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Three *Ridgeia piscesae* assemblages from a single Juan de Fuca Ridge sulphide edifice: structurally different and functionally similar

Breea W. GOVENAR[1]*, Derk C. BERGQUIST[1,2], Istvan A. URCUYO[1,3], James T. ECKNER[1] and Charles R. FISHER[1]

(1) *Department of Biology, Pennsylvania State University, University Park, PA 16802, USA.*
**Fax: (1) 814 865 9131. E-mail: bwg122@psu.edu*

(2) *Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, FL 32653, USA.*

(3) *Department of Biology, Gettysburg College, Gettysburg, PA 17325, USA*

Introduction

At the Endeavour Segment of the Juan de Fuca Ridge, Sarrazin et al. (1997, 1999) and Sarrazin & Juniper (1999) developed a dynamic succession model for sulphide edifice communities by characterizing the dominant fauna, biomass distribution, and environmental parameters of different neighbouring species assemblages on a single sulphide edifice. According to the model, *Paralvinella sulfincola* Desbruyères & Laubier, 1993, is the first metazoan to colonize sulphide edifices in areas of high temperature and active fluid flow (assemblage I). As temperatures cool and fluid flow slows, populations of *Paralvinella palmiformis* Desbruyères & Laubier, 1986, develop (assemblage II) and are eventually displaced by the recruitment of *Lepetodrilus fucensis* McLean, 1988 and *Depressigyra globulus* Warén & Bouchet, 1988, (assemblage III). Over time, *Ridgeia piscesae* Jones, 1985, start to emerge among the gastropods and come to dominate the assemblage as fluid flow slows and temperature drops (assemblage V-Low Flow). Alternatively, *R. piscesae* may appear with *P. palmiformis* in more active hydrothermal flow (assemblage V-High Flow).

In this study, we describe five quantitative collections of three epifaunal assemblage-types with the vestimentiferan *R. piscesae*, from a single sulphide edifice in the Main Endeavour Field, at the Endeavour Segment of the Juan de Fuca Ridge. A primary objective is to present the species composition, the size frequency distribution of the dominant fauna, and the total biomass within a defined sample area, for each collection, and compare this to the assemblage descriptions in Sarrazin & Juniper (1999). Using these quantifiable ecological parameters, we evaluate structural differences between the assemblage-types to develop a better understanding of the function of *R. piscesae* in these assemblages. We also compare these results to data from a previous study of a quantitative collection of a basalt aggregation in the Main Endeavour Field. This allows us to illustrate the functional similarity among the three assemblage-types that contain *R. piscesae* in the dynamic sulphide edifice environment to the *R. piscesae* basalt community in a different, more stable environment.

Material and methods

In September 1999, we employed the DSRV *Alvin* to collect five quantitative samples of three epifaunal assemblages from a single sulphide edifice, "Bastille" (47° 57' N, 129°08' W, 2200 m), in the Main Endeavour Field (Endeavour Segment, Juan de Fuca Ridge). Before each collection, we surveyed the temperature and water chemistry of each sampling site and classified the species assemblages (assemblages I-IV, V-LF, V-HF) using Sarrazin & Juniper's (1999) scheme. We collected one sample each of assemblage III and assemblage IV (*Alvin* dive 3463); and three samples of assemblage V-HF, named V_1, V_2, and V_3 respectively (*Alvin* dive 3460). Note that although the species list of assemblage III in Sarrazin & Juniper (1999) (which is based on a single grab) does not include *R. piscesae*, the original description (Sarrazin et al., 1997) indicates that small *R. piscesae* are occasionally present in this assemblage-type.

We sampled each assemblage with the "Chimneymaster", a custom built, hydraulically actuated collection device that has an open diameter of 30 cm and is lined with a 63 µm Nitex net. We considered a collection to be quantitative (all visible biological material collected from a defined surface area) if the observers in the *Alvin*

indicated that all went well, and a careful review of the video record confirmed the presence of a clean sampling scar on the surface of the sulphide edifice, and no loss of material as the sample was contained in an isolated compartment of a polyvinyl chloride (PVC) collection box. This device does not make quantitative collections from all surfaces, but the five collections considered here all met the above criteria. After the recovery of the samples on board, we preserved all of the collections in either 10% formalin or 70% ethanol for morphological and genetic identification techniques, and later moved all of the samples to fresh 70% ethanol for shipping and storage.

For each of the five collections, we sorted and identified all of the macrofauna (>250 μm) to the species level. We constructed size frequency histograms for the dominant fauna of all five collections using morphometric measurements that are highly correlated with preserved wet weight ($R^2 > 90\%$ for all, data not shown). For *L. fucensis* we used a geometrically increasing sieve series (0.25, 0.5, 1, 2, and 4 mm) to divide the species population into size classes. For *P. palmiformis*, we measured the width of the seventh setiger (see McHugh, 1989) and for *R. piscesae*, we measured the total worm length. Several morphometric measurements of *R. piscesae* were good estimates of size, including tube anterior diameter, tube length, and worm vestimentum length. From each species population, at least one quarter of the individuals were processed to determine a preserved wet weight to ash-free dry weight conversion factor. Then we calculated the total ash-free dry weight of each species population by multiplying the conversion factor by the preserved wet weight of all of the remaining individuals and adding the ash-free dry weight of the subsample. To calculate the biomass (g m^{-2}) of the two-dimensional sample area, we used the area of the open Chimneymaster collection device (0.07 m^2) to estimate the surface area originally occupied by the community. To calculate the surface area contributed by the tubes of *R. piscesae*, we calculated the surface area of the frustrum of a cone with the total length (L) and the measured radii of the anterior (A) and posterior (P) ends of the tubes (SA = (p/2)*(A+P)*L) for the individuals processed for dry weight determination (about 25% of the population). We then extrapolated to the total number of individuals in the sample.

In order to consider these assemblages in the context of the full range of *R. piscesae* assemblage types, we compared the data from our collections to that from a basaltic aggregation of *R. piscesae* collected from a very different microhabitat (Eckner, 1999; Urcuyo, 2000). This species assemblage, collected from a diffuse-flow habitat at Easter Island (47°57' N, 129° 06' W, 2200 m), in the Main Endeavour Field, was sampled with a similar, but larger, custom-built device operated by *Alvin,* named the "Bushmaster". This collection was processed using the same methods as for the sulphide edifice communities (see Eckner, 1999; Urcuyo, 2000).

We characterized the species composition in each collection with three different indices: species richness (S) = the total number of species in a sample; evenness (E) = the variability in the distribution of individuals among species; and the Shannon-Weiner index of species diversity (H'), a measure of the combined influence of species richness and evenness in quantitative samples (Begon et al., 1999). To compare species richness and evenness between assemblages, we employed the Morisita-Horn similarity coefficient (C_{MH}). This coefficient is designed to detect niche overlap between similar species of a community by calculating the proportion of common species between two samples. A value of 0 indicates no overlap, and a value of 1 indicates identical proportional species composition (Horn, 1966). From the resulting matrix of similarity coefficients of the five collections and the basalt aggregation, we constructed a dendrogram. In size frequency histograms of the dominant fauna in each collection, we illustrate a representation of the periodicity of reproduction and growth of the species population in the sample area. Next we constructed a table of the density and the biomass of all of the species in each collection. Then we used a rank abundance curve to examine niche partitioning among species of an assemblage. A geometric distribution would indicate that species within an assemblage are dividing resources evenly, while a logarithmic distribution would indicate that species within an assemblage divide niches disproportionately (May, 1975). Last we compared the species diversity to the *R. piscesae* tube surface area in all collections.

Results and Discussion

The species composition and biomass of each assemblage-type that was included in the dynamic succession model of Sarrazin et al. (1997, 1999) and Sarrazin & Juniper, (1999) was based on single collections of assemblages I, II, III, IV, V-LF and V-HF. Here we use five collections of three visibly different assemblages, using a different sampling tool, to provide additional data on species composition and biomass of different assemblage types and test the generality of their model. In our collections, the number of macrofaunal species was higher and the density of each species was generally higher in each assemblage type than reported by Sarrazin & Juniper (1999). The single exception was the density of *L. fucensis* in assemblage III, which was 3.7 times lower than their sample. The total biomass of each assemblage-type was within the range reported for all vestimentiferan assemblages at the Juan de Fuca Ridge (Sarrazin & Juniper, 1999). The biomasses of all three collections of assemblage V-HF were similar to that reported by Sarrazin & Juniper (1999), but the biomasses of our quantitative collections of assemblages III and IV were substantially higher; approximately 4.5 times higher for type III and over 40 times higher for type IV. These differences may be due in part to differences in the efficacy of the collection methods, but also likely reflect natural variation between sites and collections. Clearly, additional work will be needed to resolve these discrepancies and more completely characterize all of the assemblage types.

Community structure may be described as the distribution and abundance of component species, the number of individuals, the size frequencies of individual species populations, or the distribution of biomass among

species within a community (Begon et al., 1999). The full range of species richness among the five collections (III, IV, V_1, V_2, V_3) is found in the three samples of assemblage V-HF that show the greatest range of species richness (8-13 species) (Table 1). Assemblages III and IV have species richness values that fall within this range (Table 1). The diversity indices (H') vary between 0.90 and 1.31 for all of the collections, with all three samples of assemblage V-HF displaying the lowest values. Most of the individuals in the assemblage V-HF samples are distributed among only a few species, thus the low species evenness yields a low diversity. Conversely, assemblage III has the highest index of diversity because the individuals are more evenly distributed among species (Fig. 1). However, relative species abundances reveal important differences between assemblages that are not reflected in species richness, evenness or diversity. For example, assemblage IV has a similar species richness and diversity index to the collection V_1, but they have very different dominant species. *L. fucensis* and *D. globulus* (gastropods) dominate assemblage IV, whereas *R. piscesae* and *P. palmiformis* (polychaetes) dominate assemblage V-HF (Fig. 1).

Table 1. Three indices of species composition for each collection.

Collection	Species Richness (S)	Evenness (E)	Shannon-Weiner diversity index (H')
III	12	0.53	1.31
IV	9	0.59	1.29
V_1	8	0.49	1.01
V_2	12	0.46	1.16
V_3	13	0.35	0.90

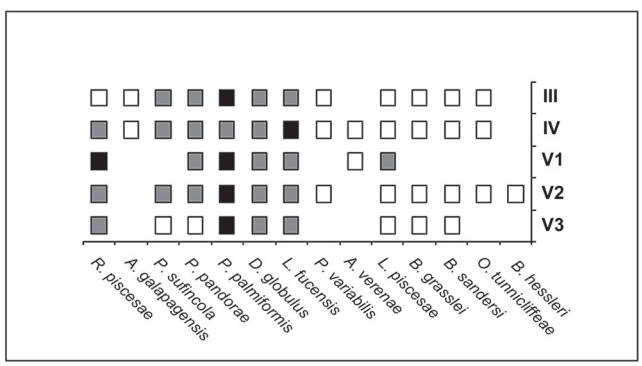

Figure 1. Relative abundance of all of the species present in a collection; no individuals present (no square), 0.01- 10% (white squares), 10- 33% (gray squares), >33% (black squares). (For the genus names see Table 2).

From the Morisita-Horn similarity dendrogram, we have illustrated that the three samples from assemblage V-HF are the most similar, with the greatest overlap between collections V_1 and V_2 (Fig. 2). It also reveals that assemblage III is more closely related to V-HF than IV (Fig. 2). The structural differences among these five collections are minimized when they are compared to a different *R. piscesae* community from a different microhabitat. The pair-wise Morisita-Horn coefficient values show very high ecological similarity among the three different assemblages of the *R. piscesae* community on the sulphide edifice and a strong difference between these assemblages and the basaltic *R. piscesae* community (Fig. 2). This is not unexpected considering the very different microhabitat conditions of the chimney and basaltic *R. piscesae* communities.

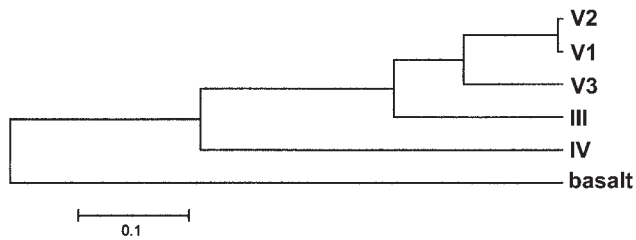

Figure 2. Dendrogram of Morisita-Horn similarity coefficients for all sulphide edifice collections and a basalt aggregation.

Community function is defined as the biological interactions among species and between species and the environment, and can be described by the role of the community in ecosystem processes (succession, trophic organization, or niche partitioning between the component species) (Begon et al., 1999). In the size frequency histograms of assemblage IV, small individuals dominate the populations of *R. piscesae* and *P. palmiformis*, and large individuals dominate the population of *L. fucensis* (Fig. 3). These size distributions suggest that there has been a recent recruitment of small worms, and smaller limpets are not replacing larger individuals. If age is proportional to size, this pattern could demonstrate the transition from assemblage IV to V-HF, where a new recruitment of *R. piscesae* and *P. palmiformis* is replacing a declining population of *L. fucensis*. According to the model of Sarrazin & Juniper (1999), IV would be replaced by V-LF in the presence of decreased hydrothermal flow. We suggest that if flow increases (as a result of a tectonic event, for example) V-HF could follow IV, and gastropods would no longer be present in high densities due to mortality or migration. In our sample of assemblage III, most (>90%) of the *R. piscesae* tubes were empty. This suggests that an environmental change in fluid flow or chemistry may have caused a reversion from assemblage V-LF to assemblage III. Although Sarrazin & Juniper (1999) do not consider this type of reversion, it is generally consistent with the mechanism of their dynamic succession model. The species composition is measurably different between assemblage-types, the biological succession from IV to V-HF and reversion from V-LF to III, suggests that the different assemblages (III, IV and V-HF) of *R. piscesae* may represent different stages within a single dynamic community.

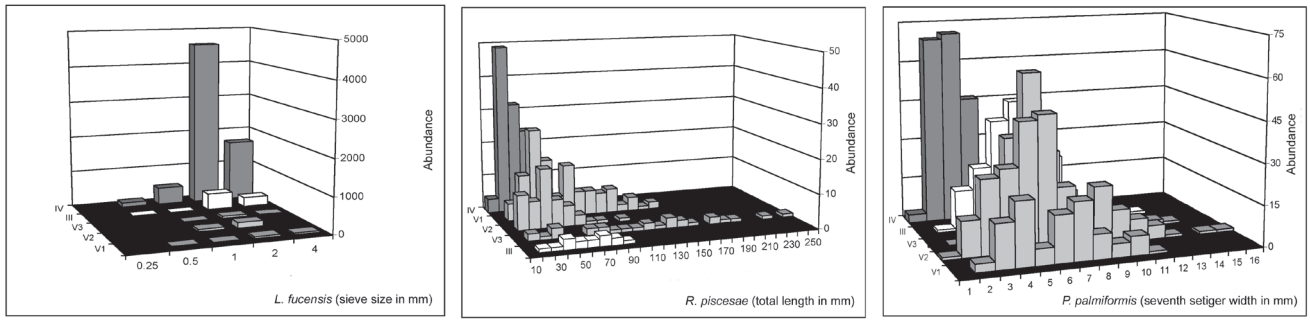

Figure 3. Size frequency distribution of *L. fucensis* (n= 705, 6831, 104, 213, 86 from collections III, IV, V_1, V_2, V_3, respectively), *R. piscesae* (n=15, 120, 118, 55, 28 from collections III, IV, V_1, V_2, V_3, respectively) and *P. palmiformis* (n=179, 197, 107, 250, 193 from collections III, IV, V_1, V_2, V_3, respectively).

Table 2. Biomass and density[1] of all macrofaunal species in each collection.

Species	Collection III	IV	V_1	V_2	V_3
Symbiont-containing species					
Ridgeia piscesae	23.3 (212)	983.2 (18250)	757.2 (14996)	1408.2 (21263)	742.4 (9903)
Primary consumers					
Amphisamytha galapagensis	<0.1 (71)	<0.1 (156)	0 (0)	0 (0)	0 (0)
Depressigyra globulus	25.0 (11445)	203.9 (27730)	0.9 (538)	1.5 (4414)	<0.1 (269)
Lepetodrilus fucensis[2]	291.0 (9974)	611.1 (95578)	203.0 (1061)	11.9 (1118)	36.4 (1217)
Paralvinella palmiformis	213.6 (24121)	129.8 (16269)	163.9 (9790)	457.4 (49204)	366.0 (25323)
Paralvinella pandorae	2.9 (3339)	2.3 (2419)	37.0 (368)	0.1 (976)	28.5 (283)
Paralvinella sulfincola	<0.1 (57)	1.1 (990)	0 (0)	23.0 (3197)	<0.1 (283)
Provanna variabilis[2]	0.3 (283)	3.7 (622)	9.2 (28)	0.4 (269)	0 (0)
Secondary consumers					
Ammothea verenae	0 (0)	<0.1 (42)	<0.1 (14)	0 (0)	0 (0)
Branchinotogluma grasslei	<0.1 (71)	7.4 (637)	0 (0)	3.9 (311)	<0.1 (28)
Branchinotogluma hessleri	0 (0)	0 (0)	0 (0)	2.7 (113)	0 (0)
Branchinotogluma sandersi	<0.1 (14)	8.1 (552)	0 (0)	2.0 (141)	<0.1 (127)
Lepidonotopodium piscesae	54.4 (283)	7.2 (325)	25.8 (297)	45.8 (552)	46.2 (241)
Opisthotrochopodus tunnicliffeae	<0.1 (71)	4.7 (170)	0 (0)	2.3 (99)	0 (0)
Total biomass (AFDW)	566.0	1935.1	1171.1	1902.8	1173.3
Total biomass (WW)	5943.9	19009.5	12893.6	14407.1	13084.1

[1] Biomass is presented as ash-free dry weight (g m^{-2}) with density (number of individuals m^{-2}) in parentheses. [2] There is inconclusive evidence that both of these gastropods may harbor chemoautotrophic symbionts, but the nutritional relation between the host and the symbiont is unknown (McLean, 1988; Eckner, 1999).

The distribution of biomass among trophic guilds in assemblages IV and V-HF is dominated first by the "primary producer" *R. piscesae* and second by the primary consumers *P. palmiformis* and *L. fucensis*. In collections IV, V_1, V_2, and V_3, *R. piscesae* comprises 48 to 72% of the total biomass. Where *R. piscesae* is not dominant (assemblage III), the biomass distribution is dominated by *P. palmiformis*, a primary consumer (Table 2). In all assemblages, secondary consumers (predators) contribute very little to the total biomass (Table 2). Predators are reported to be relatively uncommon on sulphide edifices in general, possibly due to the environmental stresses of variable high temperature and high sulphide concentration (Voight, 2000; MacDonald et al., this volume).

All the rank abundance curves of the sulphide edifice assemblages with *R. piscesae* follow a geometric series distribution (Fig. 4). According to May (1975) this suggests that most species are competing equally for a shared resource. We also observe a significant negative relationship between species diversity and *R. piscesae* tube surface area (Fig. 5). This is consistent with the trends in Sarrazin & Juniper (1999) for *R. piscesae* surface area and the species richness in assemblages IV, V-LF, and V-HF. In contrast, a basalt community from the same site shows much higher abundance and species richness, and the rank

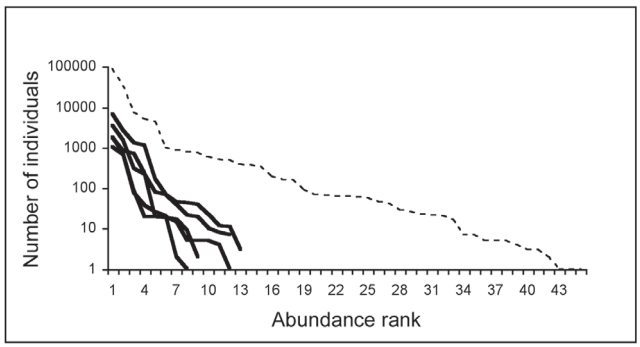

Figure 4. Rank abundance diagram of all sulphide edifice collections (black lines) and a basalt aggregation (hatched line).

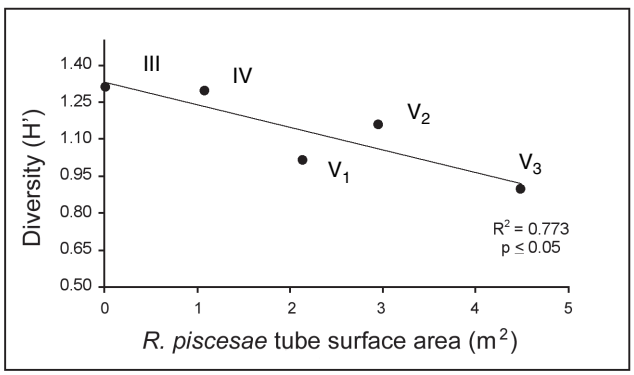

Figure 5. Relationship between Shannon-Weiner index of species diversity (H') and *R. piscesae* tube surface area (m^2) in all sulphide edifice collections.

abundance curves follow a logarithmic distribution (Fig. 4). This implies that a few dominant species occupy a greater amount of the niche. In the diffuse-flow microhabitat of basaltic aggregations, the often metre-long tubes of *R. piscesae* may increase habitat heterogeneity by spanning microhabitats that range from direct exposure to diffuse flow (around their base) to undetectable exposure to vent flow (around their anterior ends), and thus provide more niches for a greater variety of species (Urcuyo, 2000). Although *R. piscesae* is present in both sulphide edifice and basalt communities, it may play a very different ecological role in each habitat.

Conclusion

We began our investigation of the productivity and the energy flow of Northeast Pacific hydrothermal vent ecosystem with a quantification of the biomass of the different assemblage-types present on Juan de Fuca Ridge sulphide edifices. By employing measurable ecological parameters, we were able to distinguish structural differences between assemblages III, IV, and V-High Flow. Our results generally support Sarrazin et al.'s dynamic succession model (Sarrazin et al., 1997, Sarrazin & Juniper, 1999), although the community biomass and densities here are often much greater than previously reported. Overall, we demonstrate that visibly distinct species assemblages can be functionally similar and likely represent a single dynamic community. In future work, we will compare other collections of epifaunal assemblages from different sulphide edifices within the Main Endeavour Field and at High-Rise Field (sampled in August 1998) to further test the general applicability of the dynamic succession model (Sarrazin et al., 1997; Sarrazin & Juniper, 1999) and better constrain species distributions and biomass estimates for each assemblage type. This project marks a preliminary step in our long-term goal of quantitatively modeling productivity and energy flow in the hydrothermal vent ecosystem, of the Endeavour Segment of the Juan de Fuca Ridge.

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