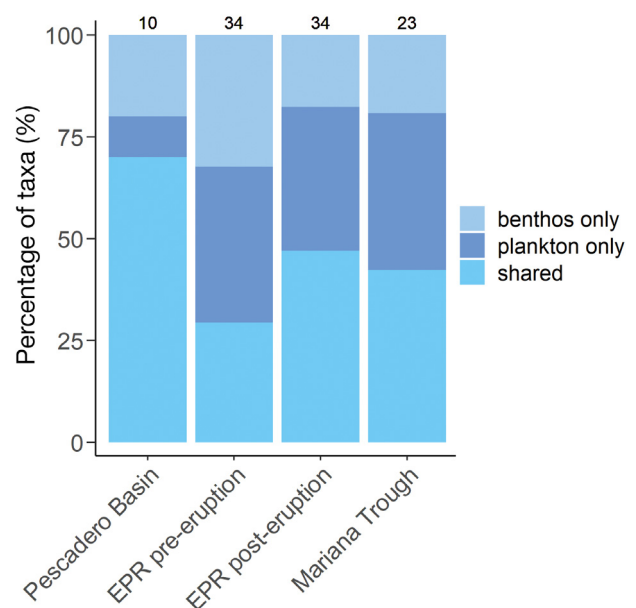

Fig. 4. Percentage of taxa found in the benthic samples only, planktonic samples only, and shared across both for Pescadero Basin, East Pacific Rise (EPR) pre-eruption, EPR post-eruption, and Mariana Trough. Total number of taxa displayed above each bar

possibly due to sampling lower volumes at greater heights above the seafloor. The distance from Pescadero Basin to the Alarcón Rise is within the maximum estimated dispersal range of some vent taxa (Marsh et al. 2001), so long-distance transport events, though rare, may occur (Mullineaux et al. 2018). For instance, the presence of the gastropods *Lepetodrilus* spp. (and the clam *Calyptogena* sp.; Supplement text 'Supplementary sample analyses') in the plankton but not the benthos at Pescadero Basin suggests these 2 taxa are widely dispersed. These taxa were found at Alarcón Rise by Goffredi et al. (2017), listed as 2 species in genus *Lepetodrilus* and 1 species in unresolved genus '*Calyptogena*'. It is certainly possible that 'false-positive' matches of pooled taxa (e.g. chaetosphaerids) between the plankton and benthos at Pescadoro Basin obscure the transport of unidentified non-local species from Alarcón Rise or other vent fields. This possibility cannot be assessed with our data but may be resolved in the future as sequences of identified adult vent specimens from this region become available in genetic databases.

On the EPR, the taxonomic compositions of larval and benthic communities were dissimilar, indicating substantial larval transport from non-local sources. Consistent along-ridge flows in this region, reported in field observations (Thurnherr et al. 2011) and models (Xu et al. 2018), could promote larval dispersal from other vent fields along the ridge, including from Medusa vent which is located 77 km away and hosts some different species than 9° 50′ N. The abundance of more proximal fields with similar composition, however, makes the EPR pattern unexpected and raises questions about whether it truly reflects larval dispersal, or results instead from limitations in sampling effectiveness. Plankton samples provide only an instantaneous view of larval supply and composition. Larval supply can be disrupted by discontinuous spawning (Tyler & Young 1999) and is known to vary on time scales of days (Beaulieu et al. 2009) to years (Mills et al. 2013), so it is possible that temporal variation in larval supply results in the episodic absence of some species from the plankton. The benthic sampling methods used could also lead to the under-sampling of some taxa. For example, colonisation surfaces cannot be deployed in the very high temperature environments (>30°C) found on vent chimneys meaning that they are less likely to sample taxa such as peltospirids and *Neomphalus fretterae* that prefer these conditions (Desbruyères et al. 2006).

The comparison of community composition in the pre-eruption and post-eruption states at EPR did not show the expected increase in similarity of benthos and plankton with time since eruption. The benthic species richness and composition was similar in the 2 states (21 and 22 taxa for pre- and post-eruption respectively, with 16 of those taxa the same), but the percentage of shared taxa between plankton and benthos was substantially lower pre-eruption (29%) than post-eruption (46%) due to the absence of 5 taxa in the plankton before the eruption that were found in both the plankton and benthos after the eruption. This pattern is contrary to the expectation from our conceptual framework, which predicted that larval taxa would be more similar to the benthos under pre-eruption conditions (Fig. 1c) than immediately after a disturbance (Fig. 1d). It is possible that the pre-eruption plankton samples were collected at a time when the missing taxa had not spawned recently, or that post-eruption populations had already become established and were spawning actively in response to higher nutrient availability. This uncertainty illustrates again the challenges of interpreting the absence of taxa in the plankton.

At Mariana Trough, the community composition of the plankton was significantly different from the benthos, as expected for a vent field experiencing larval transport from nearby fields that differ in benthic fauna. This difference was apparent in plankton samples collected directly at the vents, and from those hundreds of meters away, showing that the proximity to a vent did not influence the analysis. Biophysical models indicate that dispersal is likely between vents in the southern Mariana Trough on these spatial scales, and between the back-arc basin and the Mariana Arc (Mitarai et al. 2016). We suspect that vents on the Mariana Arc, which support different communities than those in the Mariana Trough (Giguère & Tunnicliffe 2021), are the source of species we found only in the plankton. However, the inability to identify plankton to species level in our study makes it difficult to match them to individual species reported from the Mariana Arc benthos.

We show that a comparison between larval and adult taxon composition in an individual vent field is effective for detecting limited larval exchange with other vent communities and distinguishing between larval supply and species sorting as drivers of community assembly. The approach is most useful in regions where species composition differs across vent fields. In some cases, the larval/adult comparison confirms expectations based on geographic proximity or oceanographic exchange, e.g. the determination of limited connectivity for Pescadero Basin which may limit the role of species sorting in the local community assembly. In others, however, it brings

surprises and new understanding. At the EPR, the pre-eruption and post-eruption larval pools deviated from expectation, possibly due to a mosaic of nearby vent communities in different stages of succession, recent eruptive disturbance, or sampling limitations. At Mariana Trough, the finding of substantial larval dispersal conformed to expectation but enabled the further step of identifying species sorting as the process driving community composition.

In an environment as remote and challenging to study as the deep sea it is important to gain as much information as possible from routinely collected samples. Our approach takes advantage of morphological and genetic characteristics of collected specimens and species distribution records. We acknowledge the limitations in taxonomic resolution of larvae and adults, which can obscure dissimilarities, and the limitations in sampling capabilities that can overemphasize dissimilarities. In the future, molecular identifications are likely to increase the accuracy of taxonomic comparisons by increasing taxonomic resolution and reducing the likelihood of inadvertently matching closely related species. Developments in sampling capabilities, and increasing frequency of sampling, are likely to decrease the chance of failing to detect a species in the plankton or benthos when it is present. Both of these advances are included as part of proposed deep-ocean observing programs (Cunha et al. 2020). Enhanced observations of larval supply and ecological connectivity will provide insights into community resilience and are essential for understanding the dynamics and diversity of vent species in response to natural and anthropogenic disturbance.

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