Stauromedusae on the East Pacific Rise

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Abstract: Dense aggregations of the large stauromedusae *Lucernaria janetae* Collins & Daly, 2005 are known from four sites near East Pacific Rise hydrothermal vents, but as is typical of circum-vent animals, their biology remains virtually unstudied. Observations of stauromedusae from near 8°36'N find that they are consistently near fissures from which warm, smoky water wafts. Collections of these animals and associated fauna suggest that the amphipods *Halice hesmonectes* Martin, France and Van Dover 1993 form the primary stauromedusan prey. The diversity and abundance of other taxa in the immediate area of the stauromedusae are low. The amphipods, notably sexually mature members of *H. hesmonectes,* may effectively transfer vent productivity to these stauromedusae, allowing them to reach extraordinary sizes and densities.

Keywords: *Lucernaria janetae* ● Predation ● *Halice hesmonectes* ● Distribution ● *Ventiella sulfuris*

Introduction

Deep-sea hydrothermal vents on the East Pacific Rise (EPR) have been among the most frequently targeted for submersible-based study to date, with the chemosynthetic organisms unique to vents (tubeworms, mussels and clams) having received considerable attention. Extensive, dense fields of large organisms such as "dandelions", more formally the siphonophore, *Thermopalia taraxaca* Pugh, 1983, enteropneustan "spaghetti worms", *Saxipendium coronatum* Woodwick & Sensenbaugh, 1985, nameless (and apparently uncollected) anemones (Hessler et al., 1988) and barnacles of *Neolepus* (Sarrazin et al., this volume) surround some EPR vents where they appear to feed on animals on or near the bottom. In the last 15 years, expansive fields of stauromedusae have been discovered near vents at four areas between 21°N and 20°S (Lutz et al., 1998; this volume; Halanych et al., 1999; Collins & Daly, 2005). A published towed camera image (Fig. 14C, ARGO-RISE Group, 1988) also appears to show a field of stauromedusae at an unspecified location between 10°19' to 11°53'N. Individuals collected from near 8°36'N were recently described as *Lucernaria janetae* Collins & Daly, 2005. As is typical for circum-vent taxa, other than taxonomic treatment, the stauromedusae and their potential prey had received minimal attention (Halanych et al., 1999).

Here I describe fields of stauromedusae discovered near 8°36'N on the EPR, and collections made among them and from areas of more focused fluid flow. I compare these to a similar field reported at 7°S (Halanych et al., 1999). Potential prey of the stauromedusae is also identified.

Materials and Methods

In March 2001, Autonomous Underwater Hydrophones detected an apparent earthquake swarm on the EPR between 8°37'N and 8°42'N, interpreted as indicating a magmatic triggering event. In December 2002 a single CTD tow-yow detected a hydrothermal plume restricted to the southern (8°37.25 to 8°34'N) area of the seismic event (Bohnenstiehl et al., 2003). These data led us to target a previously unexplored area near 8°36'N on the EPR for seafloor exploration. Our first ALVIN dive was made in anticipation of discovering an active hydrothermal vent field associated with the source of the plume. When extensive fields of stauromedusae were discovered instead, the sub's multichamber suction sampler was used to collect them. This sampler (or slurp pump) draws hydraulic power from the sub and has five discrete sample chambers on a rotating tray. Suction is applied to draw samples into an individual container. When suction is stopped, rotating the tray seals the container holding the sample and opens the adjacent container to receive the next sample when suction is re-initiated. However, during this dive (ALVIN 3925), the multichamber sampler failed after collecting a sample that contained only stauromedusae.

During the second dive in the area (ALVIN 3927), this suction sampler took two samples before failing, one from rock crevices at the bases of the stauromedusae, and the other from a rock fissure among tubeworms of *Tevnia jerichonana* Jones, 1985. Failure of the sampler questions whether the samples are fully discrete. A smaller, independent suction sampler sampled water venting over the tubeworms. A grab-sample of tubeworms and associated fauna was placed in a lidded box on the sub's basket for recovery. Water temperatures were measured in a crevice from which shimmering water was wafting, adjacent to a small area with *T. jerichonana*. Fluid was also sampled from this fissure using a double major water sampler. In addition to submersible operations, during two nights, a towed camera was lowered to further explore the seafloor.

All samples were put into cold seawater on recovery from the sub and preserved in either 95% ethanol or a formalin-fix. Specimens were sorted under a dissecting scope on shore and are deposited at The Field Museum (Chicago, IL, USA) with the following catalogue numbers: FMNH 10327-10328, 11101-11105, 11109-11113, 11175-11183, 11185-11188, 11209, 11458, 11472-11475, 11517, 11570 and 12492 for non-molluscan invertebrates and FMNH 307158-307161, 307186-307191, 307195, 307214-307215 for molluscan taxa. The lengths of the tubeworm tubes were determined.

To compare the reproductive status of the stauromedusae populations, stills from a digital camera mounted on the front of ALVIN were printed at a large size and the indivi-duals clearly seen in the frame were counted. Because an orange or yellow-ish color is thought to indicate ovarian development in stauromedusae (A. Collins, pers. comm.), the frequency of these colorful rather than generally transparent *L. janetae* was compared between and among populations using a contingency table and a G-test.

The frequency of maturing females of the amphipod *Halice hesmonectes* Martin, France and Van Dover 1993 was determined in the venting water sample (n = 494) and the stauromedusae sample (n = 300). Maturing females were distinguished by the darker color on the ventral surface of the pereion, and a more yellow color to the entire body.

Results

Here the location and general description of the fields are reported followed by a summary of our knowledge of their biota. The seawater near the western wall of the axial valley where ALVIN dive 3925 landed at 2560 m depth was consistently smoky. Within 15 minutes of having sighted the bottom, observers discovered a field of stauromedusae roughly 220 by 25 m near 8°36.706'N 104°12.739'W at 2559 m depth. The field was near the edge of an at least 10 m deep fissure that roughly paralleled the spreading axis. To further document the area, ALVIN transited to the eastern wall, then returned via a slightly northern track. Although no hydrothermal activity or fauna were located on this transit, an extinct and heavily weathered massive sulfide (roughly one m³) was discovered about 1 km from the closest known stauromedusae. A second field of stauromedusae was later located at 8°36.609'N 104°12.724'W in 2553 m depth through very smoky water but could not be sampled.

Towed camera operations documented a large field of stauromedusae on the lip of a large fissure (Fig. 1). Stauromedusae density increased as the fissure terminated in an area with heavy discharge of smoky water and small clumps of tubeworms of *T. jerichonana*. ALVIN dive 3927 located this roughly 20 by 15 m field at 8°36.396'N 104°12.647'W and 2553 m depth. Although water temperatures among the stauromedusae were ambient, a peak temperature of 6.4° was found among *Tevnia* in a rock fissure. The fluid sample was less saline than seawater and smelled strongly of sulfide.

In the towed camera images, the stauromedusae were often present on the lip of rock fissures or clefts, that appeared to be at least 10 m deep. A few stauromedusae also clustered around small crevices or holes among jumbled rocks that typically had what appeared to be a thin coat of bacteria. Where stauromedusae were seen near fissures, within a few meters smoke-colored water was also seen.
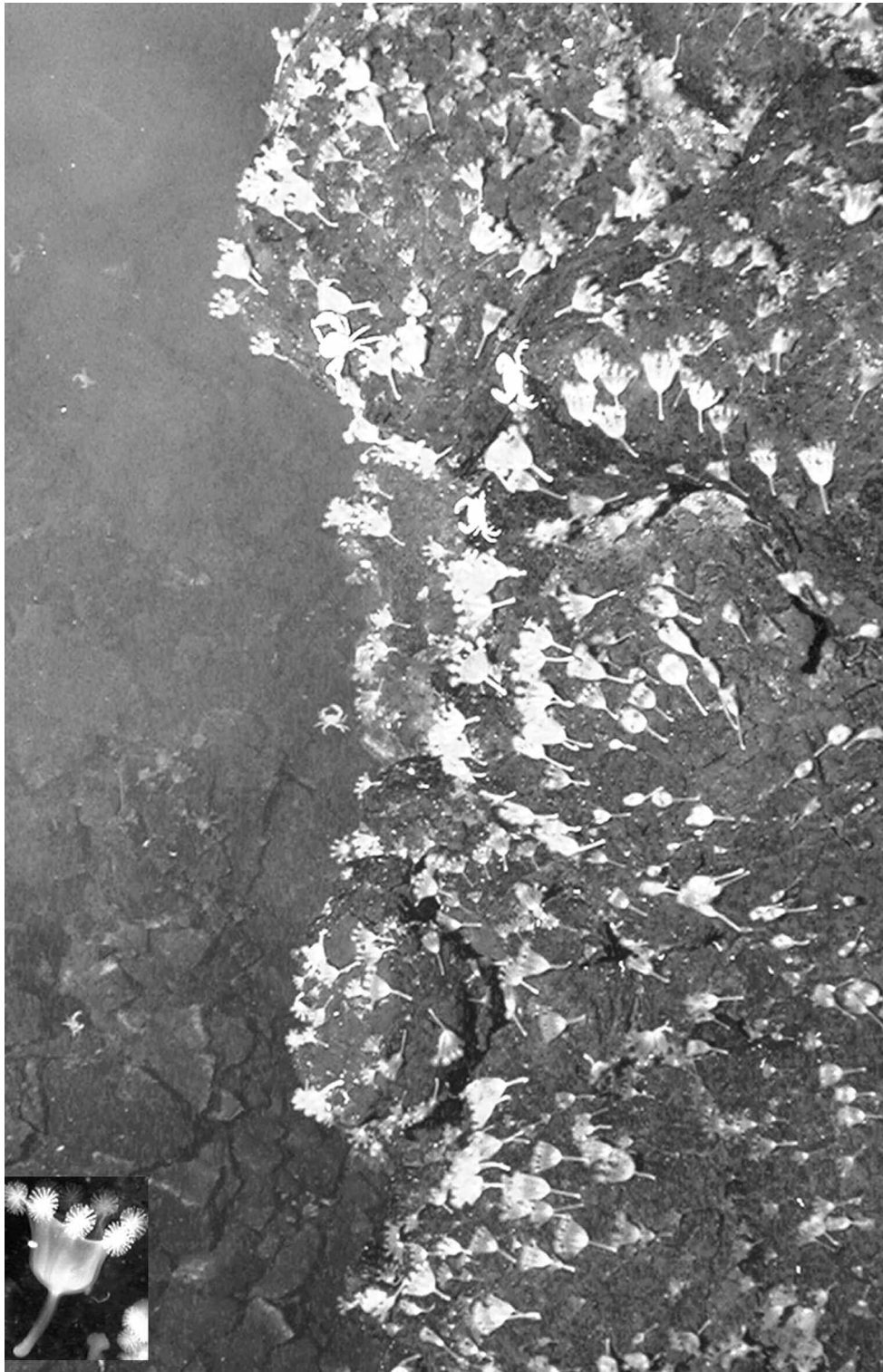
Figure 1. A small part of an extensive field of stauromedusae of *Lucernaria janetae* on the lip of a smoky seafloor fissure photographed by a towed camera at 2553 m depth near 8°36'N on the East Pacific Rise (inset in the lower left corner shows a single 4 cm tall individual).

Figure 1. Petite partie d'une population de stauroméduses de l'espèce *Lucernaria janetae* sur le bord d'une fissure fumante du fond photographiée à 2553 m de profondeur à 8°36'N sur la ride Est Pacifique (l'insert dans le coin inférieur gauche montre un individu isolé de 4 cm de hauteur).

The first indication of nearby stauromedusae was an increasing abundance of bythograeid crabs; the second was an increasing abundance of serpulid worms. Few radioles were seen emerging from the abundant serpulid tubes. Where present, the stauromedusae were densely distributed. Although most individual stauromedusae were exceptionally large (ca. 4 cm long), small individuals were also present (Collins & Daly, 2005). In areas near smoky water, the stauromedusae were lying nearly flat on the seafloor, in a posture consistent with their having been flattened by near-bottom currents. Both serpulid tubes and crabs were comparatively scarce among the stauromedusae relative to their density at the field's periphery.

In the two fields discovered in the first dive, orange or yellow-colored stauromedusae were significantly more frequent in the second, smokier field than in the first (95 of 494 vs. 10 of 160; G = 17.8; p < 0.005). The frequency of orange stauromedusae did not differ among images from the second dive (9.6 to 12.2% of 647 individuals orange, G = 0.313; p > 0.05). All 14 complete individuals of *T. jerichonana* collected were seemingly healthy; their tubes ranged in length from 31 to 42.5 cm, with a mean of 34.3.

Collections from both the stauromedusae and the tubeworms were dominated by amphipods, however the taxonomic composition of the samples differed dramatically (Table 1). The amphipod *Ventiella sulfuris* Barnard & Ingram, 1990 dominated suction and grab samples from the tubeworms; amphipods of *H. hesmonectes* were dominant in the suction sample from the stauromedusae. Five individuals of the vent mussel, *Bathymodiolus thermophilus* Kenk & Wilson, 1985 up to 5.5 mm long, were collected from among the stauromedusae. Few individuals representing limited diversity were collected (Table 1); even abundant species were represented by very small individuals (e.g. *Ophryotrocha akessoni* Blake, 1985). Taxa observed, but not collected were adult limpets of *Eulepetopsis vitrea* McLean, 1990, which were very common on vertical rock surfaces near the tubeworms, zoarcid fishes of *Thermarces*, and cardean shrimp, likely of the genus *Lebbeus* (T. Haney, pers. comm.).

Reproductively maturing individuals of *H. hesmonectes* were significantly less common in the venting water sample (3.2%) than the stauromedusae sample (16.7%; G = 43.26; p < 0.005).

Discussion

Exceptionally large, densely-distributed stauromedusae of *L. janetae* occur near faunally depauperate hydrothermally active areas associated with fissures in the basalt seafloor that emit fluid of low maximum temperatures (present study, Halanych et al., 1999). The limited data available from this study suggest that their likely prey is the amphipod *Halice hesmonectes*. Amphipods are identified as the prey because all known fields of stauromedusae report abundant swimming crustaceans (Lutz et al., 1998; Halanych et al., 1999), nine of twelve species of stauromedusae reviewed by Zagal (2004) used amphipods as prey and small pieces of crustacean legs and antennae had been ingested by individuals of *L. janetae* (Collins & Daly, 2005). Amphipods of *H. hesmonectes* are likely to be an important prey of *L. janetae*, as this species dominates the suction sample taken from among them.

Because Halanych et al. (1999) reported the taxonomic composition of samples collected during dives in areas that hosted stauromedusae at 7°S, but did not report details of where the collections were made, *H. hesmonectes* cannot be assumed to have been absent from that site. We collected different amphipods from near tubeworms and from near stauromedusae (Table 1) despite the relatively close proximity of the collection sites. Sample location is key. In addition, *H. hesmonectes* not only strongly dominated the sample taken among stauromedusae, but that sample also contained significantly more maturing females than did in the sample from water venting over the tube worms, in which the amphipods may have formed a swarm, typical of the species. Sheader et al. (2000) found that swarms of this species contain sexually immature individuals that apparently feed on bacteria sustained by warm fluid flow; the habitat of mature individuals had remained unknown, but was inferred to be benthic. Mature amphipods, which one would assume are more lipid-rich, would offer an effective means to transfer vent productivity to the stauromedusae. Although one may assume that stauromedusae suspension-feed, Collins and Daly (2005) documented the presence of muscles in the peduncle that could allow the calyx to be lowered to feed on the bottom. Whether the flattened postures seen can be strictly attributed to currents or are feeding postures cannot be determined.

The temporal stability of the stauromedusae habitat cannot be inferred, except to note that the lengths of the *T. jerichonana* tubes collected here exceed those known to be one year of age (Lutz et al., 1994). The presence of a weathered sulfide near the stauromedusae, strikingly similar in weathering and position relative to the stauromedusae to one Halanych et al. (1999) reported, indicates a long-term subsurface high-temperature system (R. Zierenberg, pers. comm.), as does the low salinity (an indicator of phase separation) of the water sample collected.

Plankton tows taken 1 to 5 m above active hydrothermal vents near 21°N contain roughly an order of magnitude more biomass than do those at non-vent habitats at comparable depths (Berg & Van Dover, 1987). Although this biomass could be argued to be the most likely source of nutrition for circum-vent animals, in these areas the low maximum tem-

Table 1. Taxonomic composition of samples taken by suction sampler near stauromedusae and near tubeworms and of those collected from a tubeworm grab during ALVIN 3927. In addition, 494 amphipods of *Halice hesmonectes* were collected from venting water near the tubeworms.

Tableau 1. Composition taxonomique des échantillons récoltés à la suceuse près des stauroméduses et près des vers tubicoles et de ceux récoltés à la benne pendant ALVIN 3927. En complément, 494 amphipodes de l'espèce *Halice hesmonectes* ont été échantillonnés dans l'eau à proximité des vers tubicoles.

	Suction of Stauromedusae	Suction of Tubeworms	Grab of Tubeworm
Crustacea			
Total Amphipoda	307	233	767
Ventiella sulfuris	6	231	767
Halice hesmonectes	300	0	0
Copepoda	7	35	1
Polychaeta			
Ophryotrocha akessoni	16	64	1
Amphisamytha galapagensis Zottoli, 1983	1	0	4
Polynoidae	2	0	1
Spionidae	4	bits	2
Mollusca			
Lepetodrilus elevatus	9	33	54
Other Gastropoda	3	1	0
Bivalvia	6	1	3

peratures would minimize fluid entrainment as is seen by the sustained smokiness of the area. The ample vent amphipods available as prey and the marginally increased temperatures to which individuals of *L. janetae* may be exposed could increase their growth rate and body sizes. Under normal deep-sea conditions of limited prey and cold temperatures, these animals may reach sizes typical of their group, making them less likely to be observed and collected.

Acknowledgements

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