Population structure and reproductive biology of two sympatric hydrothermal vent polychaetes, *Paralvinella pandorae* and *P. palmiformis*

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Abstract

The alvinellid polychaetes *Paralvinella pandorae* Desbruyères and Laubier and *P. palmiformis* Desbruyères and Laubier occur at deep-sea hydrothermal vents along the Juan de Fuca and Explorer Ridges in the northeast Pacific Ocean. The population structure and reproductive biology of both species were studied in samples taken from three vent sites during six cruises in 1983 and 1984. Size-frequency analyses of two *P. pandorae* populations produced unimodal histograms, suggesting continuous or semi-continuous juvenile recruitment; in a third population two possible size classes were evident. Histograms of *P. palmiformis* displayed size-class peaks, which most likely reflected periodic recruitment of juveniles. Both species are gonochoric and gametes develop free in the coelom. Due to the simultaneous presence of a full range of gametogenic stages in *P. pandorae* populations, including spermatozoa in males, and to the continuous or semi-continuous recruitment pattern suggested by the size-frequency histograms, continuous reproduction is proposed for this species. In *P. palmiformis* a discrete, possibly synchronized, breeding cycle is thought to occur. Although maximum fecundity of *P. pandorae* is very low, continual reproduction over a long period of time could enhance its reproductive potential. The estimate of maximum fecundity for *P. palmiformis* is comparable to estimates for other polychaetes that undergo non-planktotrophic larval development. Maximum observed oocyte size was 215 and 260 μm in *P. pandorae* and *P. palmiformis*, respectively. It is proposed that *P. pandorae* broods its young, while *P. palmiformis* probably undergoes demersal lecithotrophic larval development. The continual production of brooded young by *P. pandorae* could maintain a vent population, but severely limit dispersal to other vents. Demersal lecithotrophic larvae of *P. palmiformis* could repopulate vents, and potentially be carried by bottom currents to other vent sites.

Introduction

The high levels of chemosynthetic primary productivity at deep-sea hydrothermal vents support luxuriant biological communities. Sulphur-oxidizing bacteria provide nutrition through endosymbiosis with Vestimentifera and bivalves (Cavanaugh 1980, 1983, 1985, Cavanaugh et al. 1981, Felbeck 1981, Felbeck et al. 1981), or as a direct food source to other vent-specific invertebrates (Jannasch and Wirsen 1979, Desbruyères et al. 1985). The nutrient supply is unpredictable, however, as it ultimately depends on hydrothermal activity, which can vary in duration from one year to several decades at a vent site (Corliss et al. 1979, MacDonald et al. 1980, Lalou and Brichet 1981, Lalou et al. 1985). The geographical distribution of vents is patchy, with distances of up to tens of metres between vents in a given field of activity; fields of hydrothermal activity can be separated from others by hundreds to thousands of kilometres. It has been hypothesized that, in an unpredictable environment, selection favours early maturity, high fecundity, semelparity, large reproductive effort, and reduced parental care (Grassle and Grassle 1974, Stearns 1976). If habitat distribution is patchy, selection favours many small progeny (Stearns 1976). Desbruyères and Laubier (1983) suggest that vent fauna could be expected to display all of these life-history characteristics in the form of r-type ecological strategies. They also predict that the colonization of newly-forming or distant vents requires a dispersive phase in the life-cycle of vent species, either as pelagic larvae or swimming adults. However, such generalizations may not be appropriate. The most drastic change in vent conditions occurs when hydrothermal flow is reduced or ceases and adult populations die (Hessler et al. 1985). There are likely to be other more subtle influences, which may also contribute to selection for life-history traits. For example, larval mortality may be very high or variable in vent species because of the isolated nature of habitat distribution. Although the peculiar characteristics of the vent habitat may be expected to impose selective forces for certain life-history traits, many vent species may

not be capable of adopting such traits due to limitations imposed by ancestry, particularly with regard to modes of larval development (Strathmann 1978, 1985). Considering these factors, it seems likely that vent species will display a variety of life-history patterns.

This idea of heterogeneity in the life-history strategies exhibited by hot-vent fauna has been supported by studies on vent Mollusca (Berg and Turner 1980, Lutz et al. 1980, Fretter et al. 1981, McLean 1981, Turner 1981, LePennec et al. 1984, Berg 1985, Turner et al. 1985) and Crustacea (Van Dover et al. 1985). Few data have been published on the life-histories of the many polychaete species that inhabit vents. Zottoli (1983) described the late larval stages of *Amphisamytha galapagensis* Zottoli, an ampharetid found at vents in both the northeast and southeast Pacific. He postulated that *A. galapagensis* produces lecithotrophic demersal larvae. The erpochaete juvenile stage (11 setiger) of *Paralvinella grasslei* Desbruyères and Laubier (family Alvinellidae), found at 13 °N, was described by Desbruyères and Laubier (1986). They proposed direct larval development for this species. There are no other data on the life-histories of any of the six species and subspecies of the family Alvinellidae. The alvinellids are a recently described family of polychaetes in the order Terebellida, and they represent prominent constituents of vent communities throughout the eastern Pacific.

Two alvinellid species, *Paralvinella pandorae pandorae*[1] Desbruyères and Laubier and *P. palmiformis* Desbruyères and Laubier, have been found only at hydrothermal vent sites along the Juan de Fuca and Explorer Ridges in the northeast Pacific Ocean. *P. pandorae* is the smaller of the two species. It inhabits a self-constructed mucous sheath and is always found attached to the parchment-like tubes of vestimentiferans. *P. palmiformis* occurs free-living in a number of habitats. It is most frequently found with its caudal end coiled around the distal portion of vestimentiferan tubes. At some vents, *P. palmiformis* is found on the surface of sulphide mineral deposits covered in a sheath of inorganic particulates accumulated by mucus secretion (Desbruyères and Laubier 1986, Tunnicliffe and Fontaine 1987). Both species appear to be indirect deposit-feeders, collecting particulate organic matter with their grooved, retractable tentacles. Gut contents of the worms consist of filamentous bacteria, mucus and diatomaceous debris (Tunnicliffe et al. 1985, McHugh 1987). The gut epithelium in *P. palmiformis* appears to be colonized by bacteria; however, digestion of bacteria is not evident (E. Ishiguru personal communication).

Populations of *Paralvinella pandorae* and *P. palmiformis* have been sampled from three vent sites. In the present study, the population structure and reproductive biology of the two species have been investigated through size-frequency analysis and light microscopy. The proposed life-history strategies of both worms are discussed in relation to the
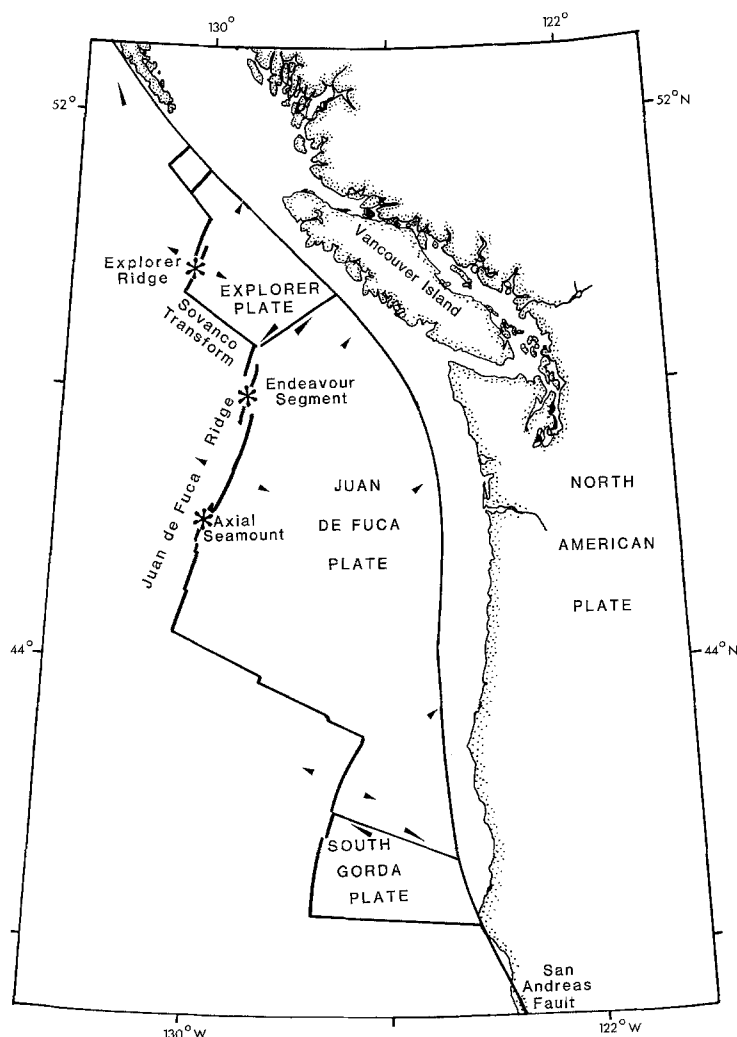

Fig. 1. Map of Juan de Fuca Ridge and Explorer Ridge showing locations of three vents sites (∗) sampled for this study

transient, isolated environment that they inhabit, and also in the light of what is known about the life-history patterns of other polychaetes, particularly those within the same order as the Alvinellidae, i.e., the Terebellida.

Materials and methods

During 1983 and 1984, six cruises using either the Canadian submersible "Pisces IV" or the American submersible "Alvin" were undertaken to four hydrothermally active sites along the Juan de Fuca and Explorer Ridges. Eight vent samples, from three vent sites, were used in this study (Fig. 1). The southernmost site is on Axial Seamount (45°59.5'N; 130°04.0'W) in the central section of the Juan de Fuca Ridge. Samples from two vents at this site, AX-1 and AX-2, were taken in August 1983 and used in this study. Three vents on the Endeavour Segment of the Juan de Fuca Ridge (47°57'N; 129°05'W) were sampled in July, August or September 1984 and designated as END-1, END-2 and END-3. The northernmost site is on Explorer Ridge (49°45.5'N; 130°18.0'W). Three vents, EX-1, EX-2 and EX-

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[1] A second subspecies, *Paralvinella pandorae irlandei* Desbruyères and Laubier is found at 13 °N. Unless otherwise stated, *P. pandorae* will refer to *P. pandorae pandorae*.
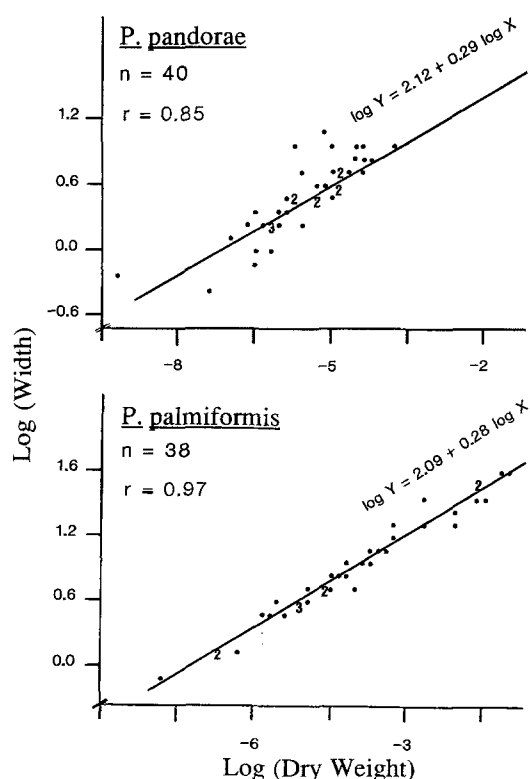
Fig. 2. *Paralvinella pandorae* and *P. palmiformis*. Relationship between log(seventh setiger width) and log(dry weight). *n:* sample size; *r:* correlation coefficient ($P < 0.01$)

3, were sampled in June, July and August 1984, respectively. Faunal samples were taken using an hydraulic claw, and were fixed in 10% seawater-buffered formalin. *Paralvinella pandorae* and *P. palmiformis* were later sorted from these bulk samples.

For size-frequency analysis of populations of *Paralvinella pandorae* and *P. palmiformis*, the width of the modified seventh setiger was used as a representation of total body size. This technique follows that used by Guillou and Hily (1983) on the ampharetid *Melinna palmata*, and by Olive (1977) and Warwick et al. (1978) for members of other polychaete orders. To validate the use of this parameter for the Alvinellidae studied, a subsample of each species was analysed for correlation (Spearman's rank coefficient) between seventh setiger width and dry weight of the worms (Fig. 2). All width measurements were made to the nearest 0.1 mm on a Zeiss dissecting microscope at $\times 20$ magnification. The correlation coefficients, $r = 0.85$ and 0.96 ($P < 0.01$), for *P. pandorae* and *P. palmiformis*, respectively, affirm this parameter as a dependable representation of total body size.

Histograms of width frequency were constructed for the populations of each species from the samples collected. Either all the specimens in a sample were measured or, if a sample was very large, a random subsample was used. Probability-paper analysis (Cassie 1954, Cerrato 1980) was carried out on histograms to determine the presence or absence of size-class peaks, and to analyse modes if present. All

statistical analyses of the data were carried out using the SAS program package (SAS Institute Inc. 1985).

Histological examination of gametes was carried out on intact worms. Thirty or more specimens of each species from each sample were dehydrated in a graded series of ethanol and embedded in paraffin. Serial sections of 5 to 7 μm thickness were stained using either haemotoxylin and eosin, or eriochrome cyanin. In sections from each female, up to 75 oocytes, in which both the nucleus and nucleolus were visible, were measured for maximum diameter at $\times 100$ magnification. Although the shape of some oocytes was irregular, a Spearman's rank correlation coefficient of $r = 0.89$ ($N = 24$; $P < 0.01$) between maximum diameter and area covered confirmed maximum diameter as a good predictor of oocyte size. Histograms of oocyte size-frequency were constructed for each population examined. To estimate fecundity, five large females were dissected and all oocytes were collected from the body cavity. Oocytes in a 4 ml subsample from a 25 ml suspension of the oocytes in water were counted. The total number of oocytes in each worm was extrapolated from the number in each subsample. Maximum oocyte size was also recorded from these coelomic samples.

In males, the frequency of occurrence of four stages of sperm development was noted; (i) single spermatogonia, or spheres of 2 to 8 cells formed by the division of spermatogonia, (ii) rosettes of spermatocytes, and larger rosettes of early spermatids; (iii) morulae composed of spermatids with tail pieces; (iv) spermatozoa in the mixonephridia. This method follows that described by Hutchings (1973) and Guillou and Hily (1983) for other terebellomorph polychaetes. In each male, all stages in ten randomly designated sections were recorded. Bar graphs of percent occurrence of the spermatogenic stages were constructed for each population examined. The number of males with spermatozoa in the paired mixonephridia was also noted.

Results

Paralvinella pandorae

Population characteristics and reproduction of *Paralvinella pandorae* were examined in three samples (AX-1, END-3, and EX-3). Width statistics for *P. pandorae* are given in Table 1, and size-frequency histograms are shown in Fig. 3. Mean widths of the three samples differed significantly from each other when tested with a Tukey test. Major differences in the range of sizes of *P. pandorae* from the three vents occurred, with the greatest size range in the AX-1 sample (Fig. 3). Two-sample Kolmogorov-Smirnov tests revealed that the distribution of size classes at AX-1 was significantly different from that at the other two sites, although END-3 and EX-3 did not differ significantly from each other.

The three size-frequency histograms differed significantly from a normal distribution when tested with the Kolmogorov test ($P < 0.01$). Two of the three size-frequency distributions, END-3 and EX-3, showed no inflection points along the curves of cumulative frequency versus width in
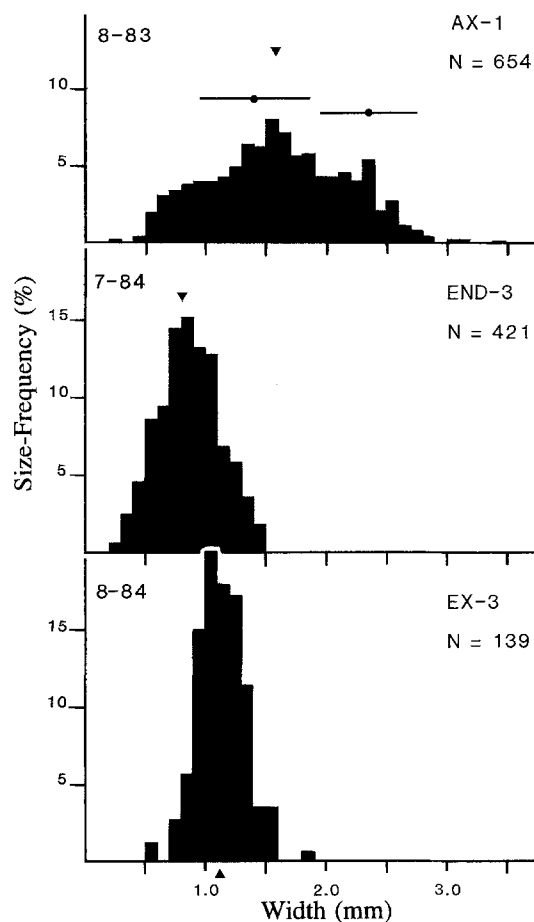
Fig. 3. *Paralvinella pandorae.* Size-frequency histograms of seventh setiger width for the three populations, with month and year of sampling shown. Arrowheads indicate mean width for each population; —●—, mean and standard deviation of modes determined from probability-paper analysis; *N:* sample size

Table 1. *Paralvinella pandorae.* Sample size (*N*), size range, mean and standard deviation (SD) of seventh setiger width for the three populations

Sample	*N*	Size range (mm)	Mean (mm)	SD (mm)
AX-1	654	0.2–3.4	1.55	0.56
END-3	421	0.2–1.4	0.82	0.25
EX-3	139	0.5–1.8	1.08	0.20

Fig. 4. *Paralvinella pandorae.* (A) Section of a female showing oocytes (O) at various stages of development in coelom (C); Lm: longitudinal muscle. (B) Section of male, showing rosettes of spermatocytes (R) and sperm morulae (M) developing in coelom; Bv: blood vessel. (C) Section through male mixonephridium containing spermatozoa (S); Nw: nephridial wall

probability-paper analysis. Analysis of the AX-1 population revealed one inflection point, resulting from two modes. The first mode comprised the main proportion of the population (86.7%); the means and standard deviations of the modal distributions are given in Fig. 3.

Histological examination of *Paralvinella pandorae* revealed that the worm is gonochoric. Chi-square tests of the three subsamples of *P. pandorae* showed no significant differences from a 1:1 male:female sex ratio. Only worms 1.0 mm in width or greater had coelomic gametes present. The paired gonads are situated laterally and are present in all segments except several at the anterior and posterior ends
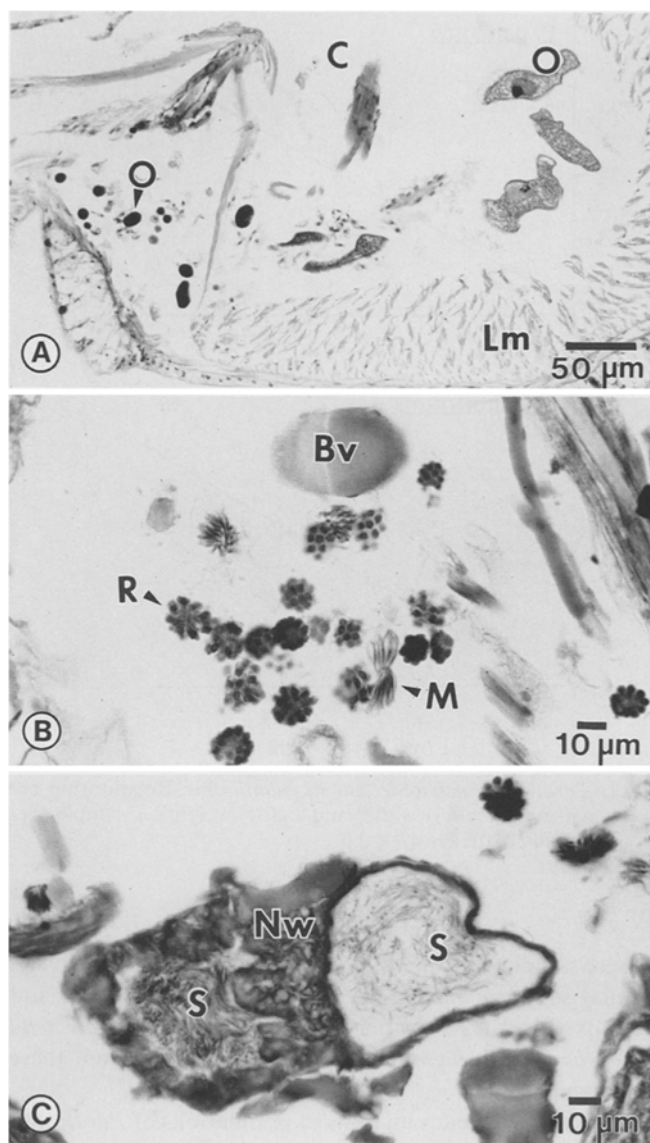
of the worm. Gametes are released into the coelom at an early stage, either as previtellogenic oocytes in females or as single spermatogonia in males. The development of gametes takes place in the coelom. The number of females in each subsample of approximately 30 worms varied between 8 and 15. Previtellogenic oocytes measured from 5 to 20 μm in diameter, vitellogenic oocytes up to a maximum of 160 μm in histological sections (Fig. 4A). During development, the oocyte changes from a spherical to an irregular shape, and then to an oval shape as maximum size is reached. The size frequency of coelomic oocytes is shown in Fig. 5. In the female population of *P. pandorae* at each of the three sites
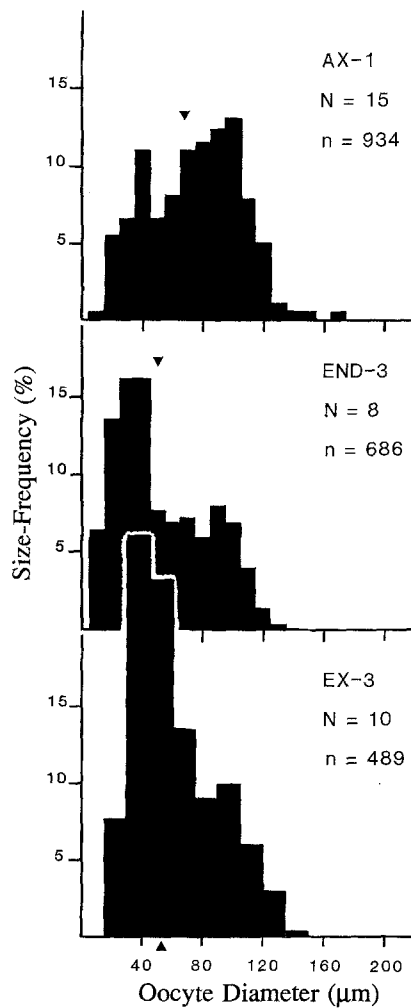
Fig. 5. *Paralvinella pandorae.* Size-frequency histograms of maximum oocyte diameter for the three subsamples. Arrowheads indicate mean oocyte diameter for each subsample; *N:* no. of specimens; *n:* no. of oocytes measured

Fig. 6. *Paralvinella pandorae.* Bar graphs illustrating percent occurrence of spermatogenic stages in males from the three subsamples; shaded portions of pie-charts represent percentage of males in which spermatozoa were observed. *N:* no. of specimens

there was a similar wide range of oocyte sizes; all individuals within each population exhibited a similar oocyte size-range. An ANOVA test revealed differences in mean oocyte size among vent samples ($F = 294.47$, $DF = 2$, $P < 0.0001$).

The frequency distributions of oocyte size differed significantly from a normal distribution ($P < 0.01$), and the END-3 and EX-3 samples were skewed towards the right. Although all individuals within each population exhibited a similar oocyte size range, ANOVA tests revealed that mean oocyte size differed significantly among individuals within each sample (AX-1: $F = 4.07$, $DF = 14$, $P < 0.0001$; END-3: $F = 8.33$, $DF = 7$, $P < 0.0001$; EX-3; $F = 7.82$, $DF = 9$, $P < 0.0001$). However, a Tukey test showed that $>80\%$ of the individuals in each population did not differ in their mean oocyte size ($P < 0.25$), thus suggesting that the significant differences shown by the ANOVA tests were accounted for by a small proportion of each population. A maximum fecundity of 4 500 oocytes/worm was recorded in a female *Paralvinella pandorae* 2.7 mm wide; the mixonephridia in the worm were packed with eggs. Maximum oocyte diameter recorded from coelomic samples was 215 μm.
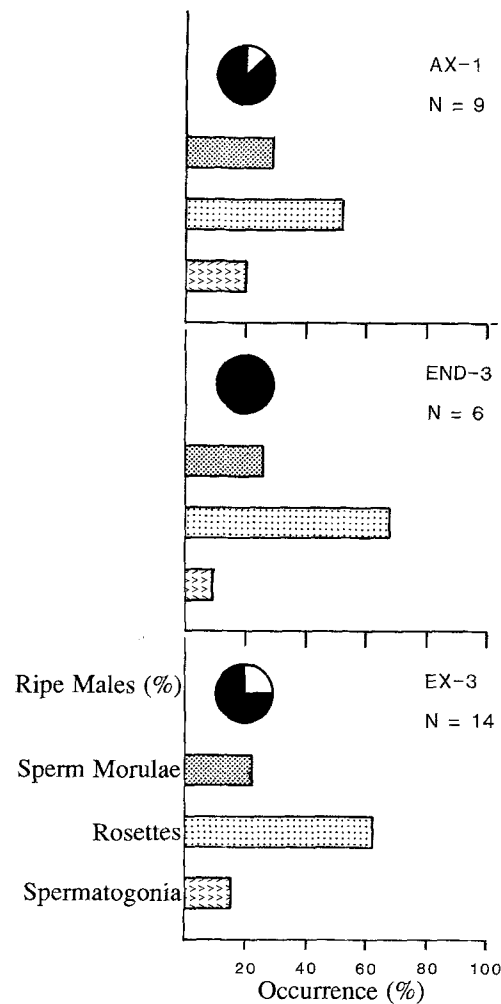
Between 6 and 14 males occurred in each of the three subsamples of *Paralvinella pandorae.* Under light microscopy, the earliest distinguishable stage of spermatogenesis is spermatogonia, which divide to give rise to rosettes of spermatocytes (Fig. 4B). Spermatocytes then form plates of tailed spermatids called sperm morulae (Fig. 4B). Ripe spermatozoa are stored anteriorly in a pair of mixonephridia (Fig. 4C). All spermatogenic stages were well represented in the male populations from the three sites (Fig. 6). All individuals within each population contained a full range of developmental stages in the coelom, and the percentage of males in each population which had spermatozoa in the mixonephridia was very high, ranging from 75 to 100% (Fig. 6).

Paralvinella palmiformis

Seven samples of *Paralvinella palmiformis* were analysed for population characteristics: AX-2, END-1, END-2, END-3, EX-1, EX-2 and EX-3. The size range varied from 0.2 mm to a maximum recorded width of 7.7 mm. As with *P. pan-*
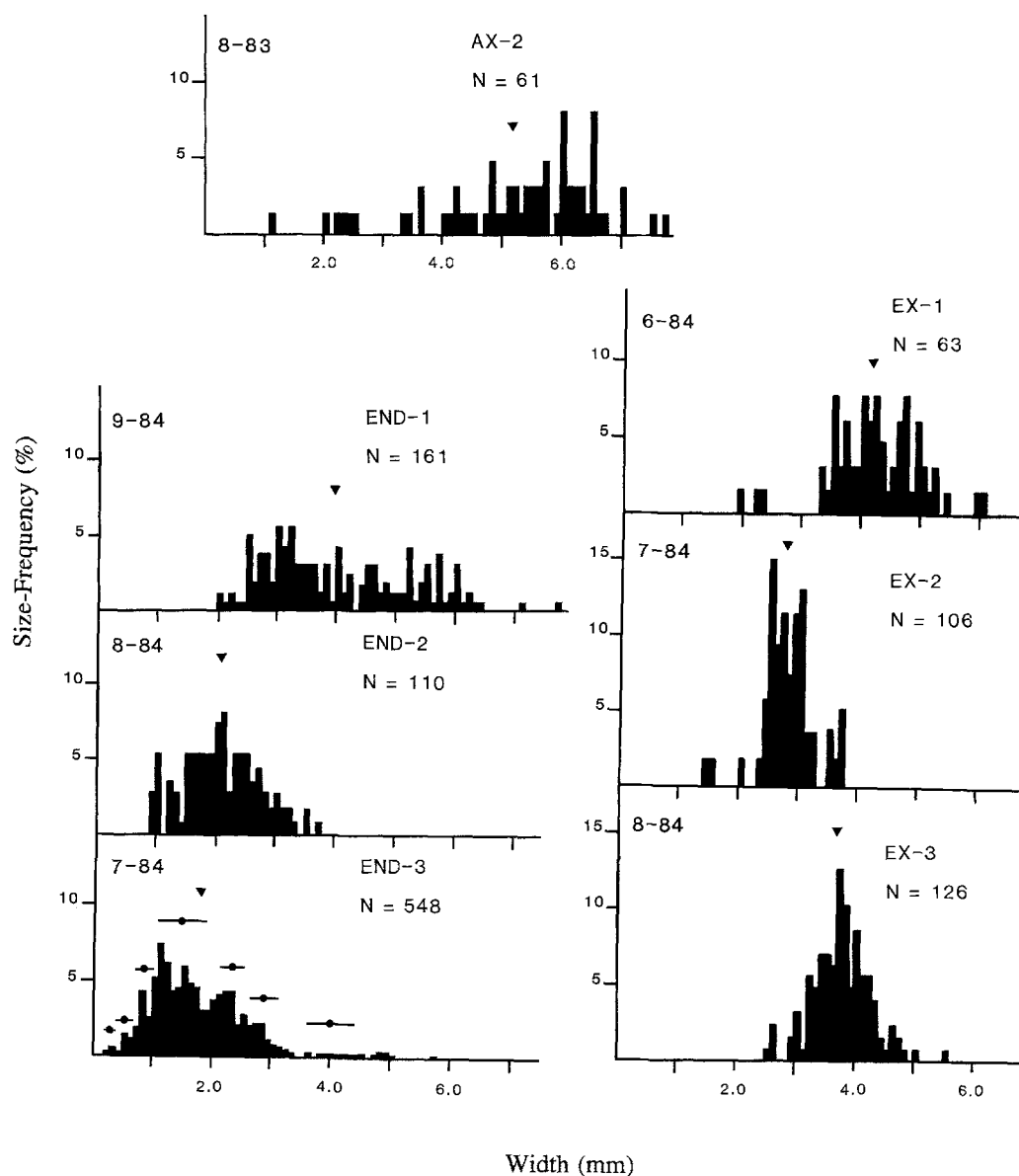
Fig. 7. *Paralvinella palmiformis.* Size-frequency histograms of seventh setiger width for the seven populations, with month and year of sampling shown. Note that very few or no gametes were present in individuals from END-2, END-3, and EX-2. Arrowheads indicate mean width for each population; —●—, means and standard deviations of modes determined by probability-paper analysis of END-3; *N*: sample size

Table 2. *Paralvinella palmiformis.* Sample size (N), size range, mean and standard deviation (SD) of seventh setiger width for the seven populations

Sample	N	Size range (mm)	Mean (mm)	SD (mm)
AX-2	61	1.1–7.7	5.17	1.42
END-1	161	2.0–7.3	4.00	1.21
END-2	110	0.9–3.7	2.07	0.64
END-3	548	0.2–5.7	1.74	0.83
EX-1	63	1.9–6.0	4.19	0.76
EX-2	106	1.4–3.7	2.78	0.45
EX-3	126	2.5–5.5	3.74	0.49

dorae, there were major differences in minimum and maximum widths of *P. palmiformis* at the seven sites (Fig. 7). Mean width ranged from 1.74 mm at END-3 to 5.17 mm at AX-2 (Table 2). A Tukey test yielded significant differences in mean widths between all pairs of samples except between END-1 and EX-1, and between END-1 and EX-3.

The size distribution of each population of *Paralvinella palmiformis* differed significantly from the normal distribution ($P < 0.01$). All seven samples differed significantly from each other in their size distributions when analysed with the two-sample Kolmogorov-Smirnov test. Histograms of the size-frequency distributions of *P. palmiformis* exhibited
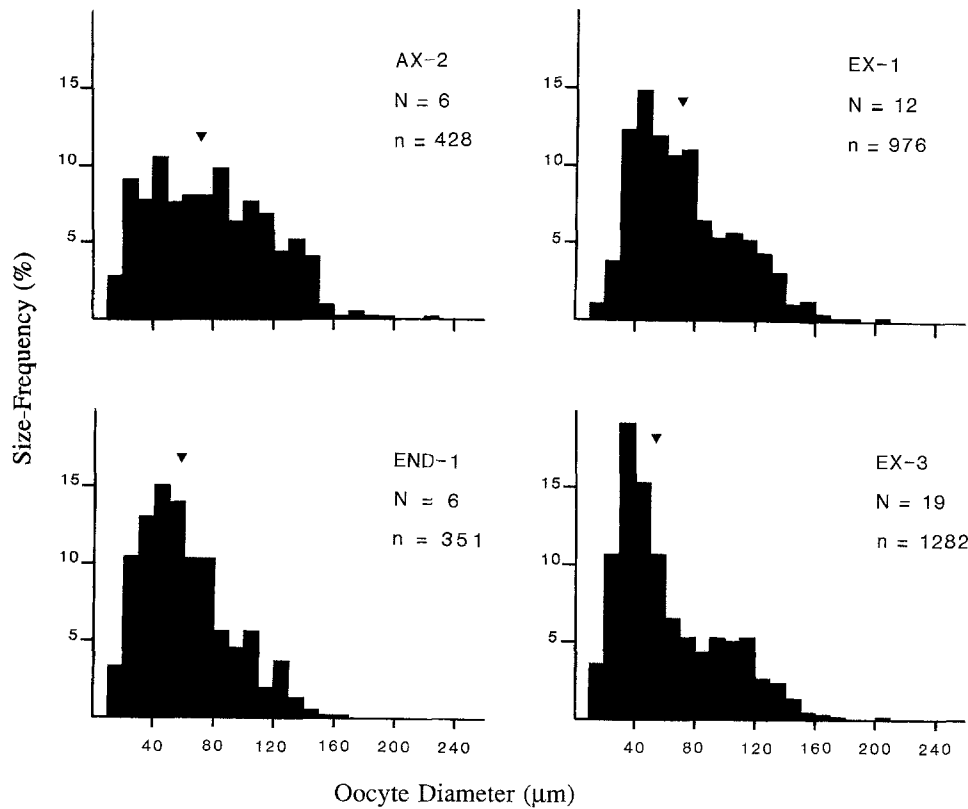
Fig. 8. *Paralvinella palmiformis.* Size-frequency histograms of maximum oocyte diameter for four subsamples. Arrowheads indicate mean oocyte diameter for each subsample; N: no. of specimens; n: no. of oocytes measured

polymodality in all but two samples, AX-2 and EX-1 (Fig. 7). Sample sizes for AX-2 and EX-1 were relatively small, and yielded disjointed histograms which are difficult to interpret. At END-1 there are numerous minor peaks evident, and possibly two major peaks defined by the absence of specimens in the 4.3 to 4.4 mm size class. There appear to be several size-class peaks in the END-2 population, and the histogram is skewed to the left. The largest sample of *P. palmiformis* was from END-3. The right-skewed histogram for this sample displays seven definite size-class peaks (Fig. 7), observed as six inflection points on the probability-paper plot. At EX-2, despite a sample size of 106, the result of size-frequency analysis was again a disjointed histogram (Fig. 7). Several possible size-class peaks were displayed by the EX-3 sample (Fig. 7).

Paralvinella palmiformis is gonochoric, and gametogenesis in this species is similar to that in *P. pandorae,* with the gametes developing free in the coelom from an early stage. In three subsamples of approximately 36 specimens of *P. palmiformis* (END-2, END-3 and EX2), very few or no gametes were observed. In the remaining subsamples, AX-2, END-1, EX-1 and EX-3, the maximum oocyte diameter recorded in sectioned specimens was 220 μm. Size-frequencies of oocytes are shown in Fig. 8, along with mean oocyte diameter for each sample. The mean oocyte sizes for AX-2 and EX-1, and for END-1 and EX-3, were not signficantly different from each other; all other pairs of sample means differed significantly according to a Tukey test. In each sample there was a wide range of oocyte sizes. The frequency

distributions of oocyte sizes for each population differed significantly from the normal distribution ($P < 0.01$). The oocyte histograms for END-1, EX-1 and EX-3 are skewed towards the right, however the AX-2 histogram is composed of almost even proportions of oocytes in the early and intermediate stages of development.

ANOVA tests revealed that mean oocyte size differed significantly among individuals within each population (AX-2: $F = 9.56$, DF = 5, $P < 0.0001$; END-3: $F = 22.55$, DF = 5, $P < 0.0001$; EX-1: $F = 10.77$, DF = 12, $P < 0.0001$; EX-3: $F = 17.37$, DF = 18, $P < 0.0001$). However, as with the *Paralvinella pandorae* females, pairwise comparisons indicate that the significant differences were accounted for by a small proportion ($< 35\%$) of each population (Tukey test: $P < 0.25$). The maximum fecundity of *P. palmiformis* was approximately 18 000 oocytes/worm, recorded from a 5.6 mm wide female. Maximum oocyte diameter in coelomic samples was 260 μm.

The three sperm developmental stages (spermatogonia, rosettes of spermatocytes, and sperm morulae) are represented in males from AX-2 (in Fig. 9). However, secondary spermatogonia and rosettes make up 95% of the noted stages, each comprising almost half of the final total (Fig. 9). Only one of the six males in this subsample contained spermatozoa in the nephridia. In males from END-1, EX-1 and EX-3, only single or small clumps of spermatogonia were observed. Larger rosettes of spermatocytes, which are composed of smaller and more condensed cells, were absent. No morulae or detached spermatozoa were present.
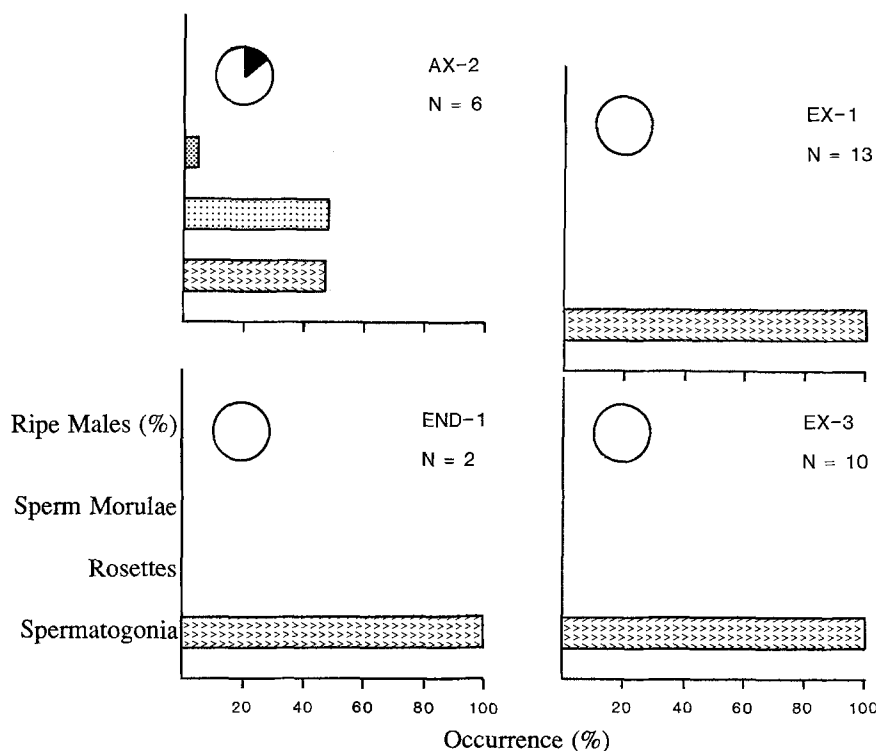
Fig. 9. *Paralvinella palmiformis*. Bar graphs illustrating percent occurrence of spermatogenic stages in subsamples of males; shaded portions of pie-charts represent percentage of males in which spermatozoa were observed in the mixonephridia. Note absence of all stages except spermatogonia in three of the four subsamples. *N*: no. of specimens

Discussion

In their demographics, *Paralvinella pandorae* and *P. palmiformis* seem to differ substantially. *P. pandorae* sample sizes were relatively large and therefore should give an accurate representation of population structure. The unimodal size-frequency histograms for this species at END-3 and EX-3 may reflect continual low recruitment to the populations studied, so that distinct peaks of juvenile input at defined intervals are not present. Alternative interpretations are that the unimodal distributions result from infrequent and irregular recruitment, as has been suggested for populations of the deep-sea holothurian *Peniagone azorica* (Tyler et al. 1985), or that each of the distributions represents a single cohort, as has been hypothesized for *Kolga hyalina,* another deep-sea holothurian (Billett and Hansen 1982). Samples of both of these sea-cucumbers yielded unimodal histograms. However, when the reproductive mode of *Paralvinella pandorae* is also considered (see discussion below), continual recruitment appears to be more likely. At AX-1, two possible peaks were evident in the size-frequency histogram, which may indicate isolated recruitment events in this population. The difference between the AX-1 distribution and those of the other samples of *P. pandorae* may have resulted from spatially patchy recruitment of juveniles among the vents.

The small samples of *Paralvinella palmiformis* from several vents displayed numerous peaks in their size-frequency distributions. However, because of the small sample sizes it is difficult to extrapolate well-defined size classes from the peaks. Fortunately the very large sample of *P. palmiformis* retrieved from END-3 yielded a histogram whose peaks

provide strong evidence of discontinuous recruitment of juveniles to the population. There appear to be seven size classes in the END-3 population, although these cannot confidently be interpreted as year classes as is often appropriate with shallow-water polychaetes (Curtis 1977, Heffernan et al. 1983, Clavier 1984, Valderhaug 1985, Christie 1986) and some deep-sea invertebrates (Tyler and Gage 1980). Nonetheless, the END-3 size classes lend support to the acceptance of definite size classes in the other, smaller samples. The size distributions of *P. palmiformis* resemble each other only in the presence of distinct classes and not in the number and location of peaks on each histogram. This may reflect patchy recruitment, or differing recruitment success or growth rates among the vents.

The size-range differences among populations of the two species from vent to vent may reflect local habitat-induced variations. A number of intertidal species which experience fluctuations in local climatic features undergo considerable variation in recruitment, growth, and maximum size in their populations (Barnes 1956, Southward and Crisp 1956, Southward 1967, Lewis and Bowman 1975). Changes in hydrogen sulphide concentration, food availability, or temperature could potentially produce similar effects in the deep-sea vent habitat. Alternatively, the different samples of each species may represent populations of varying ages, depending on the length of time a vent has been colonized. For example, the AX-1 sample of *Paralvinella pandorae* may represent an older, longer established population than that at END-3 or EX-3.

The notable absence of small size classes (<1.0 mm in width) from all but one population (END-3) of *Paralvinella palmiformis* could result from a sampling method that failed

to include juveniles, which may be spatially segregated from the adults. Alternatively, the result may reflect the lack of recent recruitment in some populations, e.g. END-1, EX-1 and EX-3. The right-hand-side truncation of one population size-frequency of *P. palmiformis*, EX-2, suggests high adult mortality at this site, possibly due to preferential predation of large worms by the crab *Macroregonia macrochira* Sakai. Tunnicliffe and Jensen (1987) reported alvinellid setae in the stomach of this crab.

Although gametogenesis is similar in *Paralvinella pandorae* and *P. palmiformis*, there are obvious differences in the reproductive cycles of the two species. ANOVA results imply a lack of synchrony of oogenesis among *P. pandorae* females in each population. However, a multiple comparison test indicates that this result may be accounted for by a small proportion of the individuals in each case. The presence of a full range of oocyte sizes in females and of all spermatogenic stages, including ripe spermatozoa, in males from the three vents, sampled in different months of different years, suggests that *P. pandorae* produces gametes continuously. Considering this observation, and the continuous or semi-continuous recruitment pattern indicated by the size-frequency histograms, it is proposed that this species reproduces continuously. Continuous breeding has been observed in a number of shallow-water polychaetes, for example in *Cirratulus cirratus* (Olive 1970) and *Arenicola ecaudata* (Southward and Southward 1958). In both studies it was postulated that suitable food is available all year round and therefore continuous reproduction takes advantage of the resources without imposing excessive seasonal demands on them (Southward and Southward 1958, Olive 1970). This is potentially the case for *P. pandorae*, as nutrients are apparently available as long as the vent remains active.

Continuous reproduction has been reported for a number of deep-sea invertebrates (Rokop 1974, Tyler and Gage 1984b, Tyler et al. 1984). The vent bivalve *Calyptogena magnifica* is thought to have great reproductive potential because it becomes reproductively active at a small size and reproduces continuously over a long period of time (Berg 1985). *Neomphalus fretterae*, a vent archaeogastropod, is also thought to spawn continuously (McLean 1981).

In *Paralvinella palmiformis*, the absence of developing gametes from three of the seven samples studied (END-2, END-3, and EX-2) implies either: (i) that none of the members of the populations had reached adulthood, at which time gametogenesis would be observed, or (ii) that those three populations had recently undergone a complete spawning of gametes. The former of the two possibilities presented seems improbable, as developing gametes were observed in worms of ≥ 2.0 mm in width in the four other populations examined, but not in worms of these sizes from END-2, END-3, or EX-2. The likelihood of complete spawning in a population is a strong indication that reproduction in *P. palmiformis* may be discontinuous, and may account for the recruitment pattern reflected in the polymodal size-frequency distributions of this species. Numerous deep-sea invertebrates have been found to exhibit a discrete reproductive pattern, similar to that suggested for *P. palmi-*

formis (Rokop 1977, Tyler and Gage 1980, Pearson and Gage 1984, Tyler and Gage 1984a, Van Praët and Duchateau 1984).

A degree of synchrony of gametogenesis between females and males in each population of *Paralvinella palmiformis* can be interpreted from the oocyte size distributions and analysis of spermatogenic stages. In AX-2 worms, both oocyte sizes and developing sperm cells were split between early and intermediate stages. In the three other samples however, the oocyte size distributions were skewed to the left, and in males the only spermatogenic stages present were spermatogonia. These three populations, END-1, EX-1 and EX-3, appeared to be at an earlier stage in the reproductive cycle. Although the ANOVA results indicated a lack of synchronization of oogenesis among females within each population at the time of sampling, a multiple comparison test showed that well over half of the individuals in each population did not differ significantly in mean oocyte size.

Synchronized reproduction has been reported in shallow-water polychaetes of the order Terebellida (Hutchings 1973, Christie 1986), to which the family Alvinellidae belongs. The means by which synchronization of gamete maturation is achieved vary among different polychaetes. In the ampharetid *Melinna cristata*, Clark (1979) suggested that hormonal regulation of ovarian activity may control synchrony of oogenesis. In many other polychaetes with synchronized spawning, gated rhythms have been proposed as a method of control (Olive 1984).

In polychaetes and other marine invertebrates there is a good correlation between maximum oocyte size and the type of larval development exhibited by a species (Thorson 1950, Strathmann and Vedder 1977, Hermans 1979). Small eggs ($< 150 \ \mu m$) are usually associated with planktotrophy in polychaetes, whilst larger eggs ($> 150 \ \mu m$) usually give rise to lecithotrophic larvae or brooded embryos (Hermans 1979). Maximum observed oocyte diameter was 215 μm in *Paralvinella pandorae*, whereas in *P. palmiformis* a substantially larger maximum oocyte size of 260 μm was observed. Oocytes of $\geq 215 \ \mu m$ diam in other, shallow-water, Terebellida produce brooded embryos that emerge from the maternal tube as a benthic stage (Marinescu 1954, Zottoli 1974, Cazaux 1982, Clavier 1984), or embryos that develop in a gelatinous cocoon to a brief pelagic stage (Eckelbarger 1974), or demersal lecithotrophic larvae (Okuda 1947, Nyholm 1951, Guillou and Hily 1983). *P. pandorae*, being a tube-dweller with large yolky eggs, exhibits the capacity to brood its young. Indeed, incubation of embryos in the maternal tube is highly probable, as the aberrant sperm ultrastructure of this species (McHugh unpublished data) provides evidence of a specialized mode of fertilization (possibly via spermatophores) which, in other polychaetes, is associated with brooding. In *P. palmiformis* it seems that brooding of young is not possible, as this worm does not usually construct a tube. In *P. palmiformis*, therefore, embryos may develop in a gelatinous cocoon to a pelagic larval stage, or a free-swimming lecithotrophic mode of larval develoment may occur. Large oocytes ($> 200 \ \mu m$) extracted from live *P. palmiformis* are not buoyant, rather they sink to the bot-

tom when placed in a container of surface seawater at 4 °C (own personal observation). Assuming similar conditions in their natural environment, this suggests that the eggs remain close to the bottom.

In the shallow-water Terebellida studied to date, demersal lecithotrophic larvae develop from eggs of 150 to 425 μm, and settle to metamorphose after three to several days (Okuda 1947, Nyholm 1951, Guillou and Hily 1983). It is not possible to confidently predict the relationship between egg size and length of larval life of hot-vent polychaetes based on those studies of shallow-water species. At the low ambient temperature around vents (2 °C) rates of metabolism may be reduced so that the length of larval life is increased, as has been demonstrated for planktotrophic and non-planktotrophic molluscan larvae (Pechenik 1984 a, b).

For some invertebrates, extended larval life has been postulated as a means of dispersal over wide geographical areas (Scheltema 1977). However, this hypothesis addresses only those larvae that develop in surface waters. Lutz et al. (1980, 1984) have suggested that the planktotrophic larvae of the vent mytilid Bathymodiolus thermophilus do not rise to the surface during development but remain close to the bottom (within approximately 500 m) throughout their free-swimming existence. Studies of deep-sea wood-borers support demersal development for some bivalve species inhabiting an isolated, ephemeral environment (Turner 1965). However, some deep-sea gastropod larvae appear to migrate to surface waters for a portion of their development (Bouchet and Fontes 1981). Demersal development of vent species would reduce the loss of larvae which would otherwise occur during surface migration.

If, as proposed, Paralvinella palmiformis has a free-swimming larval stage, it is possible that a specific cue is required to stimulate settlement and metamorphosis in the larvae. Such cues have been demonstrated for many shallow-water invertebrates (Chia and Rice 1978, Burke 1983), and may be emitted by conspecifics or the substratum. In alvinellids, specific hydrogen sulphide concentrations could act as a cue, as has been found for Capitella sp. 1 in shallow-water, sulphide-enriched habitats (Cuomo 1985, Dubilier 1986).

The suggested difference in the mode of development between Paralvinella pandorae and P. palmiformis may, in part, explain the distributional differences between the two species. P. pandorae occurs at 8 of 21 vents sampled in the northeast Pacific, whereas P. palmiformis is found at 15 vents (McHugh 1987). Brooded young of P. pandorae, produced continuously, could maintain a vent population, but severely limit dispersal to other vents. One potential means of dispersal for P. pandorae could be through hydrodynamic passive drifting of juveniles or adults. This phenomenon has been reported for sedentary polychaetes (Fauchald and Jumars 1977), and suggested for the ampharetid Melinna palmata (Guillou and Hily 1983). Demersal lecithotrophic larvae of P. palmiformis could repopulate vents, and could potentially be carried by bottom currents to other vent sites along the ridge systems. Passive mechanisms may also en-

hance the dispersal opportunities of P. palmiformis; it has been observed coiled around the leg of the highly mobile spider crab Macroregonia macrochira (Tunnicliffe and Jensen 1987). Neither P. pandorae nor P. palmiformis appears capable of dispersal to vents on the East Pacific Rise (over 3 000 km away). It has been proposed that the niche of P. pandorae pandorae at 13 °N on the East Pacific Rise is occupied by the subspecies, P. pandorae irlandei, and that of P. palmiformis by P. grasslei (Desbruyères et al. 1985, Desbruyères and Laubier 1986). It is thought that populations of a common ancestor of P. pandorae pandorae and P. pandorae irlandei have been separated since the American Plate overrode the East Pacific Rise 28 million years ago. This isolation has led to the divergence of the two subspecies, probably due to limited dispersal capabilities (Desbruyères and Laubier 1986, Tunnicliffe 1988). Populations of P. palmiformis and P. grasslei may already have been two distinct species before the separation of the Juan de Fuca and East Pacific Rise ridge systems.

The maximum fecundity of Paralvinella pandorae is very low. However, as previously mentioned, continual reproduction by P. pandorae over a long period of time would enhance its reproductive potential. The maximum fecundity estimate for P. palmiformis, although substantially higher than that of P. pandorae, appears to be relatively low. It is comparable to estimates reported for shallow-water polychaetes that undergo non-planktotrophic larval development (Olive 1970, Gibbs 1971, Gremare and Olive 1986).

Ideally, to gain complete information on the life-histories of these two polychaetes, and other hot-vent species, a time-series of samples from several vents is required. Unfortunately, the inaccessibility of the vent habitat prevents such rigorous methods. Preliminary information gained through this study indicates that two closely related hydrothermal vent polychaetes, Paralvinella pandorae and P. palmiformis, apparently employ different modes of reproduction, and methods of population maintenance.

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