

Ecology and reproductive biology of the hydrothermal vent polychaete *Amphisamytha galapagensis* (Ampharetidae)

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ABSTRACT: The ampharetid polychaete *Amphisamytha galapagensis* Zottoli, 1983 is known from hydrothermal vent sites in the eastern and western Pacific, and has been reported from the Atlantic. Pacific specimens are apparently conspecific, but closer examination of the global species is necessary. We examined ecological and reproductive features for an explanation of the wide distribution of this species, which is unusual among vent animals (unique, if truly global in distribution). The worm, present in 95% of the collections from the Juan de Fuca and Explorer Ridges in the northeast Pacific, occurs in a wide variety of vent habitats. It appears to take advantage of vestimentiferan tubes to increase substratum area but also colonizes active smokers, sediments and other animals. *A. galapagensis* is gonochoric, and all stages of egg and sperm development were present in populations sampled at different times of the year. Eggs reach 240 µm in diameter and fecundity is relatively high; no modifications in sperm ultrastructure were seen. From comparison with other polychaetes, we propose that *A. galapagensis* undergoes continuous reproduction with external fertilization resulting in demersal, lecithotrophic larvae. The proposed reproductive mode of *A. galapagensis* is not unique among vent animals, and shows no unusual adaptation for long range dispersal even though the adult distribution is wide. We propose that broad ecological tolerances, habitat flexibility and reduced dispersal may be more important in allowing establishment of *A. galapagensis* at new sites once it arrives. Further study in population genetics, systematics and development is important in a species that could provide much insight into the evolution of ecological and life history patterns at ephemeral island habitats

KEY WORDS: *Amphisamytha galapagensis* · Polychaete · Hydrothermal vent · Reproduction

INTRODUCTION

Luxuriant biological communities at hydrothermal vents are supported by chemosynthetic primary productivity. The energy source, however, is unpredictable as it depends on sustained hydrothermal activity. Hydrothermal vents, which range in age from a few to hundreds of years (MacDonald et al. 1980, Lalou et al. 1984, Campbell et al. 1988, Stakes & Moore 1989), have a global distribution that follows the mid-ocean spreading ridges and isolated back-arc

spreading centers. Discrete vent faunas are recognized in different oceanic realms corresponding to separation distance and spreading history (Tunnicliffe 1988, 1991, Van Dover 1990, D. Desbruyères pers. comm.). Vent fields on separate segments of a ridge may lie hundreds of kilometers apart. The extreme resource patchiness of vents is likely to be a major factor influencing biotic processes among the habitat's inhabitants.

Dispersal of species and maintenance of populations at these ephemeral island habitats can be interpreted from life histories of hydrothermal vent animals. Few accounts of reproduction and development of vent fauna have been published (for review see Tunnicliffe 1991), however, mainly because time-

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series samples from a vent are difficult to obtain and culture of vent species in the lab has yet to be achieved. Nonetheless, single samples of animals from different areas have yielded a great deal of information (e.g. Lutz et al. 1980, Le Pennec et al. 1984, Berg 1985, Turner et al. 1985, Van Dover et al. 1985, 1987, Berg & Van Dover 1987, Cary et al. 1989, McHugh 1989, Gustafson et al. 1991, Gardiner et al. 1992). Many of these studies show that vent species exhibit a wide range of reproductive and developmental modes reflecting phylogeny of the species rather than the opportunistic life history strategies with larval dispersal stages initially predicted for such an ephemeral and patchy environment (Desbruyères & Laubier 1983, Grassle 1985). More information on reproduction, development and growth rates is needed to understand the population dynamics of invertebrates that inhabit the vent environment (Tunnicliffe 1991, Kennish & Lutz 1992).

In this study, features of the ecology and life history of an ampharetid polychaete, *Amphisamytha galapagensis* Zottoli, 1983, are investigated. *A. galapagensis* is of particular interest because it has the widest known geographic range of all species reported from hydrothermal vents around the world. In this paper, we document the distribution, habitats and associations of this species, and examine several aspects of its reproductive and developmental biology.

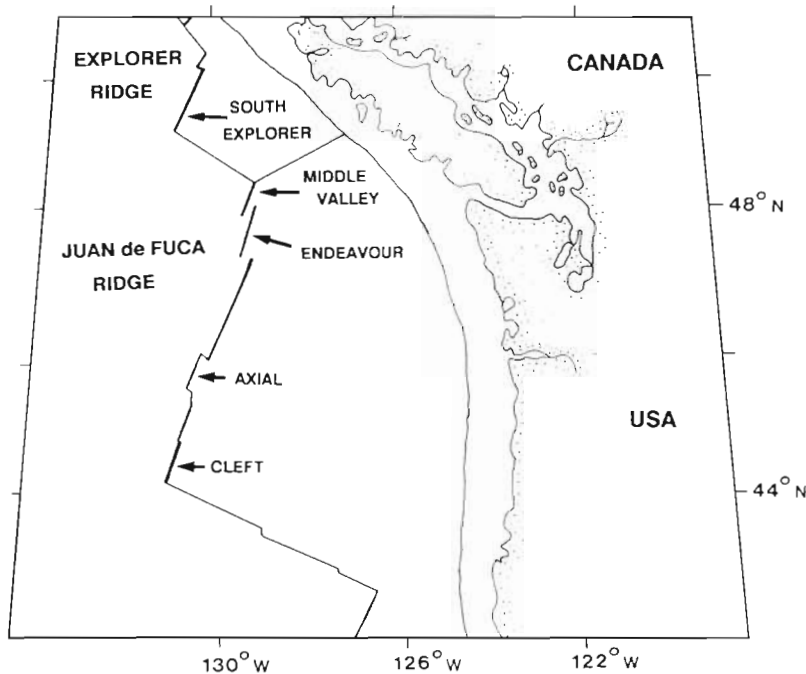


Fig. 1. Ridges of the northeast Pacific where *Amphisamytha galapagensis* was collected for this study. Vent sites are located on each of the segments indicated and may be spread over tens of kilometers

METHODS

Ecology and distribution. Specimens of *Amphisamytha galapagensis* used in this study came from Juan de Fuca and Explorer Ridges in the northeast Pacific (Fig. 1). Most collections were 'grabs-of-opportunity', and none represent targeted collection for this species. Most often, vestimentiferan tube clumps were grabbed with a submersible claw in a haphazard fashion; chimney samples might be worm grabs or the broken tops of sulphide edifices. Different pilots and observers induce different collection biases, so samples may be poor representatives of the vent fauna. Specimens were bulk fixed in 7% formalin for later sorting and storage in 4% formalin or 70% ethanol.

To examine microdistribution patterns, a high temperature smoker on Endeavour Segment was sampled as follows: a flange, measuring 30 × 40 cm, was broken from the side of the smoker; on shipboard, a 2.5 × 2.5 cm grid was overlaid and the animals within each square were preserved separately. Because of loss and displacement of some animals, results cannot be viewed as complete. Nonetheless, the relative positions of 6592 vent animals could be assigned, including 266 *Amphisamytha galapagensis*.

Reproductive biology. Specimens for study of reproductive biology came from 3 vent sites: Axial Seamount (August 1983), Endeavour Segment (September 1984) and South Explorer Ridge (June 1984) (Fig. 1). Oocytes and spermatogenic stages in formalin-fixed animals were examined under light microscopy. Specimens collected in July 1986 from Axial Seamount were fixed in 3% glutaraldehyde in Millonig's phosphate buffer for sperm ultrastructure examination with transmission electron microscopy (TEM).

Gender was determined from coelomic samples of gametes. In 10 of the largest females from each sample, 80 oocytes were measured for maximum diameter at 100× magnification. The data on oocyte sizes were log transformed and analysis of variance (ANOVA) tests were used to identify significant differences among the sample means and to examine differences in means among females in each sample. To estimate fecundity, all oocytes from the 5 largest females in each sample were collected, and the total number of oocytes in each worm was estimated by counts of three 2 ml aliquots from a 250 ml suspension of all oocytes.

Maximum oocyte size was recorded from each coelomic sample.

In males, the occurrence frequencies of 3 stages of sperm development were noted: early rosettes of spermatocytes (4 to 16 cell stage), later rosettes of spermatocytes (> 16 cell stage) and clusters of spermatids with tail pieces. In coelomic samples from each of 5 males, all stages in 4 randomly assigned squares of a hemocytometer slide were recorded. The nephromixia of males were checked for the presence of free spermatozoa. For examination of sperm ultrastructure under TEM, glutaraldehyde-fixed worms were post-fixed in 1% osmium tetroxide at 4°C for 1 h. After dehydration in a graded series of ethanol and propylene oxide, they were embedded in EPON 812 and sectioned on a Reichert ultramicrotome using glass knives. Sections were stained in lead citrate and uranyl acetate before viewing on a Philips EM-300.

RESULTS

Distribution

Table 1 documents the sites at which *Amphisamytha galapagensis* has been found. The ampharetid reported from Snake Pit of Mid-Atlantic Ridge (Segonzac 1992) resembles *A. galapagensis*; however, specimens from the Florida Escarpment were apparently misidentified and do not belong to the genus *Amphisamytha* (D. Desbruyères pers. comm.). To date, the species is known for sure only from the Pacific. Nonetheless, comparison with the distributions of

other vent species (Tunnicliffe 1991 and unpubl. data) shows that *A. galapagensis* is recorded at more sites than any other species.

On a provincial scale, it is equally ubiquitous. We have sorted collections from 56 vents along the Explorer and Juan de Fuca Ridges that span a distance of 550 km, and *Amphisamytha galapagensis* was present at 52 vents (Table 2, Fig. 1) that range from diffuse low temperature flows on new basalt to large high temperature sulphide structures in a mature field. The 4 vents with no *A. galapagensis* specimens hold no obvious common features. Often the worm has a clumped distribution and a single grab might not contain it, therefore we may have missed sampling it. The proportion of the total fauna represented by this species (Table 2) varied from negligible to 67%; in half the enumerated samples, this species represented over 4% of the total count. The few samples in which it was found in great abundance (over 25%) were old chimneys with diminished flow and many dead tubeworms.

Collections from Cleft Segment (Fig. 1) spanned many vent types, and they were analyzed together as collection methods tended to be uniform. *Ridgeia piscesae*, *Paralvinella sulfincola* and *Amphisamytha galapagensis* are 3 of the most abundant species at Cleft Segment (6 species comprise over 90% of all collections: B. Milligan pers. comm.). The abundances of *A. galapagensis* are significantly correlated with those of *R. piscesae*, the vestimentiferan (Spearman correlation coefficient = 0.488, $n = 28$, $p < 0.01$). No significant relationship was found with abundances of the polychaete *P. sulfincola*, however.

Fine-scale distribution of *Amphisamytha galapagensis* was examined on the sulphide flange collected from Endeavour Segment. Hot water pooling under the flange measured a maximum of 260°C from where it trickled upward over the nose of the flange and bathed a dense mat of animals on the upper side (J. Holden pers. comm.). The occurrence of species across the flange corresponded to water flow: where hot water emerged around one side, the polychaete *Paralvinella sulfincola* predominated; on the cooler side, *Ridgeia piscesae* tubes were abundant. *A. galapagensis* occurred on both sides. Within the sample, *A. galapagensis* abundances are correlated to those of the vestimentiferan (Spearman correlation coefficient = 0.400, $n = 108$, $p < 0.001$) and again showed no significant relationship with *P. sulfincola*. The ratio of adult *A. galapagensis* to 'juveniles' (<5 mm length, but see 'Reproductive biology' section below) in

Table 1. Reports of presence of the polychaete *Amphisamytha galapagensis*. Note that the Florida Escarpment is a seep, not a vent site

Site	Source
Equatorial Eastern Pacific	
Galapagos Rift	Zottoli (1983)
13° N, East Pacific Rise	Desbruyères et al. (1985)
21° N, East Pacific Rise	Grassle (1985)
Guaymas Basin, EPR	Grassle (1985)
Northeastern Pacific	
Juan de Fuca and Explorer Ridges	Tunnicliffe (1991)
Western Pacific	
Marianas Back-Arc Basin	Hessler & Lonsdale (1991)
Manus Back-Arc Basin	Galkin (1992)
Lau and Fiji Back-Arc Basins	D. Desbruyères pers. comm. ^a
Atlantic	
Mid-Atlantic Ridge	Segonzac (1992) ^b
Florida Escarpment	Petrecca & Grassle (1990) ^c

^aReported as *Amphisamytha* aff. *galapagensis*
^bReported as Ampharetidae gen. sp.; see text
^cSpecimens apparently misidentified (D. Desbruyères pers. comm.)

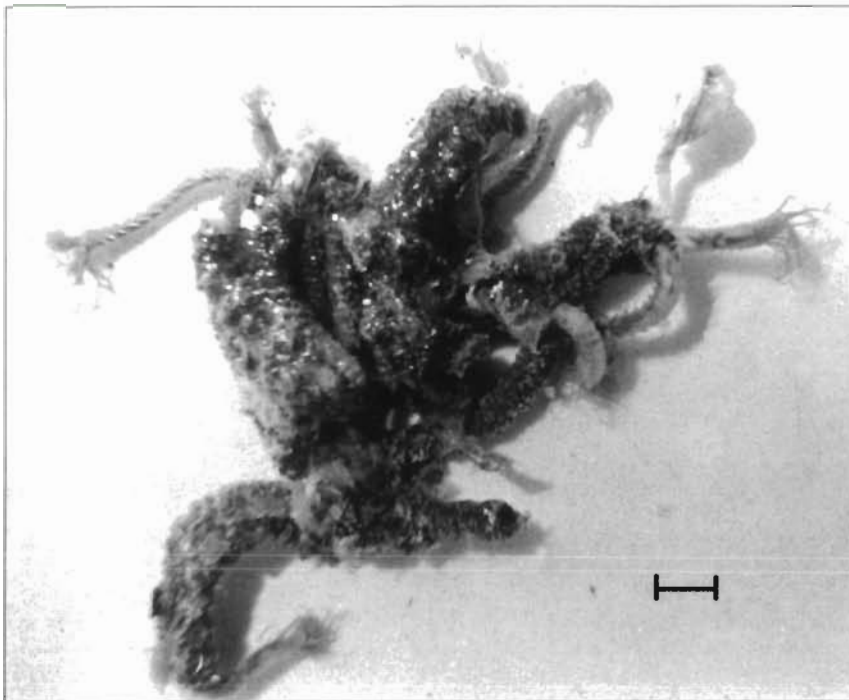


Fig. 2. *Amphisamytha galapagensis*. Live worms on shipboard. Anterior filaments are branchiae. Black mass is coalesced tubes made of sulphide particulates and mucus. Scale bar = 1 cm

this sample is 1.2:1.0. Abundances of the 2 size classes examined over the gridded flange are correlated (Spearman correlation coefficient = 0.530, $n = 108$, $p < 0.001$).

Amphisamytha galapagensis occurs in a wide variety of vent habitats. We found it most commonly attached to vestimentiferan worms in a flexible particulate tube bound by mucus, and usually free at the upper end (Fig. 2). The worm may also construct recumbent tubes on rock surfaces, and was seen on active sulphide chimneys near the venting spout. Tubes were also found projecting from sediments at the base of smoker chimneys. However, *A. galapagensis* is frequently without a tube and specimens can

crawl actively. At 13° N on East Pacific Rise, we found this species free-living around the mouthparts of the vent crab *Cyanograea praedator*; it has also been noted on the crab *Bythograea thermydron* (Desbruyères & Laubier 1983). Like other ampharetids, *A. galapagensis* apparently uses its buccal tentacles for deposit feeding; several specimens had sulphide particles and bacterial filaments in the gut.

Reproductive biology

Amphisamytha galapagensis is gonochoric and chi-square tests of the 3 samples showed no significant difference from a 1:1 male:female sex ratio ($p < 0.001$). Gametes are released at an early stage into the coelom, where development proceeds. Coelomic gametes are found in worms as small as 3.5 mm in length, which is approximately 20% of the maximum length. Fig. 3 shows size frequencies of coelomic gametes in females from the 3 sites. A similar wide range of oocyte sizes is recorded from each site and this size range is repeated in each female in the 3 samples. The ANOVA test reveals significant differences between sample means and the overall mean ($F = 63.43$, $df = 2$, $p < 0.0001$). This difference indicates variability in the reproductive cycle among the 3 populations; both the Axial Seamount and the Explorer Ridge populations have higher proportions of larger oocytes than the Endeavour Segment population (Fig. 3).

Significant differences exist between individual means of oocyte size and sample means (Axial Seamount: $F = 2.39$, $df = 9$, $p < 0.0113$; Explorer Ridge:

Table 2. Occurrence of the ampharetid polychaete *Amphisamytha galapagensis* at vents on the spreading ridges in the northeast Pacific. Listing indicates the numbers of vents at which the worm was found and, for enumerated samples, the proportion of the fauna (> 5 mm size) represented by *A. galapagensis*. n: sample size; na: not available

Ridge: Site:	Explorer			Juan de Fuca	
	South Segment	Middle Valley	Endeavour Segment	Axial Seamount	Cleft Segment
No. of vents sampled	6	3	12	17	18
No. of vents with <i>A. galapagensis</i>	6	3	12	16	15
Proportion of <i>A. galapagensis</i> (n, SD)	na	na	18.8%	6.6%	4.3%
		(8, 24.2)	(1, -)	(28, 8.7)	

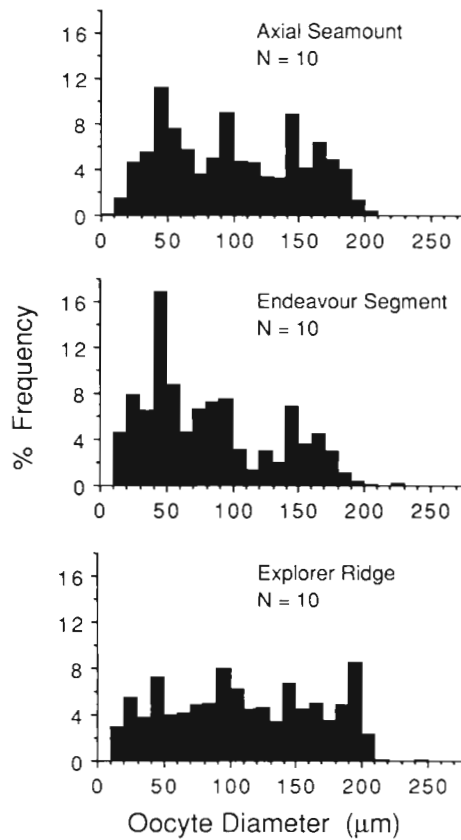


Fig. 3. *Amphisamytha galapagensis*. Size-frequency histograms of maximum oocyte diameter for the 3 samples of worms. N: number of females in each sample

$F = 6.031$, $df = 9$, $p < 0.0001$; Endeavour Ridge: $F = 4.92$, $df = 9$, $p < 0.0001$), which indicate a lack of synchronization of oocyte development among individuals in each population. In the Axial Seamount and Endeavour Segment populations, however, 1 and 2 females account for the significant differences among individuals in each sample, respectively ($p < 0.05$). Three dis-

Table 3. *Amphisamytha galapagensis*. Maximum oocyte diameter and maximum fecundity (no. of oocytes in an individual) recorded for worms from the 3 sites. n: sample size

Site	Maximum oocyte diameter (µm)	Maximum fecundity (n, \bar{x} , SD)
Axial Seamount	215	11412 (5, 5956, 3624)
Endeavour Segment	225	9625 (5, 7768, 2242)
Explorer Ridge	240	12500 (5, 9893, 2200)

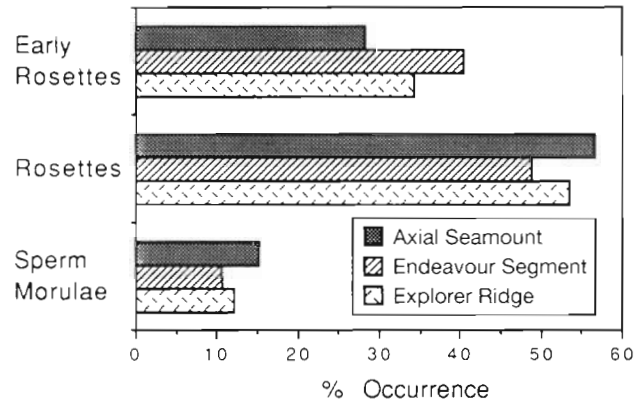


Fig. 4. *Amphisamytha galapagensis*. Percent occurrence of spermatogenic stages in 5 males from each of the 3 samples of worms

tinct peaks in oocyte sizes are evident in the Axial Seamount sample and, to a lesser extent, in the other 2 samples (Fig. 3). The maximum fecundity of *Amphisamytha galapagensis* is 12 500 oocytes in a worm of 18 mm length (0.0684 g) and mean fecundity ranges from 5600 to 9600 oocytes per worm among the 3 populations (Table 3). Maximum oocyte size of *A. galapagensis* from the 3 samples ranges from 215 to 240 µm diameter (Table 3).

While free spermatozoa were not found in the nephromixia, the 3 spermatogenic stages were well represented in the coeloms of males from the 3 sites (Fig. 4), and mature sperm were found in males fixed for TEM. In mature sperm from the coelom, the nuclear material is condensed to a bullet-shaped nucleus and the acrosomal vesicle is thimble-shaped with a thin opaque cap (Fig. 5A). Longitudinal and cross-sectional views of the vesicle reveal regional differences in electron opacity: an electron-translucent inner border lines the main portion of the vesicle, within which a regular granular substructure is apparent in some sections; a thin layer of electron-opaque material, perhaps sub-acrosomal in origin, apposes the inner proximal end of the acrosomal vesicle. A prominent gap of ca 0.1 µm separates the base of the acrosome and the anterior tip of the nucleus, and the fully condensed nucleus measures ca 2.7 µm by ca 1.6 µm (Fig. 5A). The middle piece contains 5 mitochondria surrounding the proximal and distal centrioles, and the flagellum has a 9 + 2 microtubular arrangement (Fig. 5B).

DISCUSSION

The wide distribution of *Amphisamytha galapagensis* is unique among vent species, apparently ranging across the Pacific and possibly the Atlantic. A re-

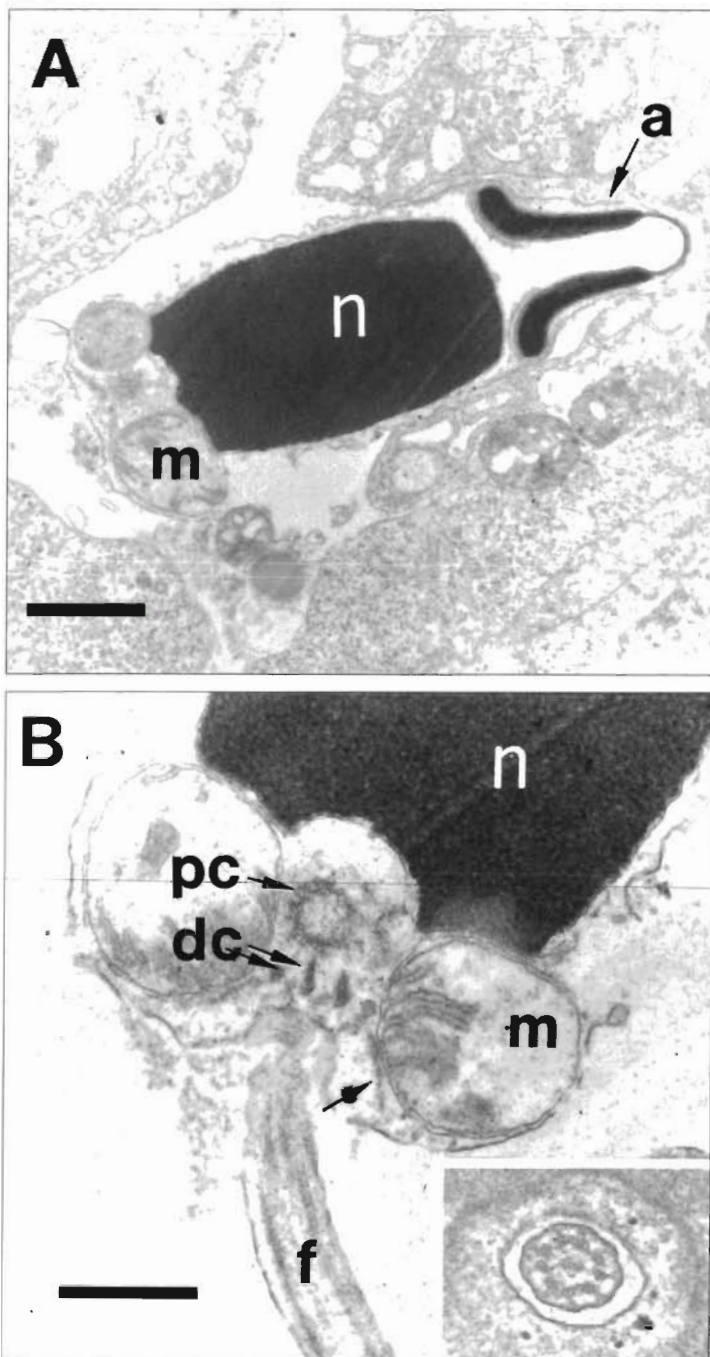


Fig. 5. *Amphisamytha galapagensis*. Transmission electron micrographs of sperm ultrastructure. (A) Median longitudinal section through a sperm cell. a = acrosome; m = mitochondria; n = nucleus. Scale bar $\approx 1.0 \mu\text{m}$. (B) Longitudinal section through the flagellar apparatus showing the proximal (pc) and distal (dc) centrioles. The unlabeled arrow points to a lateral satellite. Inset shows a cross section through a flagellum (f). m = mitochondria; n = nucleus. Scale bar $\approx 0.5 \mu\text{m}$

examination of the species characters is advisable, however, as D. Desbruyères (pers. comm.) expresses some concern over the variability of characters from

east to west Pacific, and is doubtful about the exact affinities of the Atlantic specimens. While even sub-species or sister-species relationships have biogeographic interest, further speculation on a global perspective is premature. Even with the most conservative approach, however, the wide eastern Pacific distribution remains intriguing.

The highly adaptable nature of the worm may partly explain its wide distribution. It appears to have few requirements other than proximity to a chemosynthetic source, and the extremes of habitats it occupies are impressive. We have found this animal under a 10 cm thick cracked basalt crust some 50 m distant from a vent; no other organisms were found there. It was also collected from atop a black smoker in a zone just below *Paralvinella sulfincola*, the northeast Pacific species that occupies the hottest zone (Tunnicliffe et al. 1993). *Amphisamytha galapagensis* is reported in seeping Guaymas sediments with several other polychaetes, and as the only animal in sediments at the foot of a smoker (Grassle et al. 1985). The wide range of habitats reported here and by Desbruyères et al. (1985) is seen in no other vent species to our knowledge.

Unlike other vent species with wide distributions, *Amphisamytha galapagensis* is not a rare or minor species. At over 5% mean abundance in collections, it ranks as a dominant species on Juan de Fuca Ridge. Petrecca & Grassle (1990) record densities of 2267 m^{-2} in Guaymas sediments, and we estimate a minimum density of 2995 m^{-2} on the smoker flange collected from Endeavour Segment. At such high abundances, some interactions with other species can be expected. The significant positive correlation with vestimentiferan abundances is most likely due to the increased substratum area provided by the vestimentiferan tubes. The same correlation existed whether or not the vestimentiferan tubes were occupied (tested using the flange samples). On bare chimney surfaces additional substrate is also available to this ampharetid. In neither the between-vent analysis (Cleft Segment collections) nor the within-vent analysis (Endeavour flange) did we identify a negative correlation with the alvinellid *Paralvinella sulfincola*. Nonetheless, substratum competition may occur, even though the alvinellid tends to locate within centimeters of the hottest flow (Tunnicliffe et al. 1993) while the ampharetid stays more distal.

Amphisamytha galapagensis is a deposit-feeder that appears to prefer a tubicolous habit but frequently vacates its tubes; it may be free-living when tube material is scarce. It seems to have little problem colonizing vents and maintaining populations. One Cleft Segment field is known to be young – about 10 yr at collection time (Chadwick et al. 1991, Milligan & Tunnicliffe in press) – and several Endeavour chimneys in an old field are almost extinct; *A. galapagensis* was abundant at the first and predominated at the second.

Like almost all other ampharetid polychaetes that have been studied, *Amphisamytha galapagensis* is gonochoric and its gametes develop freely in the coelom from an early stage. The presence of gametes in small worms indicates that maturity is reached at a relatively early stage in the life cycle. Mature specimens were recovered from panels deployed on the East Pacific Rise and Galapagos spreading center for 1216 d (Van Dover et al. 1988), implying that growth to maturity takes at the most 3.3 yr in this species. The presence of a full range of oocyte sizes and all spermatogenic stages in worms from 3 vents sampled in different months of different years suggests that *A. galapagensis* produces gametes continuously or semi-continuously. ANOVA results imply a lack of synchrony of oogenesis among females in the 3 populations, although multiple comparison tests indicate that this result can be accounted for by a small proportion of the individuals in 2 cases. Peaks in the oocyte size-frequency histograms may represent intermittent release of oocytes into the coelom, which may cause peaks in reproductive activity when eggs mature. In the shallow water ampharetid *Ampharete acutifrons*, 2 spawning peaks in the females are separated by 2 mo (Clavier 1984), and peaks are also known in the continuous reproduction of the brackish water ampharetid *Hypaniola kowalewskii* (Marinescu 1964). The alvinellid polychaete *Paralvinella pandorae*, found at north-eastern Pacific vents, is thought to reproduce continuously (McHugh 1989). Reproductive potential in the vent bivalve *Calyptogena magnifica* may be high because it becomes reproductively active at a small size and apparently reproduces continuously over a long time (Berg 1985). Also, gametogenesis occurs continuously in the vestimentiferan *Riftia pachyptila* (Gardiner et al. 1992).

The Polychaeta exhibit a variety of sperm morphologies, which generally correspond to fertilization modes. In species with ect-aquasperm (sensu Rouse & Jamieson 1987), the spermatozoon generally has a short, rounded or conical head, a middle piece containing 4 to 6 mitochondria and a long flagellum with a 9 + 2 microtubular arrangement. Broadcast spawning polychaetes from many families have such characteristics (for reviews see Sawada 1984, Jamieson & Rouse

1989, Rice 1992). Specializations for the mode of fertilization (e.g. within the tube, spermatophore transfer, pseudocopulation, copulation) are usually associated with spermatozoan modifications such as an elongated nucleus, a complex acrosome or fused mitochondria. Sperm ultrastructure is known in few polychaetes of the Order Terebellomorpha and we report the first observations for an ampharetid. The invaginated conical acrosomal vesicle of *Amphisamytha galapagensis* is reported in other polychaete families, including the terebellid *Streblosoma acymatum* (Jamieson & Rouse 1989). The variation in acrosomal electron opacity seen in *A. galapagensis* is common in polychaetes and may reflect compositional differences of acrosome components (Eckelbarger & Grassle 1987). The nucleus, middle piece and tail of *A. galapagensis* sperm show no unusual characteristics. The condensed nucleus length to width ratio of 1.8 lies within the range observed among polychaetes with external fertilization (Sawada 1984). Only the acrosome of *A. galapagensis* sperm shows any complexity which may be related to egg envelope specializations rather than the fertilization mode. Based on these results, it is proposed that *A. galapagensis* has neither internal fertilization nor spermatophore formation. We can only speculate whether fertilization occurs in the water or in the tube. In the terebellids *Ramex californiensis* and *Nicolea zostericola* eggs are fertilized in the tube and in a mucus mass at the tube opening, respectively (Eckelbarger 1974, McHugh 1993), and both species have elongated sperm nuclei (ca 10 µm; pers. obs.); the terebellid *Streblosoma acymatum* fertilizes in the water column and has a sperm head of ca 2 µm (Jamieson & Rouse 1989). If such characteristics can be generalized, then broadcast spawning seems likely for *A. galapagensis*.

While polychaete larvae have been sampled in the plankton at and near vents on the East Pacific Rise and in the Guaymas Basin, their identification has not been possible because of their early stages of development and damaged condition (Berg & Van Dover 1987). Therefore, we base our predictions of the development mode of *Amphisamytha galapagensis* on indirect evidence. In marine invertebrates, maximum oocyte size correlates well with type of larval development (Thorson 1950, Strathmann & Vedder 1977). In polychaetes, small eggs (<150 µm) are usually associated with planktotrophy while larger eggs (>150 µm) give rise to lecithotrophic larvae or brooded embryos (Hermans 1979). Among ampharetids, oocytes greater than 150 µm in diameter give rise to lecithotrophic, demersal larvae (Okuda 1947, Nyholm 1951, Hutchings 1973, Guillou & Hily 1983) or to direct developing larvae (Wesenberg-Lund 1934, Marinescu 1964, Zottoli 1974, Cazaux 1982, Clavier 1984). The eggs of shallow water ampharetids sink, in some cases sticking

to the bottom for a few days after fertilization, and emerging lecithotrophic larvae are demersal (Thorson 1946, Nyholm 1951, Clavier 1984). The relatively large eggs of *A. galapagensis* (200 µm) probably produce non-feeding demersal larvae or develop directly into crawl-away juveniles. We have yet to find larvae or early stage juveniles of *A. galapagensis*; the earliest juvenile stages retrieved have 9 setigers (pers. obs.). We propose, therefore, that *A. galapagensis* undergoes lecithotrophic larval development near the bottom. The longest planktonic period recorded for ampharetid larvae is 3 to 5 d in *Melinna cristata* (Nyholm 1951). Metabolism may be reduced at the low ambient temperature around vents (ca 2°C), making it impossible to confidently predict the length of larval life of vent polychaetes based on studies of shallow water species.

The maximum fecundity of *Amphisamytha galapagensis*, 12 500 oocytes, is comparable to estimates for shallow water polychaetes that undergo non-feeding larval development (George 1964, Olive 1970, Fauchald 1983, Gremare & Olive 1986), and the vent alvinellid polychaete *Paralvinella palmiformis* (McHugh 1989). If *A. galapagensis* does reproduce continuously, then each breeding event may involve just a portion of the eggs in the coelom. Nonetheless, fecundity in *A. galapagensis* is much higher than that of the only other ampharetid for which an estimate exists; *Hypaniola kowalewskii*, which is comparable in size and reproduces continuously, spawns 40 to 110 eggs at a time (Marinescu 1964) and undergoes direct development within the maternal tube.

The proposed life history features of *Amphisamytha galapagensis* are continuous reproduction, external fertilization and non-feeding, demersal larval development. A short larval life would ensure that a vent population is maintained. We find large numbers of small individuals (<5 mm) associated with adults, which indicates more than 1 recruitment event, and recruitment experiments at and near vents confirm local repopulation (Van Dover et al. 1988, Tunnicliffe 1990). Recruitment to new sites within a ridge requires a dispersal mechanism of larvae. The strong along-ridge component to the movements of deep water (Thomson et al. 1990, Cannon et al. 1991) around vents may be important in providing such a mechanism.

The proposed life history does not explain the unique distribution of *Amphisamytha galapagensis*. While it has been suggested that long planktonic development promotes wide dispersal (e.g. Mileikovsky 1971, Scheltema 1986), the observation is not universal and many other factors may influence distribution patterns (Johannesson 1988). Active dispersal of *A. galapagensis* between northern and equatorial Pacific vent fields would be compromised by a short larval life; further dispersal across the Pacific is even less probable.

However, there are numerous examples of marine species with short-lived or brooded larvae that have wide geographic ranges; some authors describe mechanisms of adult dispersal by rafting or wafting (e.g. Highsmith 1985, Ó Foighil 1989, Martel & Chia 1991). If this highly adaptable species has located a dispersal agent in the deep sea, it is not yet known.

The ecology of *Amphisamytha galapagensis* may contribute to its ability to become widely established. In addition to having the widest distribution, it also has the widest ecological range presently documented among the common vent species. Vent animals may enter distant provinces frequently but be unable to locate an appropriate habitat. The key to the wide distribution of *A. galapagensis* may lie in its ability to adapt to whatever habitat is available in a new site. Indeed, long-lived larvae may not be an advantage to a hot-vent animal with a localized habitat. As Johannesson (1988) points out, the colonizing potential of short dispersers may be higher, as they can maintain a population once it becomes established.

Amphisamytha galapagensis is an exception to the high species endemism shown by vent communities of different provinces. A better understanding of its biology would contribute to interpretation of many aspects of vent biology, such as the roles of dispersal, habitat specialization, speciation and population structure in the development of vent communities. Studies on the systematics and population genetics of this species would make valuable contributions.

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