The Life-History Patterns of Two Hydrothermal Vent Polychaetes, *Paralvinella pandorae* Desbruyères and Laubier and *Paralvinella palmiformis* Desbruyères and Laubier

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"The limitations of our biological equipment may condemn us to the role of 'peeping toms' at the keyhole of eternity, but at least let us take the stuffing out of the key-hole which blocks even our limited view."

Koestler, 1964

Supervisor: Dr. Verena Tunnicliffe

ABSTRACT

The population structure and reproductive biology of two polychaetes of the Family Alvinellidae, *Paralvinella pandorae* Desbruyères and Laubier and *Paralvinella palmiformis* Desbruyères and Laubier, have been studied from eight vents at three hydrothermal sites on the Juan de Fuca Ridge and Explorer Ridge. The Alvinellidae are found exclusively in hydrothermal vent habitats; *P. pandorae* and *P. palmiformis* are known only from hot vents of the northeast Pacific. This restricted distribution appears to be due to dispersal limitations between vent fields along the Juan de Fuca and Explorer Ridges, and those situated thousands of kilometers to the south along East Pacific Rise and Galapagos Rift. Abundance of both species at different vents varies, possibly as a result of competition for space and/or food, or differences in recruitment. Absence of either species from a vent may be due to inability to disperse, unsuitable settling substratum, or inappropriate physico-chemical conditions.

Size-frequency analysis of two *P. pandorae* populations produces unimodal histograms, suggesting continuous or semi-continuous juvenile recruitment; in a third population two possible size classes are evident. Histograms of *P. palmiformis* display definite size class peaks, which indicate periodic recruitment of juveniles. Local, habitat-induced variations in environmental conditions are thought to produce the observed size range variations in both species from different vents.

Histological studies of gametogenesis show that both species are gonochoric, and gamete development is similar to that described for other polychaetes in the Order Terebellida. All populations of *P. pandorae* examined exhibit a full range of gametogenic stages, including spermatozoa in males. This species appears to reproduce continuously or semi-continuously. *P. palmiformis*, on the other hand, appears to possess a discrete breeding cycle. The control of synchronization of gametogenesis and spawning in *P. palmiformis* is not known.

Maximum oocyte size in *P. pandorae* and *P. palmiformis* is approximately 330µm and 440µm, respectively. Larval development, extrapolated from this parameter and based on previous terebellid studies, is thought to be lecithotrophic and demersal in both species. Such development would provide for repopulation of a vent, or colonization of new vents. Extended larval life facilitated by low ambient temperatures would allow dispersal, possibly via bottom currents along the ridge systems, to other vents. The larger maximum oocyte size of *P. palmiformis* suggests a longer larval developmental period than that of *P. pandorae*. Despite this, neither *P. palmiformis* nor *P. pandorae* appears capable of dispersal over the long distances to southeastern Pacific vents.

P. pandorae and *P. palmiformis* do not exhibit extreme r-selected or K-selected life-history strategies. Neither species shows a high reproductive potential, rather they tend to be more K-selected in their life-history patterns. Both produce relatively small numbers of large, lecithotrophic larvae.

The life-histories of *P. pandorae* and *P. palmiformis* appear to be influenced more by the limitations of their evolutionary history than the selective pressures of the environment that they inhabit. These results are in agreement with the

suggestions of several authors that reproductive modes of vent fauna are mainly a function of phylogenetic constraints.

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(Frontispiece courtesy of ASHES Expedition, 1986)

INTRODUCTION

The occurrence of extraordinary assemblages of invertebrates, existing independently of photosynthetic primary production, around sources of hydrothermal activity along ocean spreading centres, has been one of the most surprising ecological discoveries of this century. The initial discovery was made in the mid 1970's, when discharge of hydrothermal fluids from the seafloor along the Galapagos Rift was detected by temperature and isotopic anomalies (Weiss *et al.*, 1977). Further investigations, involving a deep-tow camera survey of that area, revealed the presence of a unique faunal community surrounding sources of hydrothermal emissions (Lonsdale, 1977). In 1977 and 1979, *in situ* expeditions to this area with the manned submersible *Alvin* obtained the first specimens from the hydrothermal vent faunal assemblage (Galapagos Biology Expedition Participants, 1979; Corliss *et al.*, 1979). Since then several other hydrothermally active areas in the Eastern Pacific have been explored and found to support faunal communities similar in many respects to that found at Galapagos Rift, i.e., 21°N, 13°N and 17°S on the East Pacific Rise (Desbruyères *et al.*, 1982), Guaymas Basin (Grassle, 1982), Juan de Fuca Ridge and Explorer Ridge in the northeast Pacific (Canadian American Seamount Expedition, 1985; Tunnicliffe *et al.*, 1985; Tunnicliffe *et al.*, 1986).

Large bivalves, crabs, vestimentiferans and polychaetes form the distinctive community at vents on Galapagos Rift (Galapagos Biology Expedition Participants, 1979). This type of faunal assemblage has become the signature community at all hydrothermal vents in the southeast Pacific. However, variations at all taxonomic levels of vent fauna occur between northern and southern vent sites. For example, limpets and snails are the dominant molluscs at northern vents, as compared to bivalves at southern vents. The diverse and luxuriant biological communities associated with sources of hydrothermal activity contrast starkly with the typically depauperate deep-sea floor (Sanders and Hessler, 1969). Even at cold hydrogen sulphide and methane seepage sites at the base of the Florida Escarpment, in the Gulf of Mexico, and along the subduction zone off the Oregon coast, communities of vent related organisms have been discovered (Paull *et al.*, 1984; Hecker, 1985; Suess *et al.*, 1985). Although these sites resemble the hot vent environment in many physical aspects and the community is taxonomically similar to that of other vents, no elevated temperatures have been recorded. The key factor for the presence of lush faunal assemblages at vents and seepage sites is the elevated concentration of a reducing substance, hydrogen sulphide or methane, in the hydrothermal effluent. These substances are oxidized to derive energy by chemoautotrophic bacteria, thus forming the basis of a relatively simple food chain at hydrothermal vents (Jannasch and Wirsen, 1979; Rau, 1981; Karl *et al.*, 1980). Many vent species exhibit intimate associations with these bacteria, while others possess physiological adaptations that enhance their uptake of bacterially derived nutrients (for reviews see Somero *et al.*, 1983 and Felbeck *et al.*, 1985). Vestimentifera are gutless; they depend on the metabolic byproducts of endosymbiotic bacteria in the trophosome as a source of nutrition (Felbeck, 1981; Cavanaugh *et al.*, 1981). *Calyptogena magnifica* Boss and Turner and

Bathymodiolus thermophilus Kenk and Wilson also have symbiotic relationships with chemoautotrophic bacteria (Rau, 1981; Cavanaugh, 1983; Le Pennec and Prieur, 1984). De Burgh and Singla (1984) describe the colonization of limpet gills by bacteria that are endocytosed, which is an intermediate type of association of bacteria with a vent species. The high biomass of free-living bacteria provides a direct food source in the form of particulate organic matter in the water and mats of microbial material, which are eaten by suspension-feeders, deposit-feeders and grazers at the vents.

Vents, when active, appear to represent a favourable environment with high levels of available nutrients. It is an unpredictable environment, however, as vent activity is variable in duration, lasting from one year to several decades (Lalou and Brichet, 1981; MacDonald *et al.*, 1980). The ephemeral nature of hydrothermal vents is just one of the many problems to which sedentary vent-specific animals must adapt. Temperatures experienced by animals living at a vent may be from 4°C to 100°C or greater, and the temperature at a single vent can vary irregularly over short periods of time (Tunnicliffe *et al.*, 1985; Fatton *et al.*, 1981). Elevated concentrations of minerals (particularly sulphides of iron, zinc and manganese) in the form of suspended particulate matter are characteristic of vent effluent, and organic particulates are often concentrated around vents (Karl *et al.*, 1980). Large variations in rate of hydrothermal flow over a few hours, and even complete interruption of discharge have been observed (Desbruyères and Laubier, 1983).

Suitable habitat for a vent population is patchily distributed. In a given field of hydrothermal activity, distances between vents may be up to tens of metres.

The degree of isolation of separate vent fields is not yet fully known. From explorations to date it appears that some hydrothermally active areas can be separated from others by hundreds to thousands of kilometers. The patchy and transient nature of the hot vent environment suggests that vent-specific animals, if they are to be successful, must possess life-history traits suited to such a situation. The colonization of newly-forming or newly-encountered vents requires a dispersive phase in the life-history of these species, either as pelagic larvae or swimming adults, or by passive transportation of either stage.

It has been theorized that in unstable environments, early maturity, high fecundity, semelparity, no parental care, and large reproductive effort represent the optimum life-history traits (Grassle and Grassle, 1974; Stearns, 1976). These tactics are collectively referred to as an 'r-type' life-history strategy (MacArthur and Wilson, 1967). Conversely, a 'K-type' strategy, i.e., delayed reproduction, low fecundity, iteroparity, parental care, and smaller reproductive effort, is favoured in an environment of stable conditions. Clearly, the r-strategy (high reproductive rate) and the K-strategy (reduced reproductive effort) represent endpoints of a continuum (Pianka, 1983). No organism is completely r-selected or K-selected, rather all must reach some compromise between the two extremes. An organism is usually considered an r-strategist or a K-strategist only in comparison with some other organism. An organism in a given environment at a given time can only be placed somewhere along the r to K selection continuum (Pianka, 1983).

An alternative theory put forward by Schaffer (1974b) regards variable mortality of the young or the adults as the major force which directs selection of certain life-history characteristics under given conditions. When variations in mortality affect the number of young that survive to breed, then reduced reproductive effort, small clutches, and longevity are favoured. On the other hand, environmental variability that affects adult survival favours increased reproductive effort, larger clutches, and short-lived organisms.

The hydrothermal vent environment may be considered an unstable one in which fluctuations occur randomly in time. Relatively stable and favourable periods at a vent are punctuated by the flow or ebb of hydrothermal fluid, which provides the essential ingredients for the survival of the community. Stearns (1976) proposes that in an unstable, fluctuating environment, such as hydrothermal vents, a mixed life history tactic is favoured. Desbruyères and Laubier (1983) suggest that vent fauna could be expected to have r-type ecological strategies, i.e., adapted to an unstable, short-term environment. However, such a generalization may not be possible. Selective pressures in the vent environment may occur on a number of levels. The most drastic change in vent conditions occurs when hydrothermal flow ceases and the faunal populations die out. There are likely to be other more subtle variations which affect the outcome of vent populations, and thus may also contribute to the selection of life-history traits. Larval mortality may be very high and/or variable in vent species because of the patchiness of the habitat, and may represent as great a selective pressure on the life-history pattern of a vent species as the localized extinction of an adult population. Intermittent alterations in temperature, bacteria concentration, mineral composition or concentration, etc., may influence a vent population, e.g., increase or decrease food availability, increase or decrease the developmental rate of gametes, or precipitate spawning. Although the peculiar environmental fluctuations of vents may be expected to impose selective forces for a certain set of life-history traits, many vent species may not have the ability to adopt those traits due to strong phylogenetic constraints. Considering all these factors, it seems likely that vent species will display a variety of life-history tactics. Some will be more successful than others in the vent environment, but no one strategy will characterize the vent faunal community.

The life-history patterns of a number of vent species have been studied, with the vent Mollusca receiving most attention to date. The large bivalve, *Calyptogena magnifica* produces large numbers of relatively large yolk-filled eggs which suggest the development of lecithotrophic larvae (Berg, 1985; Berg and Turner, 1980; Turner, 1981), although it is not known if these larvae develop within egg cases or swim freely. Growth rates in *C. magnifica* approximate 0.58cm/year to an estimated maximum age of between 23 and 37 years (Lutz *et al.*, 1984, 1985; Roux *et al.*, 1985).

The vent mussel, *Bathymodiolus thermophilus*, produces large numbers of small eggs (Berg, 1985); the larvae are thought to develop planktotrophically and near bottom dispersal has been proposed (Lutz *et al.*, 1980). Size-frequency distributions imply discontinuous recruitment of juveniles (Rhoads *et al.*, 1982). The growth rates of *B. thermophilus*, like those of *C. magnifica*, are among the highest recorded for deep-sea species at 1cm/year (Rhoads *et al.*, 1982). The largest mussel collected is estimated to be 19 ± 7 years old (Rhoads *et al.*, 1981).

The archaeogastropod, *Neomphalus fretterae* McLean, spawns continuously and undergoes direct development within coated eggs (McLean, 1981; Fretter *et al.*, 1981). Protoconch size of *N. fretterae* supports the suggestion of non-planktotrophic development (Turner *et al.*, 1985). These and other molluscs studied to date exhibit no unique adaptations for living in a transient, patchy environment. Data on developmental modes of molluscan vent species are typical and within the range of variation for the systematic group to which they belong (Turner *et al.*, 1985).

Van Dover *et al.* (1985) report the mode of larval development in four decapod crustaceans found at hot vents. *Alvinocaris lusca* William and Chace, a vent shrimp, and the brachyuran crab, *Bythograea thermydron* Williams have planktotrophic larval development, while two species of squat lobster, *Munidopsis lentigo* Williams and Van Dover and *M. subsquamosa* Henderson, undergo lecithotrophic larval development. Van Dover and her colleagues suggest that phylogenetic constraints, rather than the vent habitat, dictate the life-history strategy of these species.

Few data have been published on the life-cycles of the many polychaete species that inhabit vents. Zottoli (1983) describes the late larval stages of *Amphisamytha galapagensis* Zottoli, an ampharetid found at vents in both the northeast and southeast Pacific. He hypothesizes that *A. galapagensis* produces lecithotrophic demersal larvae. The erpochaete juvenile stage (11 setiger) of *Paralvinella grasslei*, (Desbruyères and Laubier, 1982), an alvinellid found at 13°N, was reported by Desbruyères *et al.*, 1985. They propose direct larval development and a very early benthic stage for this species. There are no other data on the population structure or reproductive biology of any polychaetes of the Family Alvinellidae, which represent prominent members of the communities at a wide range of vents and sites.

The Family Alvinellidae, (Desbruyères and Laubier, 1986) is a recently described family of primitive terebellid polychaetes. All known alvinellids are associated with hydrothermal vents. Originally the alvinellids were described as a subfamily of the Ampharetidae (Desbruyères and Laubier, 1980), with *Alvinella pompejana*, (Desbruyères and Laubier, 1980) and *A. caudata*, (Desbruyères and Laubier, 1986) being the first described members of that subfamily. *A. pompejana* builds U-shaped, parchment-like tubes on the surface of zinc sulphide diffuser vents and, in a few cases, on the walls of black smokers where both living and fossilized tubes have been observed (Desbruyères *et al.*, 1985). The geographic distribution of *A. pompejana* is relatively wide; specimens have been recovered from three sites on the East Pacific Rise at 21^{o}N, 13^{o}N and 17^{o}S.

A. caudata is similar to and found associated with *A. pompejana* at the 21^{o}N and 13^{o}N sites. It has not been found at 17^{o}S, possibly due to insufficient sampling (Desbruyères and Laubier, 1986). *A. caudata* differs from *A. pompejana* in that it has a greater number of setigerous segments and an extreme modification of the posterior parapodia. Filamentous bacteria and sulphur accumulations are found on digit-like expansions of the posterior notopodia (Desbruyères *et al.*, 1983; Laubier *et al.*, 1983); the bacteria appear to be chemoautotrophic and may provide nutrition to the worm (Tuttle, 1985; Alayse-Danet *et al.*, 1986). The gut also contains bacteria associated with organic matter and sulphide particles. The tubes of both *Alvinella* species are lined with sulphur-oxidizing bacteria that enrich the tube medium with organic molecules that can be absorbed across the body surface of the worm (Desbruyères *et al.*, 1985).

A second alvinellid genus, *Paralvinella*, was erected by Desbruyères and Laubier (1982). The type species, *Paralvinella grasslei*, was originally described from vent collections on Galapagos Rift, and since then has been found on the East Pacific Rise at 21°N and 13°N, and in the Guaymas Basin (Desbruyères and Laubier, 1986). *P. grasslei* builds tubes on a variety of surfaces: basalts, sulphides, vestimentiferan tubes and bivalve shells (Desbruyères and Laubier, 1986). From genetic studies of the *Alvinella* species and *P. grasslei*, Autem *et al.* (1985) concluded that the divergence of *Paralvinella* and *Alvinella* occurred long before that of the two *Alvinella* species.

Two other species of the Family Alvinellidae, *Paralvinella pandorae*, (Desbruyères and Laubier, 1986)[1] and *P. palmiformis*, (Desbruyères and Laubier, 1986), have been collected from four sites along two relatively small ridge systems in the northeast Pacific. The two ridges, Juan de Fuca Ridge and Explorer Ridge, separated from each other approximately 6.5 million years ago (Riddihough, 1978). They are joined by the 200km long Sovanco Transform fault. The Juan de Fuca Plate split from the Cocos Plate approximately 28 million years ago (Riddihough, 1981; Ingersoll, 1982) as the American Plate overrode the East Pacific Rise (Atwater and Molnar, 1973). This separation of the Juan de Fuca and Explorer Ridges from the East Pacific Rise has been steadily increasing with the southwestern movement of the American Plate.

To date, no information on the population structure or reproductive cycle of either *P. pandorae* or *P. palmiformis* has been published. The purpose of this study is to determine the life-history strategies of these two closely-related polychaetes

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[1] Unless otherwise specified, *Paralvinella pandorae* will refer to *P. p. pandorae* Desbruyères and Laubier, and not *P. p. irlandei* Desbruyères and Laubier.

that are found, often co-occurring, at hydrothermal vents on the aforementioned ridge systems in the northeast Pacific. Samples of both species from three vent sites in that area have been used to achieve this goal. From size-frequency analysis of population structures, the demography and recruitment patterns of the two species have been ascertained. The reproductive cycle and type of larval development have been deduced from gametogenic studies. On the basis of these initial data, colonization, reproduction, and dispersal by these two polychaetes are discussed in relation to the fluctuating, transient environment of hydrothermal vents, which *P. pandorae* and *P. palmiformis* inhabit, and also in the light of what is known about the life-history patterns of polychaetes in the same order as the Alvinellidae, i.e., the Order Terebellida.

Many limitations are inherent in a study of this nature. Due to the inaccessibility of the hot vent environment, and the expense incurred by submersible expeditions, only one sample is available from any one vent. This unfortunately rules out the possibility of observing temporal changes in population structure, or following gametogenesis in a population over a period of time. Faunal samples are taken using hydraulic submersible claws thus excluding quantitative sampling of a vent. One must assume that a population sample taken in this manner represents a random sample, and is not biased towards any particular portion of the population, e.g., large members. Time constraints and technical difficulties encountered during a submersible dive can sometimes prevent the sampling of water or temperature at a vent. Consequently, many faunal samples lack supporting physico-chemical data.

To gain a complete understanding of the life-cycle of a species it is often desirable to complement analyses of population structure and gametogenesis with the culture of larvae from fertilized eggs to metamorphosed juveniles. This has not yet been achieved with any vent species. Even if vent animals are alive on retrieval to the surface, they are difficult to maintain in ship-board aquaria for extended periods of time.

Despite these restrictions, this study provides the first insights into an important aspect of the biology of a polychaete family that is eminent in the hydrothermal vent habitat.

MATERIALS AND METHODS

Collection Sites

During 1983 and 1984 there were six submersible research cruises to four hydrothermally active sites along the Juan de Fuca and Explorer Ridges, located in the north-east Pacific. Either the Canadian submersible, *Pisces IV*, or the American submersible, *Alvin*, was used to make dives on the four vent sites (Table 1). Of the vents investigated in detail, eight of them, from three vent sites, were used in this study. In other vent samples, alvinellid numbers were insufficient, or the specimens were used for other studies. Each faunal sample was taken using an hydraulic claw operated by the submersible pilot, and was fixed in 10% seawater-buffered formalin on board ship. Two alvinellid species, *Paralvinella pandorae* and *Paralvinella palmiformis*, were later sorted from these bulk samples. Temperature recordings were made at each vent and, when possible, water samples were retrieved and used by other scientists to determine bacterial counts, hydrogen sulphide concentration and other physico-chemical parameters. Environmental data for the eight vents from which the two alvinellid species were sampled are given in Table 2.

The southern-most site used in this study, at $46^{\circ}00.0'$N, $130^{\circ}04.0'$W, is on Axial Seamount in the central section of the Juan de Fuca Ridge (Fig. 1). The northern end of this seamount was explored in August, 1983. The summit of Axial Seamount is a flat-floored collapse feature, called a caldera, with rim walls of up

Table 1: A list of all submersible research cruises to hydrothermally active sites on the Juan de Fuca Ridge and Explorer. The number of vents sampled, and the number of vent samples used in this study, are also given.

VENT SITE	EXPEDITION	DATE	NO. VENTS SAMPLED	NO. VENTS USED	REFERENCE
Axial Seamount	UVIC/UBC	8-1983	3	2	a, b
	UVIC/NOAA	7-1986	12	0	c
Endeavour Segment	NOAA	7-1984	4	1	d
	UW	8-1984	6	2	e
Explorer Ridge	UVIC	6-1984	9	2	f
	UofT/UBC	8-1984	?	1	g
Southern Juan de Fuca	USGS	9-1984	3	0	h

UVIC = University of Victoria; UBC = University of British Columbia; NOAA = National Oceanic and Atmospheric Administration; UW = University of Washington; UofT = University of Toronto; USGS = United States Geological Survey.

a = Canadian American Seamount Expedition, 1985,
b = Tunnicliffe *et al.*, 1985,
c = ASHES Expedition, 1986,
d = Malahoff *et al.*, 1984,
e = Karsten *et al.*, 1984,
f = Tunnicliffe *et al.*, 1986,
g = Scott *et al.*, 1984,
h = USGS Juan de Fuca Study Group, in press.

Table 2: Temperature, hydrogen sulphide/SO_4 concentration and bacterial concentration from the vents used in this study. Omissions from this table are due to incomplete sampling at some vents.

VENT SITE	VENT	TEMPERATURE	H_2S/SO_4 CONCENTRATION	BACTERIAL CONCENTRATION	REFERENCE
Axial Seamount	AX-1	29°C	H_2S 330μmol kg^{-1}	3.5×10^4 ml^{-1}	a
	AX-2	35°C	-	-	a
Endeavour Segment	END-1	17°C	SO_4 27.4mmol kg^{-1}	5.6×10^6 ml^{-1}	b, c
	END-2	113°C	SO_4 27.8mmol kg^{-1}	1.7×10^4 ml^{-1}	b, c
	END-3	warm	-	-	d
Explorer Ridge	EX-1	44°C	H_2S 2.8μmol kg^{-1}	41×10^4 ml^{-1}	e
	EX-2	25°C	H_2S 29.6μmol kg^{-1}	4.2×10^4 ml^{-1}	e
	EX-3	25°C	-	-	f

a = Canadian American Seamount Expedition, 1985,

b = S. K. Juniper, pers. comm.,

c = R. E. McDuff, pers. comm.,

d = M. L. Jones, pers. comm.,

e = Tunnicliffe *et al.*, 1986,

f = S. Scott, pers. comm.

to 60m in height. Its northern rim and the floor of the caldera are transected by fissures. Older basalts of the upper rim are covered with a thin sediment layer; young glassy sheet flows found on the caldera floor suggest that the lava flows are recent (Canadian American Seamount Expedition, 1985). Along a 20m deep fissure, which traverses 200m of the caldera floor and continues through the north wall, there were numerous vents seeping hydrothermal fluids. These vents were surrounded by limpets and polynoid polychaetes, or by small numbers of vestimentiferans. There was considerable water flow from two major vents in the fissure, designated as AX-1 and AX-2.[2] Both AX-1 and AX-2 were surrounded by dense mounds of vestimentiferans. The temperatures measured at AX-1 and AX-2 were 29°C and 35°C respectively (Table 2). Both vents were within an approximate 30m range of other, less active, biotic vents (Tunnicliffe *et al.*, 1985).

The Endeavour Segment of the northern Juan de Fuca Ridge, located 217km north of Axial Seamount, was explored in July, 1984 and again in August, 1984 (Fig. 1). Endeavour Segment is approximately 90km long and forms an elongate S-shaped ridge bounded north and south by overlapping spreading centres (Tivey and Delaney, 1986). The summit of the ridge crest lies at a depth of 2100m. Geological features of this site indicate that this area has been vigorously hydrothermally active (Karsten *et al.*, 1984). The vents at this site lay in an axial valley of the ridge at 2200m, at 47°57.0'N, 129°00.0'W, and the three used in this study are designated as END-1, END-2 and END-3. They were sampled for fauna, water and temperature. Temperatures measured at the vents varied from 17°C at

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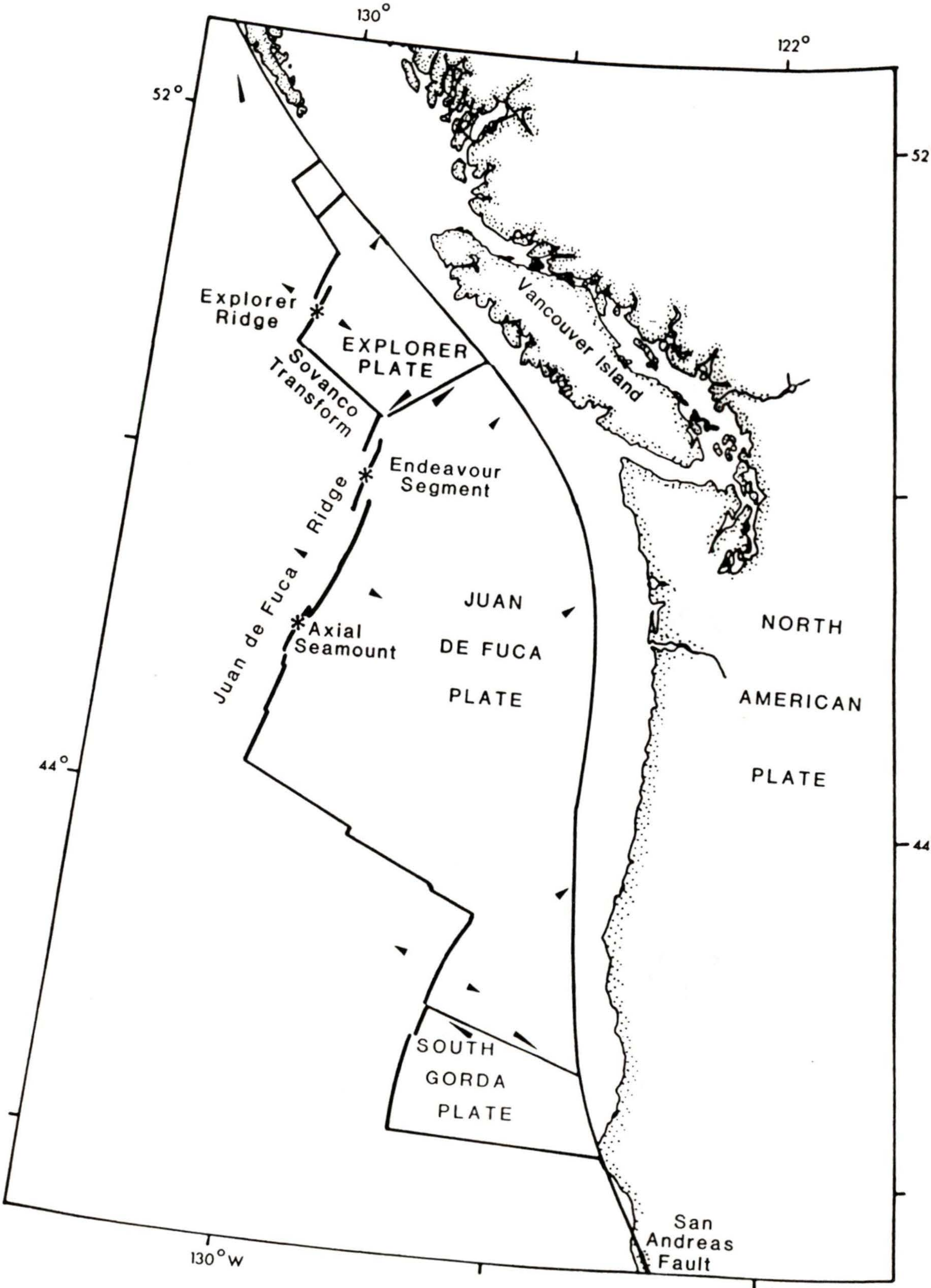
[2] Appendix A lists all corresponding vent names used to date in publications, on specimen labels, etc.

Figure 1: Map of Juan de Fuca Ridge and Explorer Ridge showing the locations of the three vent sites sampled for this study.

Arrows indicate areas of spreading, faulting or subduction.


130°
122°
52°
52°N
44°
44°N
130°W
122°W
Explorer Ridge
EXPLORER PLATE
Sovanco Transform
Endeavour Segment
Vancouver Island
Juan de Fuca Ridge
Axial Seamount
JUAN DE FUCA PLATE
NORTH AMERICAN PLATE
SOUTH GORDA PLATE
San Andreas Fault

END-1 to 113°C at END-2.

The northern-most site, at 49°45.5'N, 130°16.0'W, is on Explorer Ridge. This ridge was investigated in June, 1984 and in August of the same year. Explorer Ridge is offset to the northwest of the Juan de Fuca Ridge by the 200km long Sovanco Transform fault (Fig. 1). At 49°42.0'N, two northerly branches of a 100m deep axial valley rise to a large plateau that rises to approximately 1800m. The axial floor is made up of relatively old pillow basalts, with light to moderate sediment cover. Inactive mounds of oxidizing sulphides were present in the southwest, while northwards there were larger and younger deposits. Massive hydrothermal flows, venting 25°C to 310°C fluid, were found at the eastern apex of the valley (Tunnicliffe *et al.*, 1986). Alvinellid samples from several vents were retrieved. Three of these samples, EX-1, EX-2 and EX-3, were used in this study. EX-1 exhibited diffuse venting, which supported luxuriant thickets of large vestimentiferans over many square meters. At EX-2 a restricted warm-water source was surrounded by a small vestimentiferan clump. EX-3 was a 1-2m high, low temperature diffuser vent, covered with vestimentiferan tube worms (S. K. Juniper, pers.comm.). Temperatures at the three vents ranged from 25°C to 44°C (Table 2).

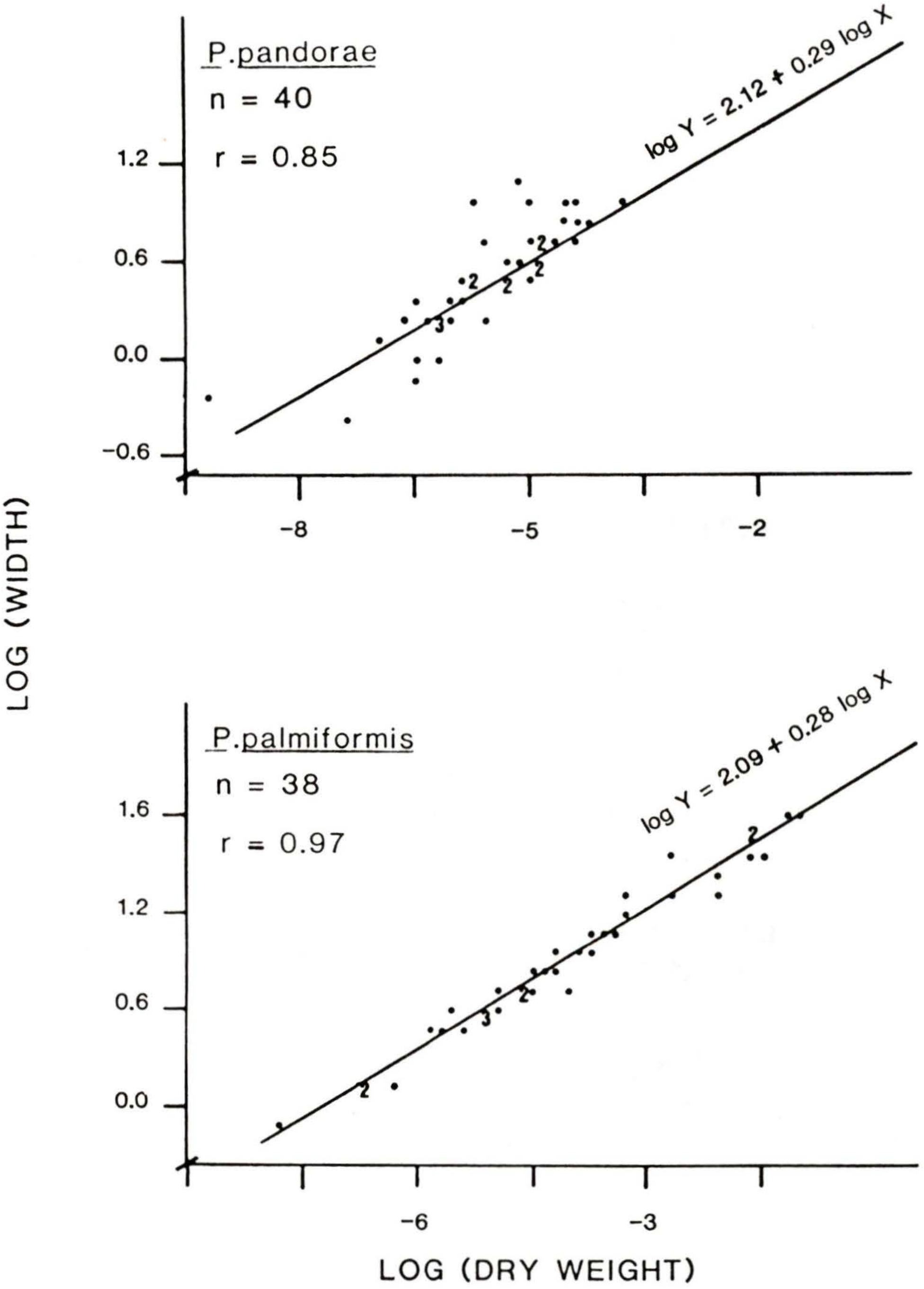
Population Structure

For size-frequency analysis of all populations of *P. 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 terebellid *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 the correlation (Spearman's rank coefficient) between the seventh setiger width and dry weight of the worms. All width measurements were made to the nearest 0.1mm on a Zeiss dissecting microscope at X20 magnification. Figure 2 shows the resulting relationship for both *P. pandorae* and *P. palmiformis*. The correlation coefficients, $r = 0.85$ and 0.96 ($P<0.01$) for *P. pandorae* and *P. palmiformis* respectively, affirm the width of the seventh setiger as a dependable parameter for representing total body size.

Histograms of width-frequency were constructed for the populations of each species from all sites sampled. Either all of the specimens in a sample were used for this analysis or, if a sample was very large, a subsample was randomly taken and used. Probability paper analysis (Cassie, 1954; Cerrato, 1980) was carried out on all histograms to determine the presence or absence of size-class peaks. The two-sample Kolmogorov-Smirnov test was used to test for statistically significant differences between size-frequency distributions. Total segment numbers of specimens of worms were counted and used to determine whether different morphs of a species occurred at various sites.

Figure 2: The relationship between log (width) and log (dry weight) for *Paralvinella pandorae* and *P. palmiformis*.

n = sample size,
r = correlation coefficient ($P<0.01$).


P.pandorae
n = 40
r = 0.85
log Y = 2.12 + 0.29 log X
1.2
0.6
0.0
−0.6
−8
−5
−2
LOG (WIDTH)
P.palmiformis
n = 38
r = 0.97
log Y = 2.09 + 0.28 log X
1.6
1.2
0.6
0.0
−6
−3
LOG (DRY WEIGHT)

Gametogenesis

Attempts to obtain mature eggs and active sperm from *P. pandorae* and *P. palmiformis*, kept alive in ship-board aquaria for several days, were unsuccessful.

Histological examination of gametogenesis was carried out only on well-preserved and undamaged worms. Thirty or more specimens representing the size ranges of both species from each site sampled were prepared for histology by impregnation with Tissue Prep (Fisher ®). A detailed outline of the tissue-processing schedule is given in Table 3. This schedule was modified for very large specimens of *P. palmiformis* which required longer periods to allow full penetration of the tissues by the processing solutions. Serial sections of 5 - 7 μm thickness were stained using either haemotoxylin and eosin, or eriochrome cyanin.

Table 3: Tissue processing schedule used for histology of *Paralvinella pandorae* and *P. palmiformis*.

PROCESSING FLUID	HOURS IMMERSED
70% Ethanol	8
95% Ethanol	16
Absolute Alcohol I	2
Absolute Alcohol II	2
Absolute Alcohol III	2
Xylene I	2
Xylene II	16
Xylene III	1
'Tissue Prep' I	2
'Tissue Prep' II	2
'Tissue Prep' III	1
'Tissue Prep' IV	1

Female Specimens

In each female specimen up to 75 oocytes were measured for maximum oocyte diameter at X100 magnification. To avoid repeated measurements of a single oocyte, only those oocytes in which both the nucleus and nucleolus were seen were measured. Although the shape of the oocytes became rather irregular with increasing size, a Spearman's rank correlation coefficient of $r = 0.86$ ($P<0.01$) was determined between maximum oocyte diameter and area. This indicates that maximum diameter is a good predictor of oocyte size (Fig. 3). Histograms of oocyte size-frequency were constructed for each sample.

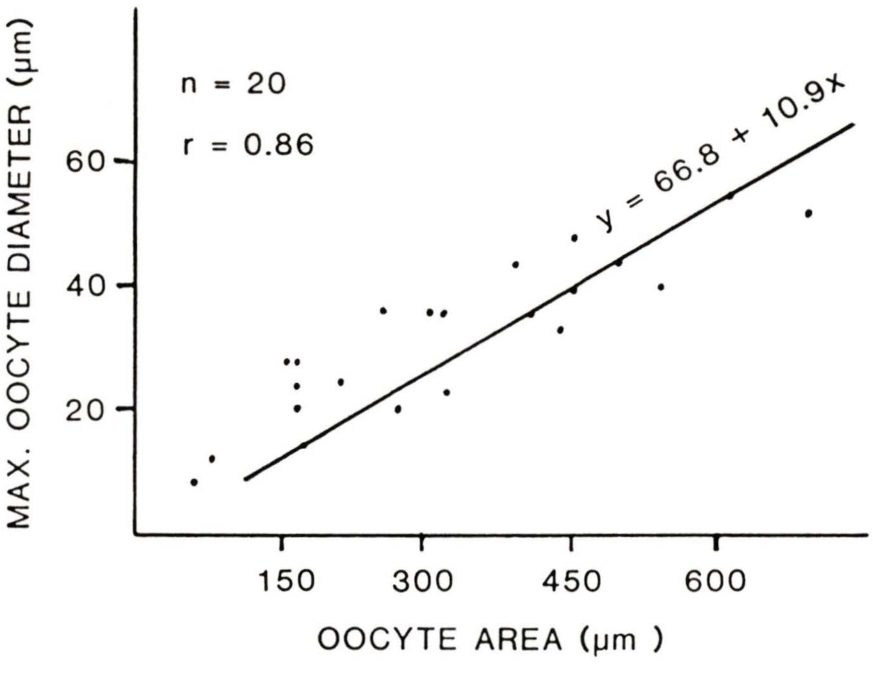
Fecundity measurements were made by calculating the mean number of oocytes per millimeter body length for five worms of each species. This number was then extrapolated to give an estimate of the total number of oocytes in a worm of 30mm in length for *P. pandorae*, and 60mm in length for *P. palmiformis.*

Male Specimens

In all male specimens, the frequency of occurrence of four gametogenic stages was noted: (i) single or small clumps of spermatogonia, (ii) rosettes of spermatocytes, (iii) sperm morulae and (iv) detached spermatozoa within the modified nephridial organs. This method follows that described by Fauvel (1897), Hutchings (1973) and Guillou and Hily (1983) for other terebellid polychaetes. In each male, all stages in ten randomly designated sections were recorded. Bar graphs of percent occurrence of each spermatogenic stage were constructed for each population examined. The percentage of males with spermatozoa in the paired modified nephridia was also noted.

Figure 3: The relationship between maximum diameter and the cross sectional area of oocytes.

n = sample size,
r = correlation coefficient ($P<0.01$).


n = 20
r = 0.86
y = 66.8 + 10.9x
MAX. OOCYTE DIAMETER (μm)
20
40
60
150
300
450
600
OOCYTE AREA (μm)

Statistical Methods

All statistical analyses of the data collected were carried out using the SAS program package (SAS Institute Inc., 1985) on the University of Victoria IBM ® mainframe computer.

Photographic Techniques

Transmission light micrographs were taken on a Zeiss Ultraphot ® microscope using a Balzers interference filter narrow band pass at 552nm. Standard developing and printing procedures were followed.

In Situ Observations

In July and August, 1986, *in situ* explorations of the Juan de Fuca Ridge were made with the Canadian submersible *Pisces IV* on the southern end of Axial Seamount. Although samples from this site are not examined in this study, visual observations of *Paralvinella pandorae* and *P. palmiformis* in their natural habitat made by the author during three dives have aided greatly in understanding the biology and ecology of both species.

RESULTS

Paralvinella pandorae Desbruyères and Laubier.

Biology

Paralvinella pandorae inhabits a self-constructed mucous sheath and is always found attached to the parchment-like tubes of vestimentiferans (Fig. 4). Worm sheaths are not attached to very small Vestimentifera, nor to the extreme bases of the tube-worms (pers. obs.). Apart from this, there appear to be no restrictions on the location of *P. pandorae* along the length of the vestimentiferan tubes.

From within the mucous sheath, the anterior end of the worm emerges to expose four pairs of branchiae and the buccal apparatus with numerous retractable feeding tentacles. Each branchia is composed of a central stalk from which two adjacent rows of filaments extend (Fig. 5). The branchiae are well supplied with blood vessels and thus provide an efficient respiratory surface for the animal. These structures may also function in nutrition by gathering organic debris, which is then gleaned by the feeding tentacles (Desbruyères *et al.*, 1985).

The feeding tentacles are grooved and may be retracted into the mouth. *P. pandorae* is presumably a modified indirect deposit feeder, collecting particulate organic matter. Gut contents of the worm consist of some foraminiferan debris and other unidentifiable material (pers.obs.). Bacterial matter probably makes up a large portion of the worm's diet.

Figure 4: *Paralvinella pandorae* attached by means of its mucous sheath to vestimentiferan tubes at a warm water vent on Axial Seamount.

P = *P. pandorae*,
V = vestimentiferan.

(Photograph courtesy of S. Scott).


V
P

Figure 5: Photographs showing the branchiae and feeding tentacles in preserved specimens of *Paralvinella pandorae* and *P. palmiformis*.

(A) *P. pandorae* in its mucous sheath. Note the paired branchiae with adjacent rows of filaments, and the numerous feeding tentacles.

(B) The anterior end of *P. palmiformis* showing the paired branchiae with opposing rows of filaments, and numerous feeding tentacles.

B = branchiae,
F = feeding tentacles,
M = mucous sheath.


F
B
M
A
B
F
B

Geographic Distribution

The known geographic distribution of *Paralvinella pandorae* extends over a 350km long portion of the northeast Pacific, and is limited to the four known major hydrothermally active fields within that range (Fig. 6). At its southern-most location, at 44°40'N and 130°22'W on the Juan de Fuca ridge, *P. pandorae* represents a rare member of vent specific fauna (Desbruyères and Laubier, 1986). This contrasts with its high abundance at two of the three vents sampled on Axial Seamount, 46°60'N and 130°04'W (Table 4). At both of these sites *P. pandorae* constituted a substantial proportion of the total biomass (Tunnicliffe *et al.*, 1985). At the southern end of the Axial Seamount caldera, this species has been recorded at eight of the twelve vents sampled recently (pers. obs.).

Although the number of *P. pandorae* from one of the vents sampled on Endeavour segment, END-3, is high, it is present in very low numbers and only in small sizes at two of the other four vents sampled in this area (Table 4). On Explorer Ridge, the northern-most vent field to have been explored, *P. pandorae* is present at two of the ten sampled sites, being abundant only at EX-3 (Table 4).

Apart from the vents sampled on the Juan de Fuca and Explorer Ridges, *P. pandorae pandorae* has not been recorded at any other sites. However, the other subspecies named *P. pandorae irlandei*, has been described by Desbruyères and Laubier (1986) from a vent site at 13°N, which is over 3000km from the nearest site at which *P. pandorae pandorae* has been found (Fig. 6).

Figure 6: A map of all the sampled hydrothermal vent sites in the Pacific, showing the geographic distribution of *Paralvinella pandorae pandorae* and *P. p. irlandei*.

Site 1: Explorer Ridge,
Site 2: Endeavour Segment,
Site 3: Axial Seamount,
Site 4: Southern Juan de Fuca,
Site 5: Guaymas Basin,
Site 6: East Pacific Rise at 21°N,
Site 7: East Pacific Rise at 13°N,
Site 8: Galapagos Rift,
Site 9: East Pacific Rise at 17°S.

P. pandorae pandorae is found at sites 1 - 4 (circled),
P. p. irlandei occurs at site 7 (squared).

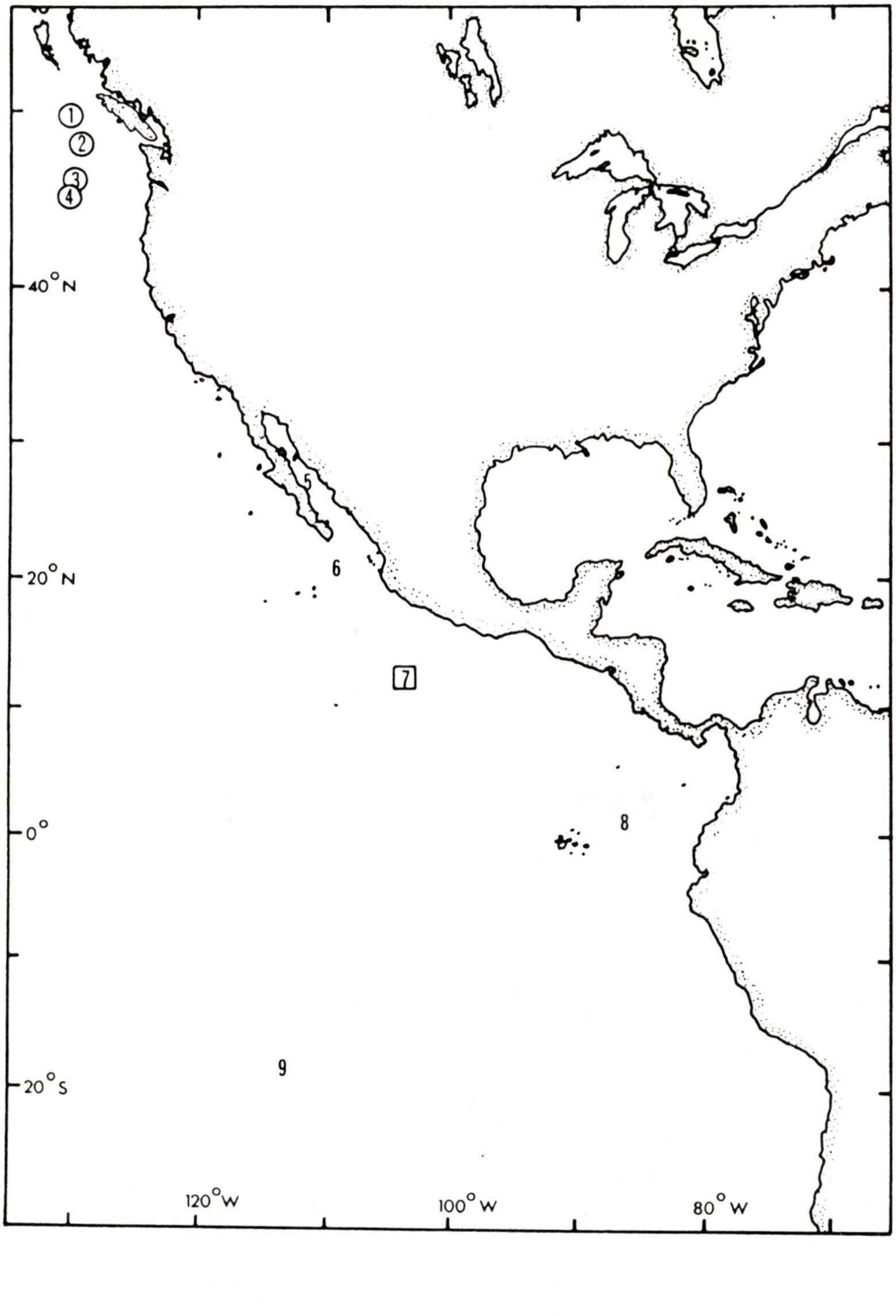

①
②
③
④
40° N
5
6
20° N
7
8
0°
9
20° S
120° W
100° W
80° W

Table 4: Relative abundance of *Paralvinella pandorae* and *P. palmiformis* in a single claw sample from each of twenty one vents on the Juan de Fuca Ridge and Explorer Ridge.

An asterisk marks those samples used in this study. A dash denotes the absence of a species from a sample.

LOCATION	VENT	#*P. pandorae*	#*P. palmiformis*
Axial Seamount	AX-1	4411 *	43
	AX-2	367	108 *
	AX-3	-	15
Endeavour Segment	END-1	36	161 *
	END-2	5	110 *
	END-3	421 *	2292 *
	END-4	-	3
	END-5	-	27
Explorer Ridge	EX-1	-	63 *
	EX-2	-	110 *
	EX-3	139 *	126 *
	EX-4	?	49
	EX-5	-	?
	EX-6	-	-
	EX-7	-	-
	EX-8	-	-
	EX-9	-	-
	EX-10	-	-
Southern Juan de Fuca	SJdF1	-	-
	SJdF2	3	?
	SJdF3	-	15

Population Structure

At three vents *Paralvinella pandorae* was present in sufficient numbers to allow detailed analyses of population characteristics. These three sites are: AX-1, END-3 and EX-3 (Table 4). The smallest specimen collected measures 0.2mm in width; the maximum width recorded is 3.4mm. Mean width of *P. pandorae* from the three vents ranges from 0.82mm at END-3 to 1.55mm at AX-1; the EX-3 population has a mean size of 1.08mm (Table 5). All means differ significantly from each other when tested with Tukey's range test.

Table 5: Size range, mean and standard deviation of widths for the three populations of *Paralvinella pandorae*

n = sample size. * = significant difference in the means of two samples at $\alpha = 0.05$.

SAMPLE	n	SIZE RANGE (mm)	MEAN (mm)	S.D. (mm)		
AX-1	654	0.2-3.4	1.55	0.56		
		(3.2)			}*	
END-3	421	0.2-1.4	0.82	0.25		}*
		(1.2)			}*	
EX-3	139	0.5-1.8	1.08	0.20		
		(1.3)				

Figure 7 shows size-frequency histograms for the three populations of *P. pandorae*. The frequencies of body width measurements each show a single blunt peak over the full range of size classes in all of the samples. Although all three populations have size-frequency distributions that appear approximately bell-shaped, all of them differ significantly from a normal distribution when tested with the Kolmogorov test (Table 6). Distinct size class peaks are not immediately evident in any of the histograms. This impression is supported by probability paper analysis (Cassie, 1954) of two of the three size-frequency distributions, END-3 and EX-3. In this analysis no strong inflection points occur along the curves of cumulative frequency plotted against seventh setiger width for those samples (Fig. 8). The AX-1 histogram displays two possible size class peaks (Fig. 7), which are reflected as inflection points in probability paper analysis (Fig. 8). Such inflection points indicate periodic or seasonal recruitment of juveniles.

Although the general characteristics of the histograms are similar, major differences in the size range of *P. pandorae* from the three vents can be seen. At AX-1 the maximum width recorded is 3.4mm, whereas at END-3 and EX-3 the largest sizes measured are 1.3mm and 1.7mm respectively (Table 5). The minimum size at EX-3 is 0.5mm, which is 0.3mm greater than the smallest worms from both AX-1 and END-3 (Table 5). Two-sample Kolmogorov-Smirnov tests show that the distribution of size classes at AX-1 is significantly different from that of the other two sites at $\alpha = 0.05$; however, END-3 and EX-3 do not differ significantly from each other (Table 6). The difference observed may be due to (i) the occurrence of a large morph of *P. pandorae* at AX-1, or (ii) the presence of younger populations at END-3 and EX-3, or (iii) slower growing or growth limited populations at those two sites. Total segment number was compared among 5-10 worms of a single size, 1.3-1.5mm, from each of the three sites, and also among worms of maximum sizes from each site. Results of this analysis are given in Table 7. Mean segment number does not differ significantly among worms of the same width from the three samples. However, when worms of maximum widths from AX-1 are compared with those of maximum widths from either of the other two sites, a significant difference is seen, with the larger worms having more segments (Table 7).

Figure 7: Size-frequency histograms of seventh setiger width of *Paralvinella pandorae* from the three populations.

Possible size class peaks are marked with arrows. N = sample size.

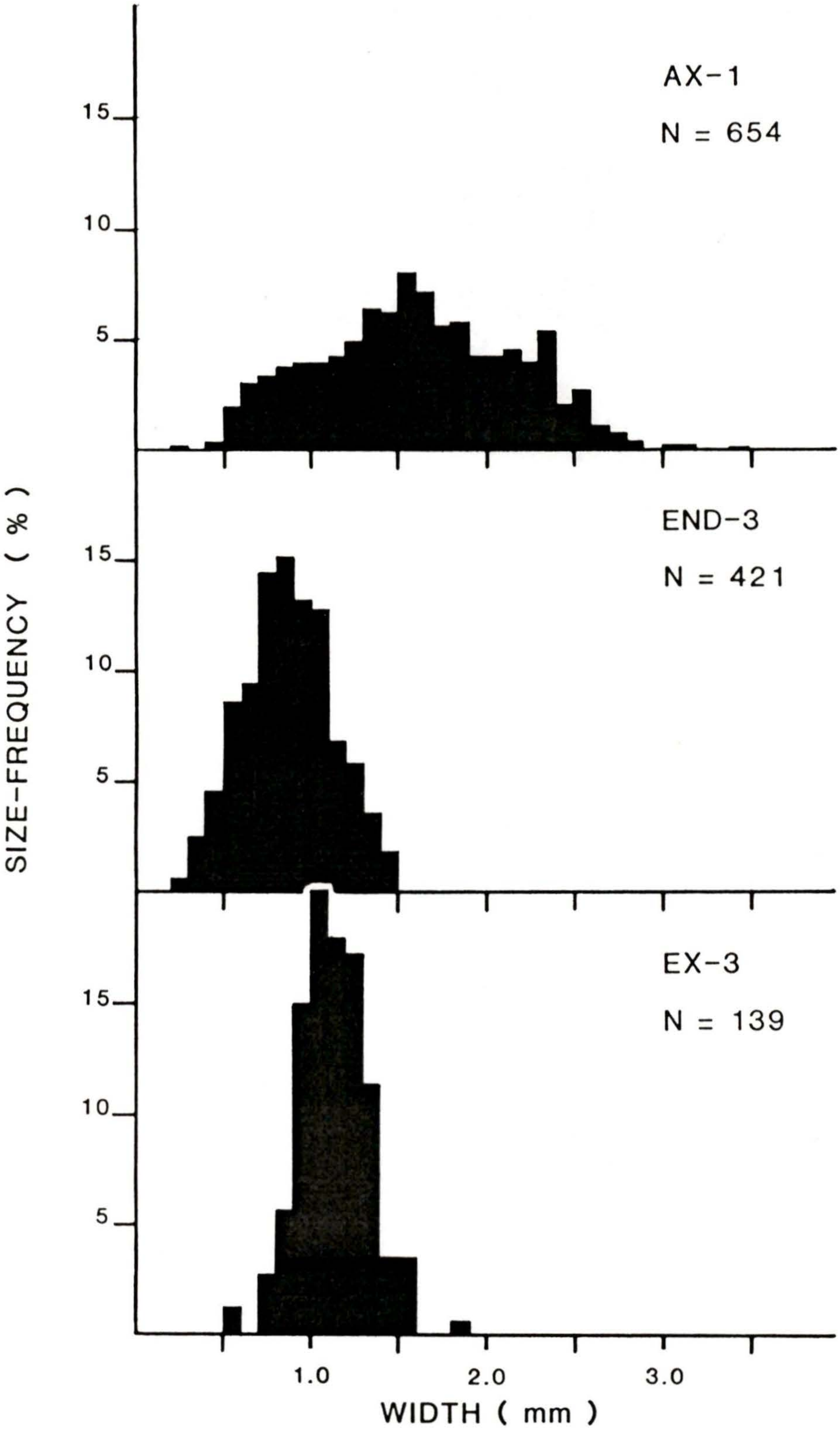

AX-1
N = 654
END-3
N = 421
EX-3
N = 139
SIZE-FREQUENCY (%)
15
10
5
1.0
2.0
3.0
WIDTH (mm)

Figure 8: Probability paper analysis of widths for the three populations of *Paralvinella pandorae*.

N = the number of worms measured in each sample.

Seventh setiger width is plotted against cumulative percentage on log paper.

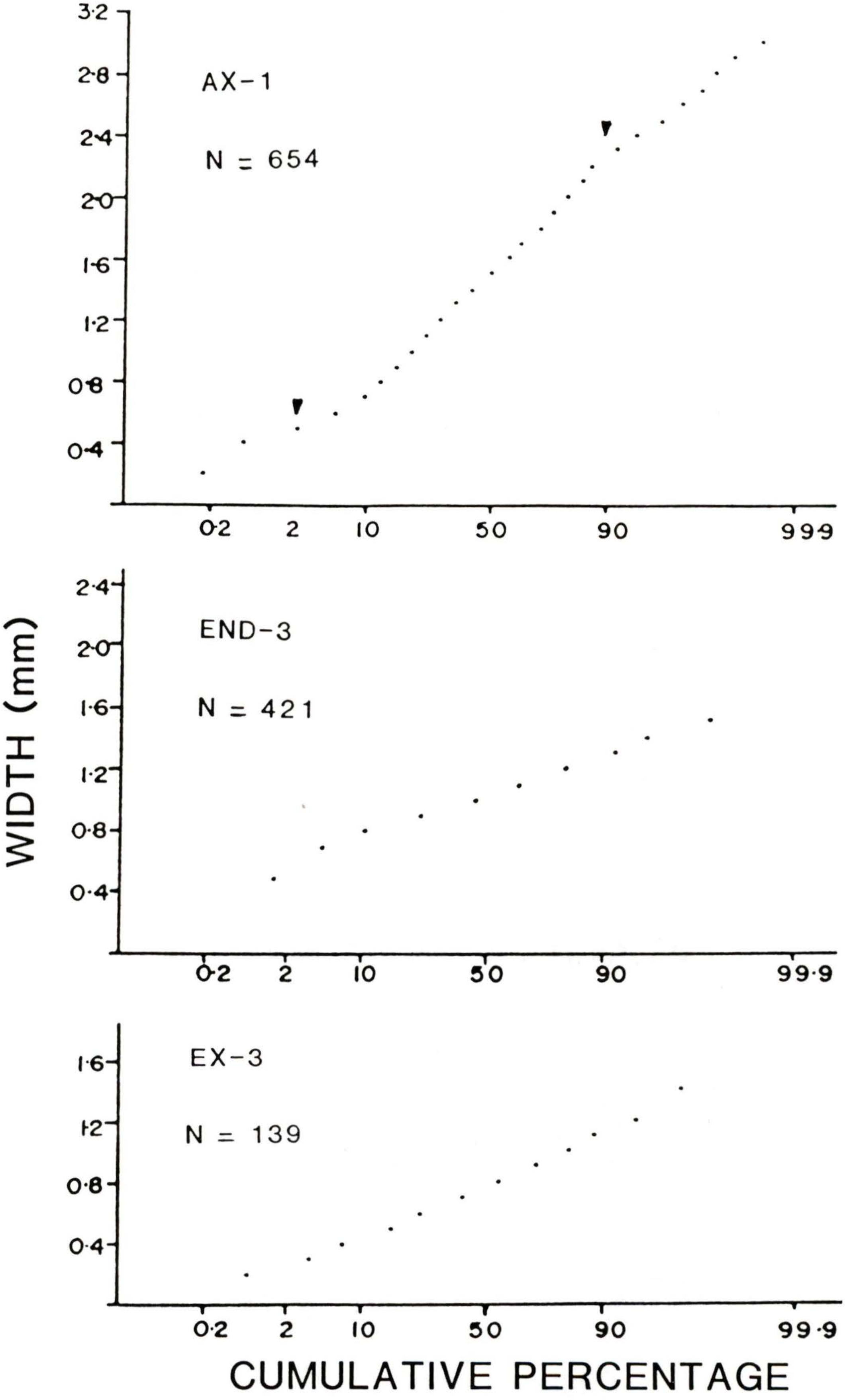

3·2
2·8
2·4
2·0
1·6
1·2
0·8
0·4
AX-1
N = 654
0·2
2
10
50
90
99·9
2·4
2·0
1·6
1·2
0·8
0·4
END-3
N = 421
0·2
2
10
50
90
99·9
1·6
1·2
0·8
0·4
EX-3
N = 139
0·2
2
10
50
90
99·9
WIDTH (mm)
CUMULATIVE PERCENTAGE

Table 6: Results of tests of normality of *Paralvinella pandorae* size distributions, and differences in distributions.

α = 0.05, N.S = no significant difference, * = significant difference.

SAMPLE	KOLMOGOROV STATISTIC		KOLMOGOROV-SMIRNOV TESTS			
AX-1	0.04997	* P<0.01				
			}0.0848	* P<0.01		
END-3	0.08361	* P<0.01			}0.0118	* P<0.01
			}0.1328	N.S. P>0.05		
EX-3	0.11024	* P<0.01				

Table 7: Mean and standard deviation of segment numbers in *Paralvinella pandorae* from the three populations.

Samples of different size ranges that differ significantly in their mean segment number according to Tukey's test are listed below the table. N = sample size; * = significantly different.

SAMPLE	SIZE (mm)	N	MEAN SEGMENT NUMBER	S.D.
AX-1a	1.3-1.5	10	53.8	3.1
AX-1b	2.5-3.0	6	57.0	2.0
END-3	1.3-1.4	10	52.1	2.8
EX-3	1.3-1.5	10	54.0	3.0

AX-1b	Vs	AX-1a	*
AX-1b	Vs	END-1	*
AX-1b	Vs	EX-3	*

No other comparisons differ significantly.

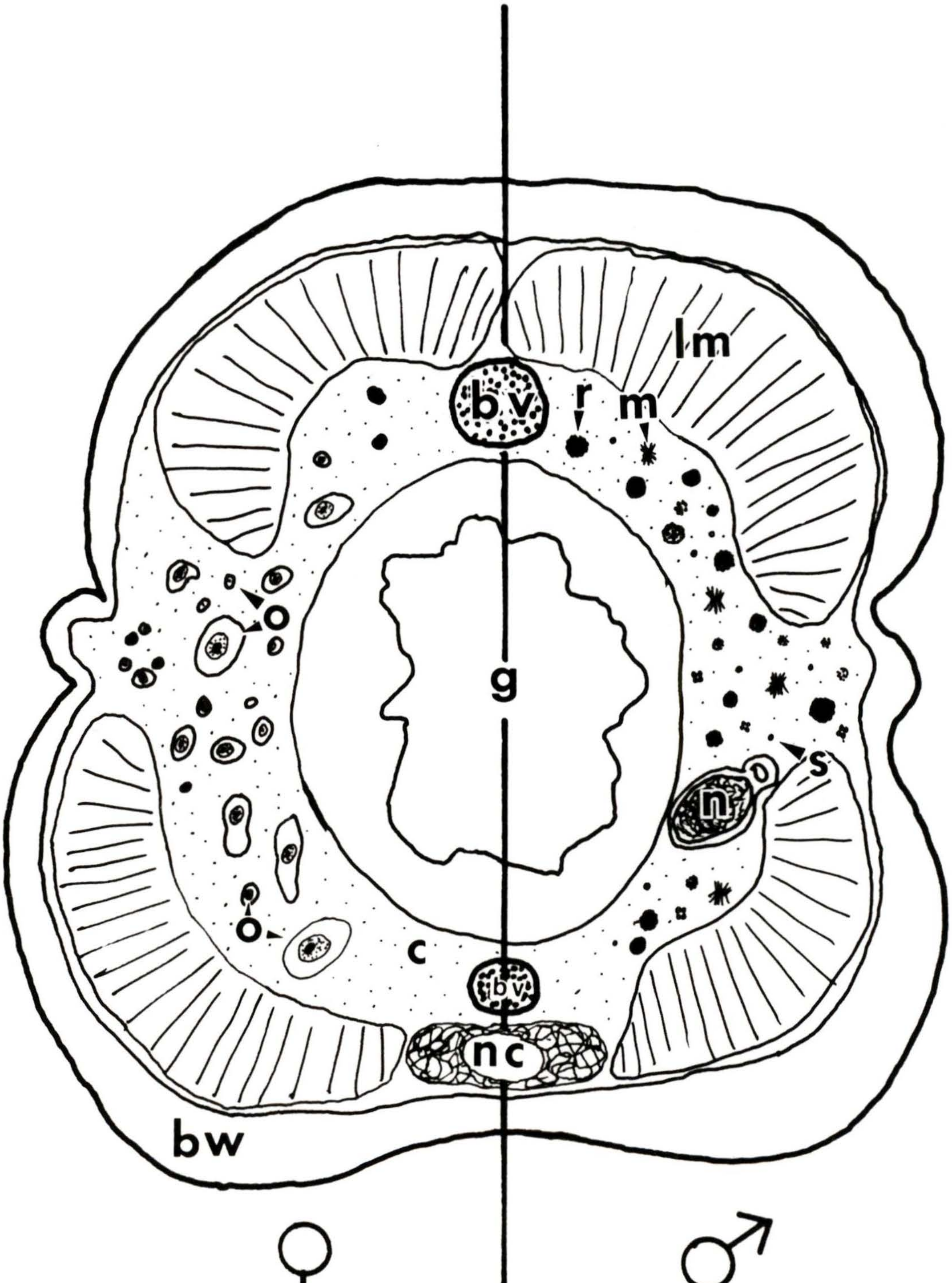
Gametogenesis

Histological sections of *Paralvinella pandorae* reveal that the worm is gonochoric. Chi-squared tests of the three subsamples of *P. pandorae* show no significant differences from a 1:1 male:female sex ratio (AX-1: $P<0.50$; END-3: $P<0.50$; EX-3: $P<0.75$). Only those worms of 1.0mm in width or greater have distinguishable gametogenic stages present.

The paired gonads are situated lateroventrally 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. Spawning of gametes presumably takes place through the external openings of two pairs of modified nephridia at the anterior end of the animal, and leads to external fertilization. Although no oocytes have been observed in these modified nephridia, they are known to occur in *P. grasslei* (D. Desbruyères, pers. comm.). It appears that sperm is stored there as is the case in other terebellid polychaetes (Hutchings, 1973; Guillou and Hily, 1983). Figure 9 is a diagrammatic representation of the internal anatomy of male and female *P. pandorae* based on histological sections.

Figure 9: A schematic drawing of the internal anatomy of male and female *Paralvinella pandorae* based on histological sections.

bv = blood vessel,
bw = body wall,
c = coelom,
g = gut,
lm = longitudinal muscle,
m = sperm morula,
o = oocyte,
n = nephridium,
nc = ventral nerve cord,
r = rosettes of spermatocytes,
s = secondary spermatogonia.


lm
bv
r
m
o
o
g
s
n
o
c
bv
nc
bw
♀
♂

Female Specimens

The number of females in each subsample of approximately thirty worms varied between eight and fifteen. In sections of females, oocytes smaller than 5 µm could not be recognized. Previtellogenic oocytes measure from 5 to 20 µm in diameter. Yolk granules accumulate in the cytoplasm of the oocytes as the diameter increases. Vitellogenic oocytes measure from 30 µm up to a maximum of 160 µm (Fig. 10). As the diameter increases the developing oocyte changes from a spherical to irregular shape, and then to an oval shape as maximum size is reached. Percentage frequency of coelomic oocyte diameter is depicted in histogram form in Figure 11. In the female population of *P. pandorae* at each site there is a similar wide range of oocyte sizes, despite the differences in the size ranges of worms from AX-1 and the other two sites. An ANOVA test revealed differences in mean oocyte size among vent samples ($F = 294.47$; $df = 2$; $P<0.0001$). Mean sizes from all three samples, shown in Table 8, differ significantly from each other when tested with Tukey's range test at $\alpha = 0.05$.

The frequency distributions of oocyte size differ significantly from a normal distribution (Table 9), and the histograms of oocyte size-frequencies for the END-3 and EX-3 samples are skewed towards the right. Although the oocyte size distributions for each individual resemble those for corresponding populations (see Appendix B), ANOVA tests show that mean oocyte size differs significantly among individuals within each subsample (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, Tukeys range tests show that > 80% of the individuals in each population do not differ in their oocyte size ($P<0.25$).

The fecundity of *P. pandorae* is estimated at a mean and standard deviation of $23.7 \times 10^3 \pm 18.3 \times 10^3$(n = 5).

Male Specimens

Between six and fourteen males occurred in the three subsamples of the worm. In male specimens the earliest distinguishable stage of spermatogenesis is spermatogonia, which divide to give rise to rosettes of spermatocytes; spermatocytes then develop flagellae and form plates of spermatids called sperm morulae (Fig. 12). The three spermatogenic stages are well represented in the male populations from the three sites (Fig. 13). This is also the case for the stages within individual worms from each population. Ripe spermatozoa are stored anteriorly in pairs of modified nephridia, termed mixonephridia (Goodrich, 1945) (Fig. 14). The percentage of males in each population which have spermatozoa in the mixonephridia is very high, ranging from 75% to 100% (Fig. 13).

Table 8: Oocyte size range, mean and standard deviation for the three subsamples of *Paralvinella pandorae* females.

* = significant difference in the means of two samples at $\alpha = 0.05$.

SAMPLE	n	OOCYTE SIZE RANGE (µm)	MEAN	S.D.		
AX-1	934	7-164	66	27		
					}*	
END-3	686	9-118	48	27		}*
					}*	
EX-3	489	15-165	54	28		

Table 9: Results of tests of normality for oocyte size distributions for *Paralvinella pandorae* females.

* = significantly different at $\alpha = 0.05$, $P < 0.01$.

SAMPLE	KOLMOGOROV STATISTIC	
AX-1	0.10100	*
END-3	0.18116	*
EX-3	0.20514	*

Figure 10: Light micrographs of oogenesis in *Paralvinella pandorae*

(A) Section of a female from AX-1 showing oocytes at different stages of development in the coelom of the worm.

(B) Cross section of an EX-3 female with developing oocytes, some of irregular shape, within the coelom.

(C) Cross section of an oocyte showing the nucleus and nucleolus. Only those oocytes in which both the nucleus and nucleolus were seen, were measured.

BV = blood vessel,
C = coelom,
CS = coelomic sac,
G = gut,
LM = longitudinal muscle,
N = nucleus,
Nu = nucleolus,
NC = ventral nerve cord,
O = oocyte.

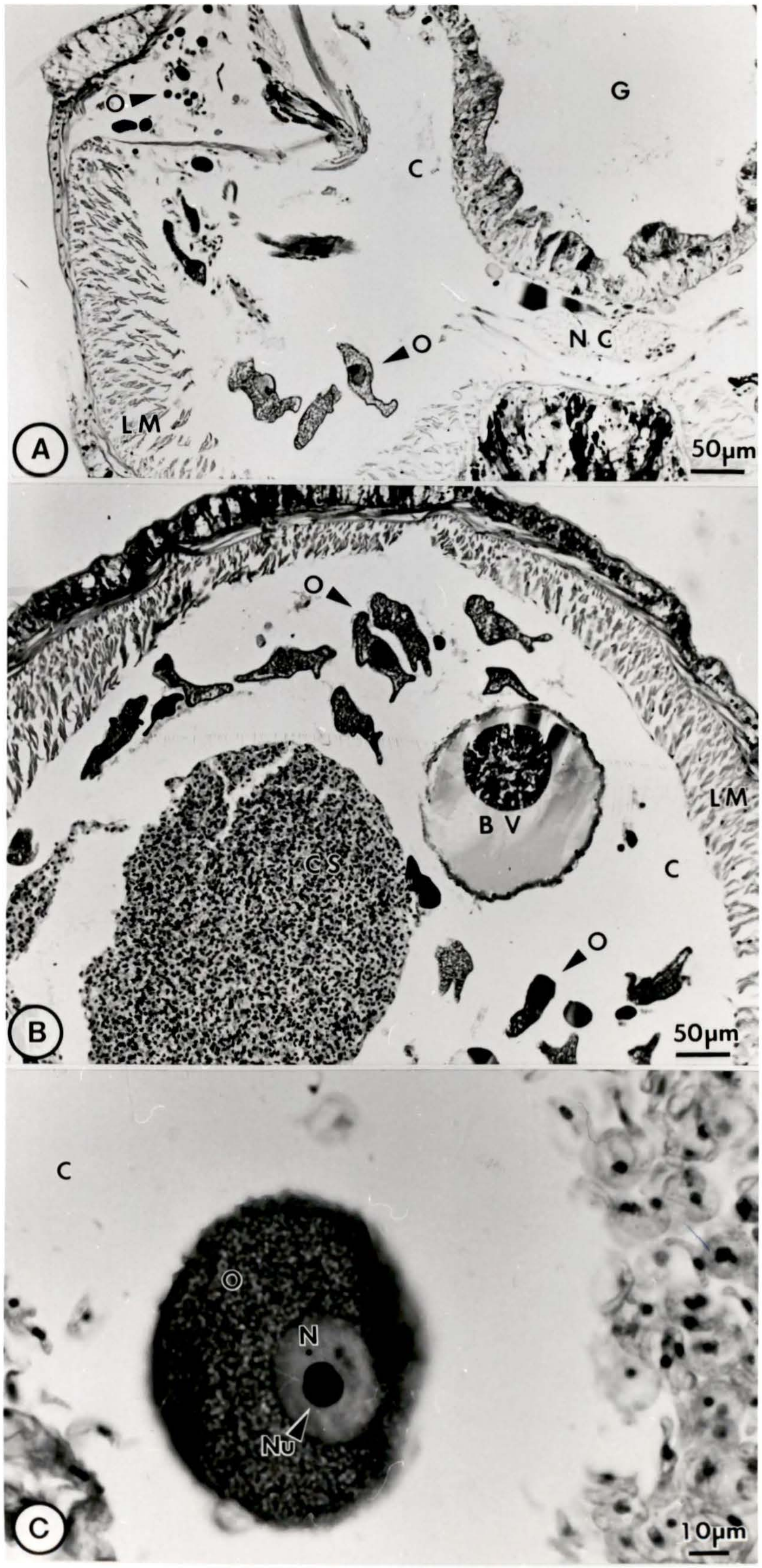

O
G
C
O
N C
L M
A
50µm
O
L M
B V
C S
C
O
B
50µm
C
O
N
Nu
C
10µm

Figure 11: Size-frequency histograms of maximum oocyte diameter for subsamples of *Paralvinella pandorae* from the three populations.

N = number of female specimens in each subsample,
n = total number of oocytes measured in each subsample.

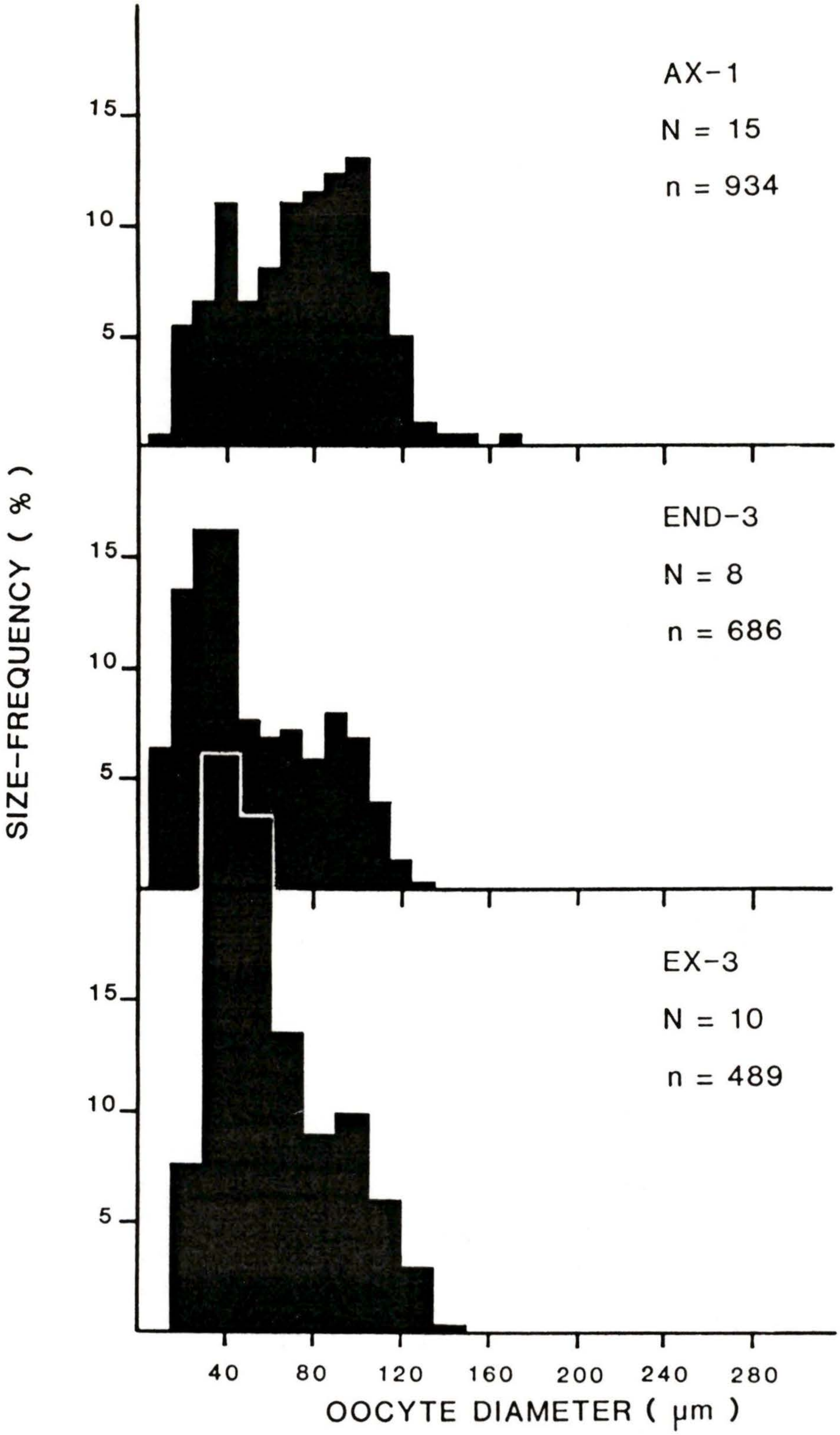

AX-1
N = 15
n = 934
END-3
N = 8
n = 686
EX-3
N = 10
n = 489
15
10
5
SIZE-FREQUENCY (%)
40
80
120
160
200
240
280
OOCYTE DIAMETER (µm)

Figure 12: Light micrographs of spermatogenesis in *Paralvinella pandorae*

(A) Cross section of a male from AX-1 showing various stages of spermatogenesis in the coelom of the worm.

(B) The percent occurrence of secondary spermatogonia, rosettes of spermatocytes and sperm morulae, shown in this micrograph at X400 magnification, was noted in each male in all three population subsamples.

BV = blood vessel,
BW = body wall,
C = coelom,
G = gut,
M = sperm morulae,
N = nephridia,
R = rosettes of spermatocytes,
S = secondary spermatogonia.

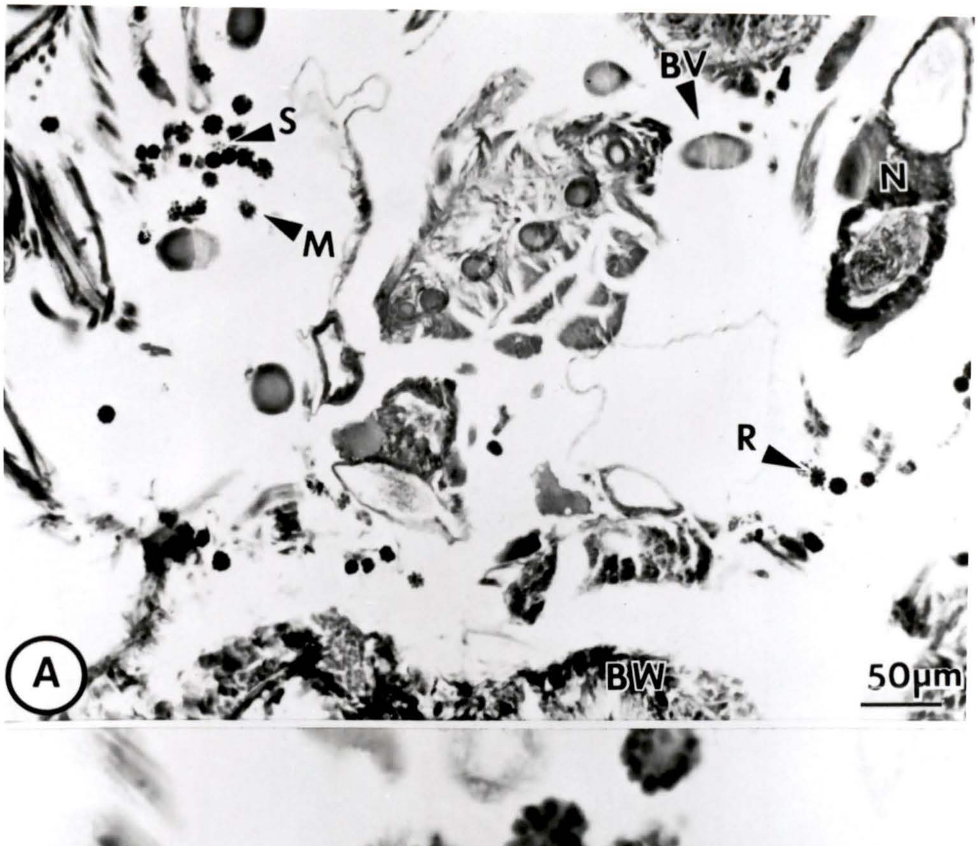

S
M
BV
N
R
A
BW
50μm
M
R
BV
B
10μm

Figure 13: Bar graphs showing the percent occurrence of the spermatogenic stages in subsamples of males of *Paralvinella pandorae* from the three populations.

The shaded portions of the pie-charts represent the percentage of males in which ripe spermatozoa were observed in the mixonephridia.

N = number of males in each subsample.

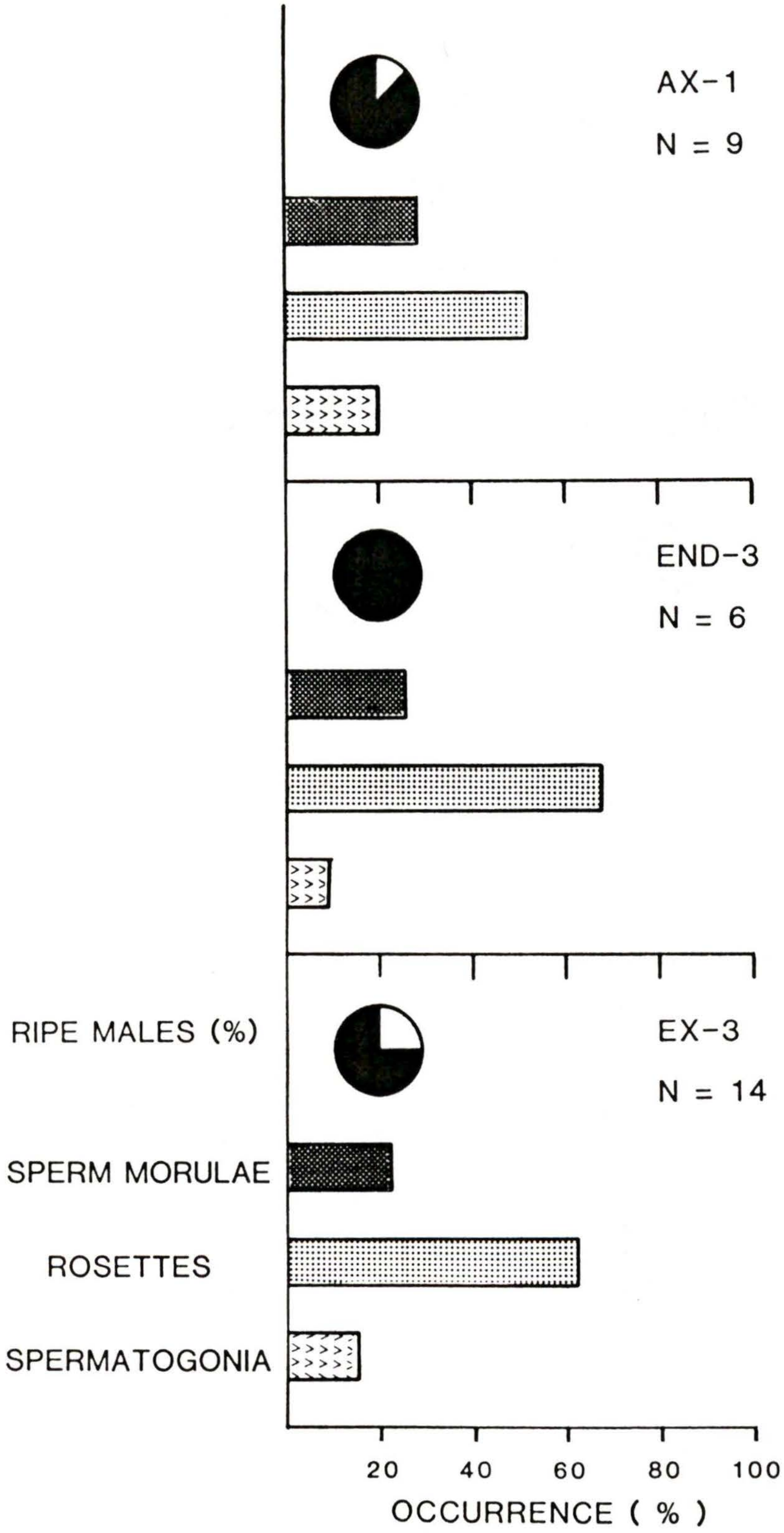
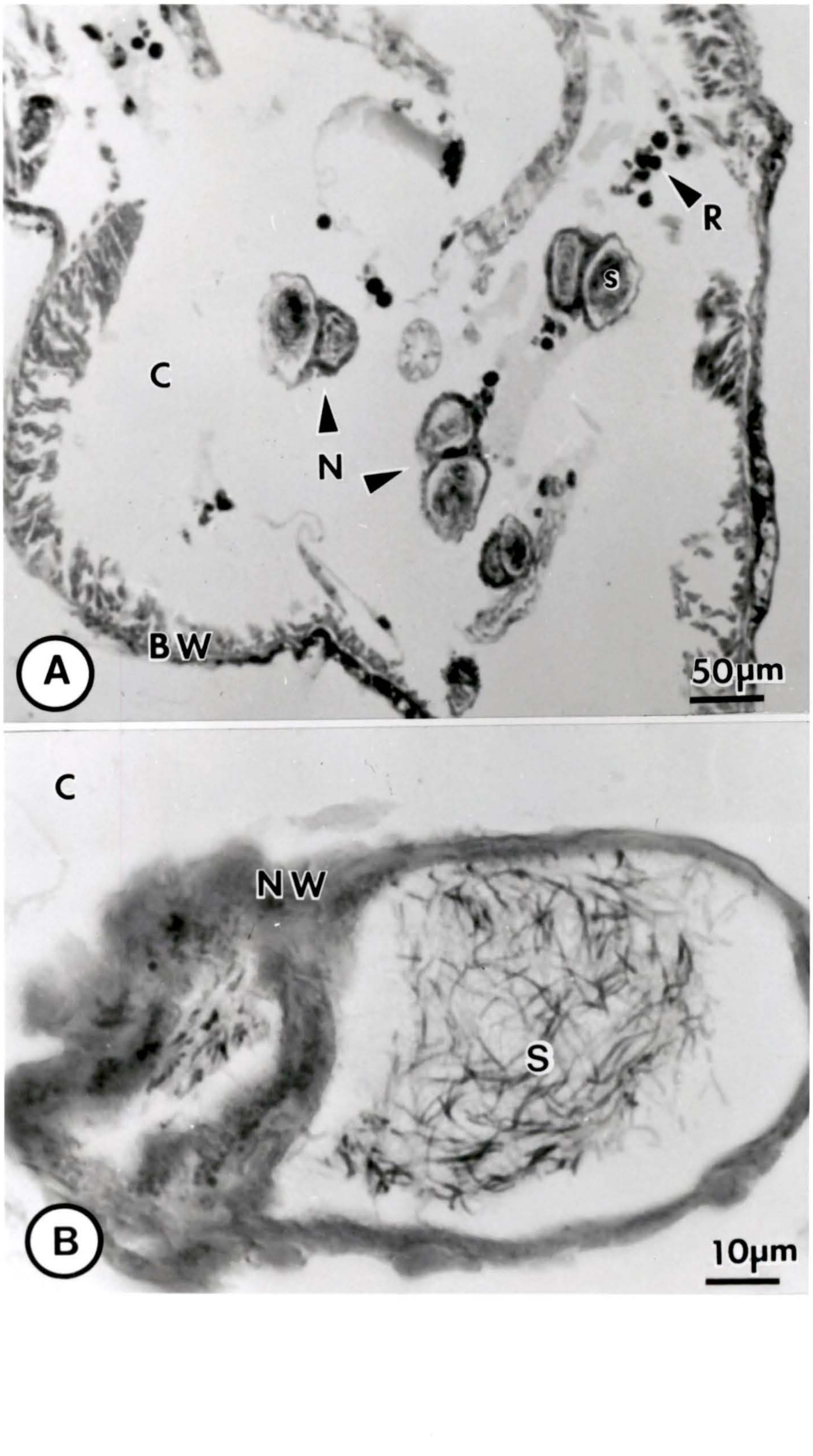

AX-1
N = 9
END-3
N = 6
EX-3
N = 14
RIPE MALES (%)
SPERM MORULAE
ROSETTES
SPERMATOGONIA
20
40
60
80
100
OCCURRENCE (%)

Figure 14: Light micrographs showing the paired, U-shaped nephridia of *Paralvinella pandorae*.

(A) Cross section of an END-3 male showing the two pairs of modified nephridia, which function in sperm storage.

(B) Section through a nephridium containing spermatozoa.

C = coelom,
G = gut,
N = nephridia,
NW = nephridial wall,
R = rosettes,
S = spermatozoa.


R
S
C
N
N
BW
A
50µm
C
NW
S
B
10µm

Paralvinella palmiformis Desbruyères and Laubier.

Biology

Paralvinella palmiformis does not form a tube or sheath although it does secrete large amounts of mucus which trap inorganic particulate matter (Tunnicliffe and Fontaine, in press). The worm is found naked in a number of habitats. Although it is most frequently found with its caudal end coiled around the distal portion of vestimentiferan tubes (Fig. 15), *P. palmiformis* is not always associated with tubeworms. For example, at Vent 12a on Explorer Ridge (Tunnicliffe *et al.*, 1986), all individuals were covered with mineral particles solidly attached to the cuticle (Desbruyères and Laubier, 1986) (Fig. 15). At one vent at the Southern Juan de Fuca site, a few specimens were retrieved from the surface of a sulphide spire within 10cm of a 224^{o}C spout of hydrothermal fluid (Tunnicliffe and Fontaine, in press).

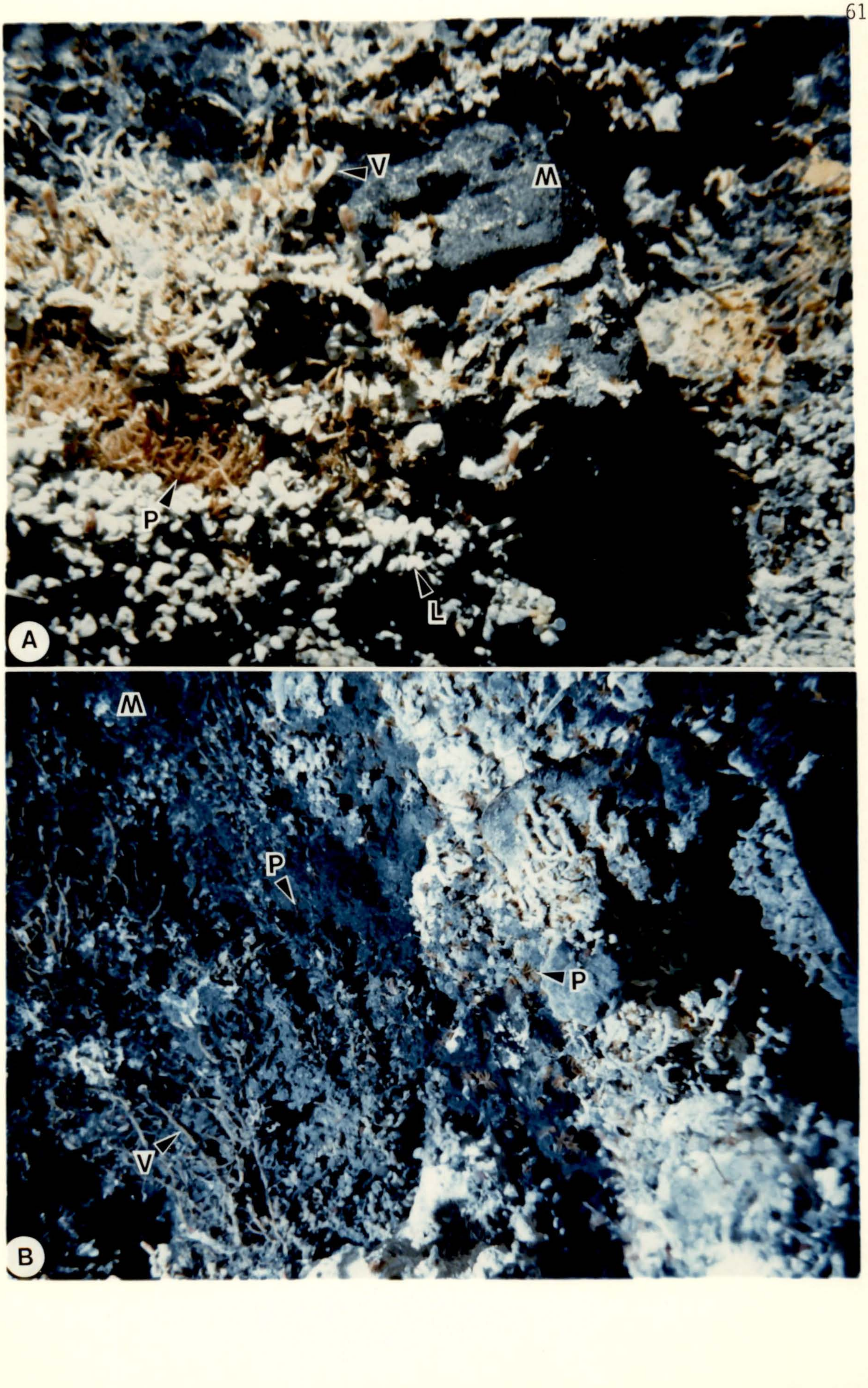
The anterior end of the worm bears four pairs of branchiae with numerous filaments arranged in two opposing rows (Fig.5). The buccal apparatus is situated below these structures. Numerous grooved, retractable feeding tentacles emerge from the buccal apparatus. *P. palmiformis* is a modified indirect deposit-feeder. Gut contents of the worm consist mainly of filamentous bacteria, mucus and possible diatomaceous debris (Tunnicliffe *et al.*, 1985). The gut epithelium appears to be colonized by bacteria, however digestion of bacteria is not evident (E. Ishiguro, pers. comm.).

Figure 15: *In situ* photographs of *Paralvinella palmiformis.*

(A) *P. palmiformis* associated with vestimentiferans. (Photograph courtesy of ASHES Expedition, 1986)

(B) *P. palmiformis* embedded in mineral deposits. (Photograph courtesy of V. Tunnicliffe)

L = limpets,
M = mineral deposits,
P = *P. palmiformis,*
V = vestimentiferan.


V
M
P
L
A
M
P
P
V
B

Geographic Distribution

Paralvinella palmiformis is common to all four known hydrothermally active sites in the northeast Pacific (Fig. 6). At its southern-most location, at 44 °40'N, 130°22'W on the Juan de Fuca Ridge, it is abundant on sulphides at two vents, but absent at a third vent sampled (Tunnicliffe and Fontaine, in press). At all vents sampled on Axial Seamount, *P. palmiformis* is present in low numbers only (Table 4), although it nonetheless contributed substantially to the biomass at those sites (Tunnicliffe *et al.*, 1985). At the southern end of the Axial Seamount caldera, the worm occurs at all of the four major vents and eight smaller ones sampled on the most recent cruise to that area (pers. obs.).

The abundance of *P. palmiformis* at three vents on Endeavour Segment is high (Table 4). In three other vent samples from this vent site, the number of worm specimens is very low (< 50 per claw sample). On Explorer Ridge, it is present at five of the ten sites sampled, occurring in abundance at only three of these sites (Table 4).

P. palmiformis has not been found at any non-vent locations, and is not known to occur at any vents south of the Juan de Fuca Ridge.

Population Structure

Paralvinella palmiformis was present in sufficiently large numbers at five vents to allow analysis of population characteristics: END-1, END-2, END-3, EX-2 and EX-3 (Table 4). Two other samples, AX-2 and EX-1, were included for analysis despite the relatively small sample sizes from these sites.

The smallest worm measures 0.2mm in width, and the maximum width recorded is 7.7mm. Mean width ranges from 1.74mm at END-3 to 5.17mm at

AX-2. The mean sizes of *P. palmiformis* from all seven vents are given in Table 10. The mean size for END-1 does not significantly differ from either EX-1 or EX-3. Tukey's range test yielded significant differences in mean widths between all other pairs of samples. The distribution of each population differs significantly from the normal distribution (Table 11).

Table 10: Size range, mean and standard deviation of widths for seven populations of *Paralvinella palmiformis* samples.

n = sample size. Those samples whose means do not differ significantly, at $\alpha = 0.05$ are listed in the bottom rows of the table.

SAMPLE	n	SIZE RANGE (mm)	MEAN (mm)	S.D. (mm)
AX-2	61	1.1-7.7 (6.6)	5.17	1.42
END-1	161	2.0-7.3 (5.3)	4.00	1.21
END-2	110	0.9-3.7 (2.8)	2.07	0.64
END-3	548	0.2-5.7 (5.5)	1.74	0.83
EX-1	63	1.9-6.0 (4.1)	4.19	0.76
EX-2	106	1.4-3.7 (2.3)	2.78	0.45
EX-3	126	2.5-5.5 (3.0)	3.74	0.49
END-1	Vs	EX-1	N.S.	P>0.05
END-1	Vs	EX-3	N.S.	P>0.05

Figure 16 shows a histogram of the size-frequency distribution of *P. palmiformis* from AX-2. Due to the small sample size at this site, the histogram of population structure is discontinuous and therefore is difficult to interpret. Probability paper

Table 11: Results of tests of normality of *Paralvinella palmiformis* size distributions, and differences in distributions.

$\alpha = 0.05$, $P < 0.01$. * = significantly different from a normal distribution.

SAMPLE	KOLMOGOROV STATISTIC	
AX-2	0.1032	*
END-1	0.1166	*
END-2	0.0659	*
END-3	0.0922	*
EX-1	0.0872	*
EX-2	0.1349	*
EX-3	0.0816	*

analysis shows a number of possible peaks in the histogram (marked with arrows on Figure 17). Despite the discontinuity in the histogram, it is easy to recognize that it is skewed to the right. This may reflect the stacking of size classes as maximum size is reached, or perhaps the difficulty of sampling small individuals.

The three vent sites on Endeavour Segment have larger sample sizes which results in continuous size-frequency histograms (Fig. 18). At END-1 there are numerous minor peaks evident and/or possibly two major peaks defined by the absence of specimens of the 4.3mm size class. At END-2, there again appears to be a number of size-class peaks in the population structure, and the histogram is skewed slightly to the left. The largest sample of *P. palmiformis* is from END-3 and therefore this sample probably gives the most accurate representation of *P. palmiformis* population structure. The size-frequency histogram, also shown in

Figure 16: Size-frequency histogram of seventh setiger width of *Paralvinella palmiformis* from AX-2.

N = sample size.

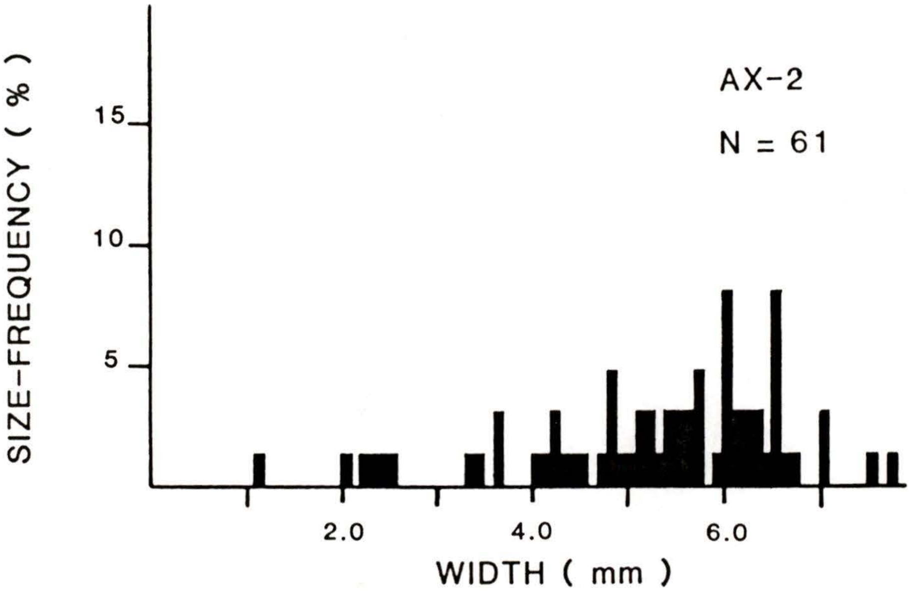

AX-2
N = 61
SIZE-FREQUENCY (%)
15
10
5
2.0
4.0
6.0
WIDTH (mm)

Figure 17: Probability paper analysis of widths for the AX-2 sample of *Paralvinella palmiformis*

Possible size class peaks, reflected by inflection points on the curves, are marked with arrows.

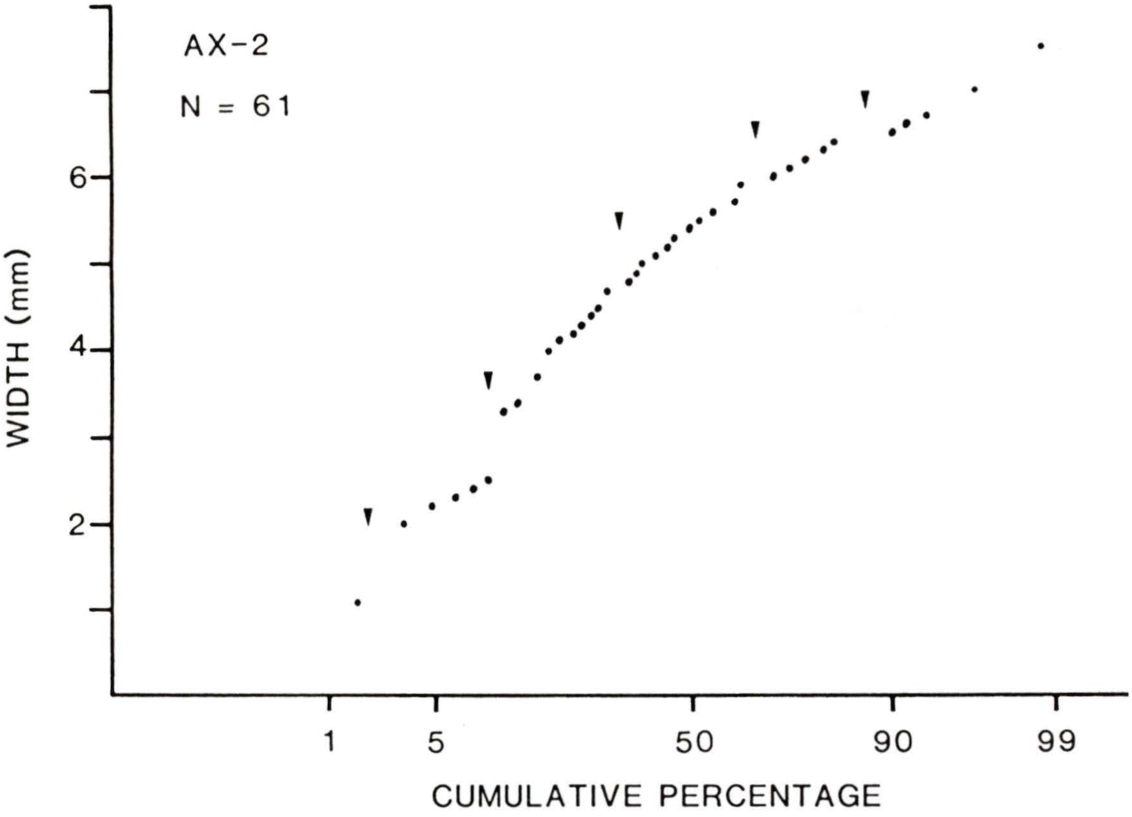

AX-2
N = 61
6
4
2
WIDTH (mm)
1
5
50
90
99
CUMULATIVE PERCENTAGE

Figure 18, displays at least five definite size classes and is also skewed to the left. Probability paper analysis shows several definite inflection points in the plots for all three Endeavour Segment samples (Fig. 19). As previously mentioned, these inflection points likely reflect size-class peaks. These peaks may be a result of periodic/seasonal recruitment of juveniles to a population.

The population structure of the three vent samples from Explorer Ridge are illustrated in Figure 20. The sample size for EX-1 is relatively small and yields a discontinuous histogram. The peaks in this sample are therefore difficult to define. At EX-2, despite a larger sample size of 106, the result of size-frequency analysis is again a disjointed histogram (Fig. 20). There appear to be three or four size classes present. The size-frequency histogram for the third sample from Explorer Ridge, EX-3, is also shown in Figure 20. It exhibits a number of definite size-classes. The results of analysis of the Explorer Ridge populations using the probability paper method are shown in Figure 21. For all three populations, strong inflection points (marked with arrows in the figure) are present, thus giving supporting evidence for the existence of definite size-classes in the populations.

Major differences occur in the maximum and minimum widths of *P. palmiformis* from the seven sites (Table 10), and also in size ranges. AX-2 has the widest size range, 6.6mm, although many sizes within that range are not represented in the sample. Of the Endeavour Segment populations studied, END-1 and END-3 have similar size ranges of 5.3mm and 5.2mm respectively. This contrasts with the narrow range of 2.8mm at END-2 (Table 10). All three Explorer Ridge populations have relatively narrow ranges of size classes: EX-1 has a range of 4.1mm, with many size intervals not represented; EX-2 has the

Figure 18: Size-frequency histograms of seventh setiger width for the three Endeavour samples of *Paralvinella palmiformis*.

N = sample size.

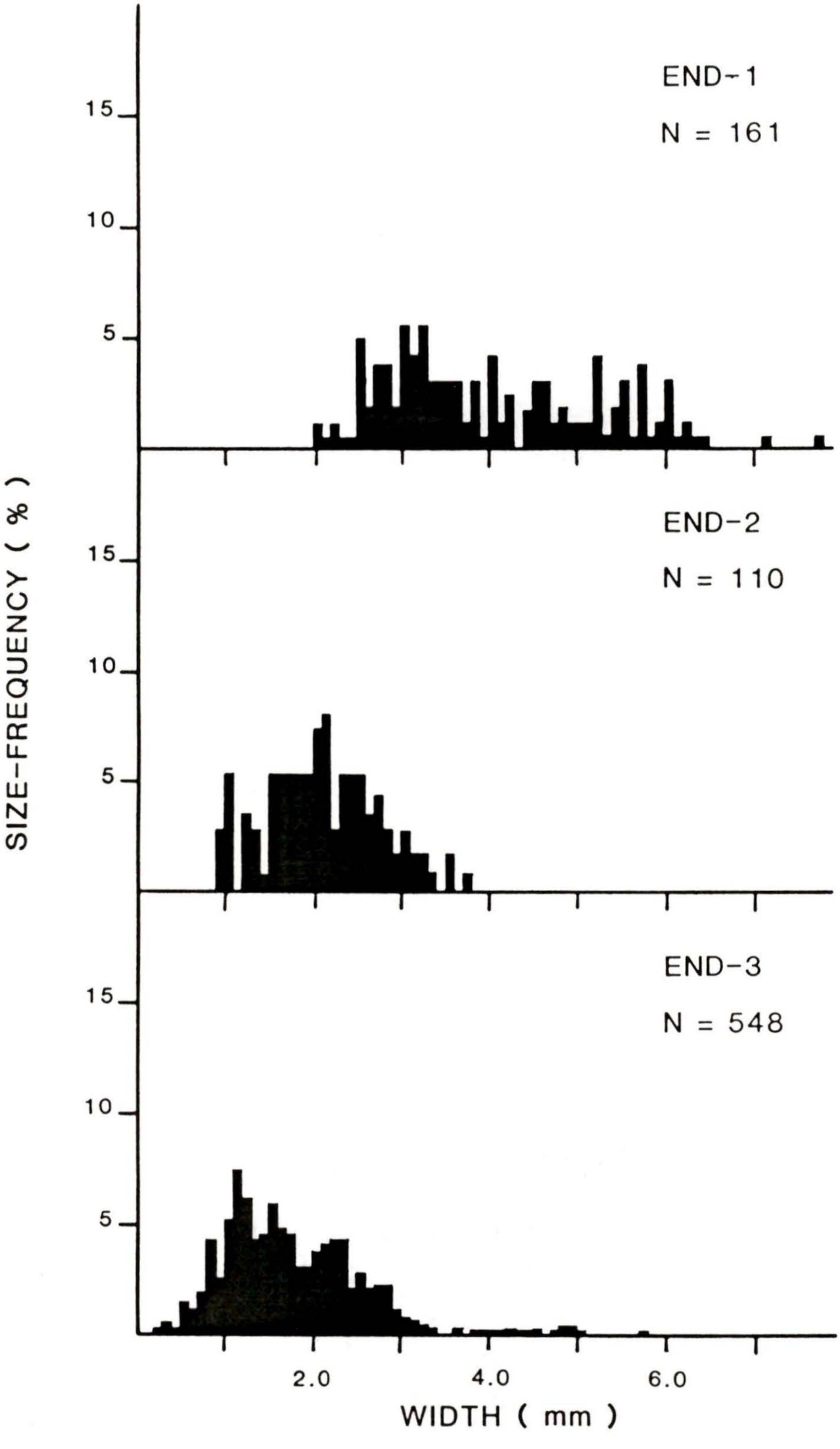

END-1
N = 161
END-2
N = 110
END-3
N = 548
15
10
5
SIZE-FREQUENCY (%)
2.0
4.0
6.0
WIDTH (mm)

Figure 19: Probability paper analysis of widths for the three samples of *Paralvinella palmiformis* from Endeavour Segment.

Inflection points are marked with arrows.

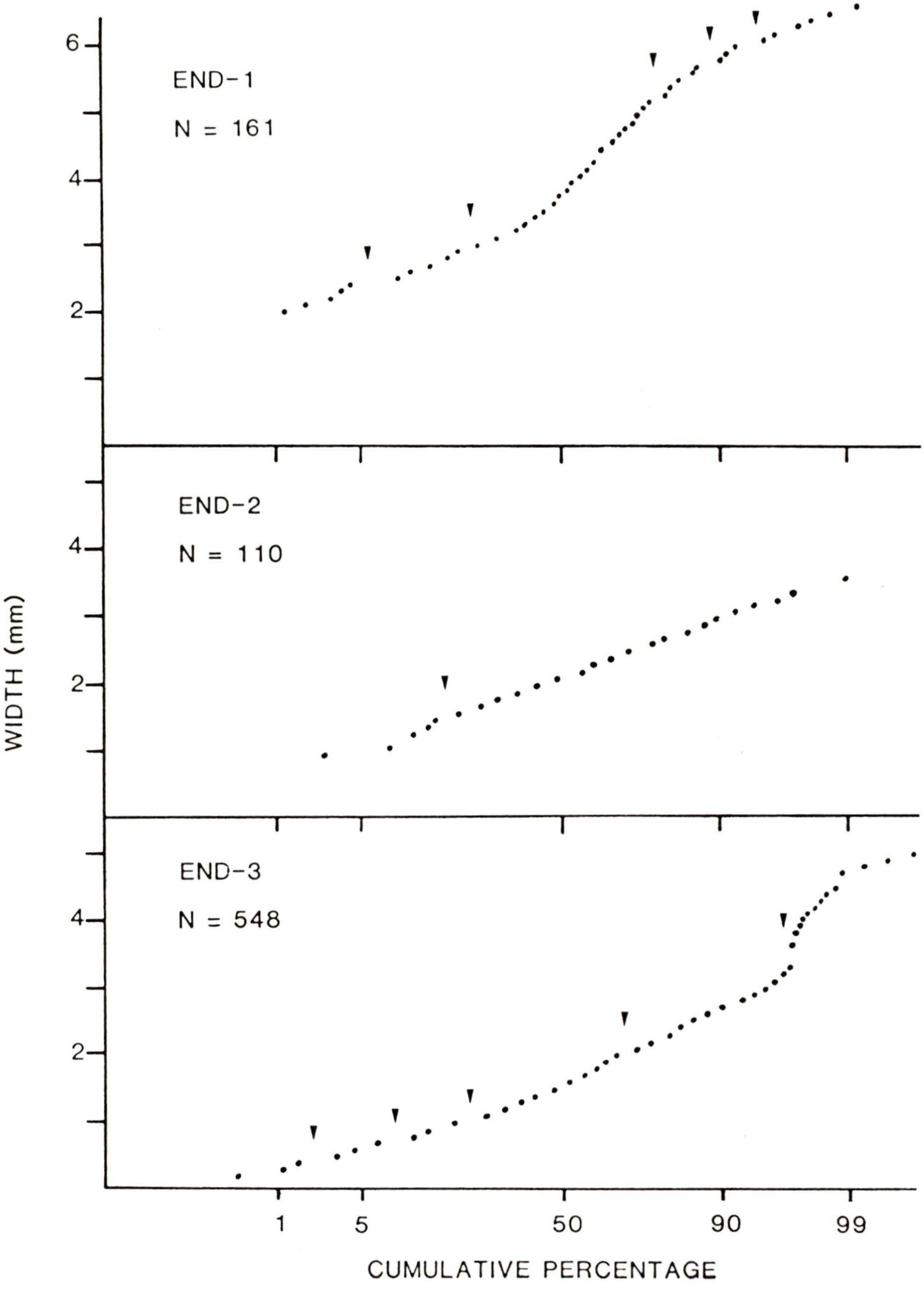

END-1
N = 161
END-2
N = 110
END-3
N = 548
WIDTH (mm)
6
4
2
4
2
4
2
1
5
50
90
99
CUMULATIVE PERCENTAGE

Figure 20: Size-frequency histograms of seventh setiger width for *Paralvinella palmiformis* from three Explorer Ridge vents.

N = sample number.

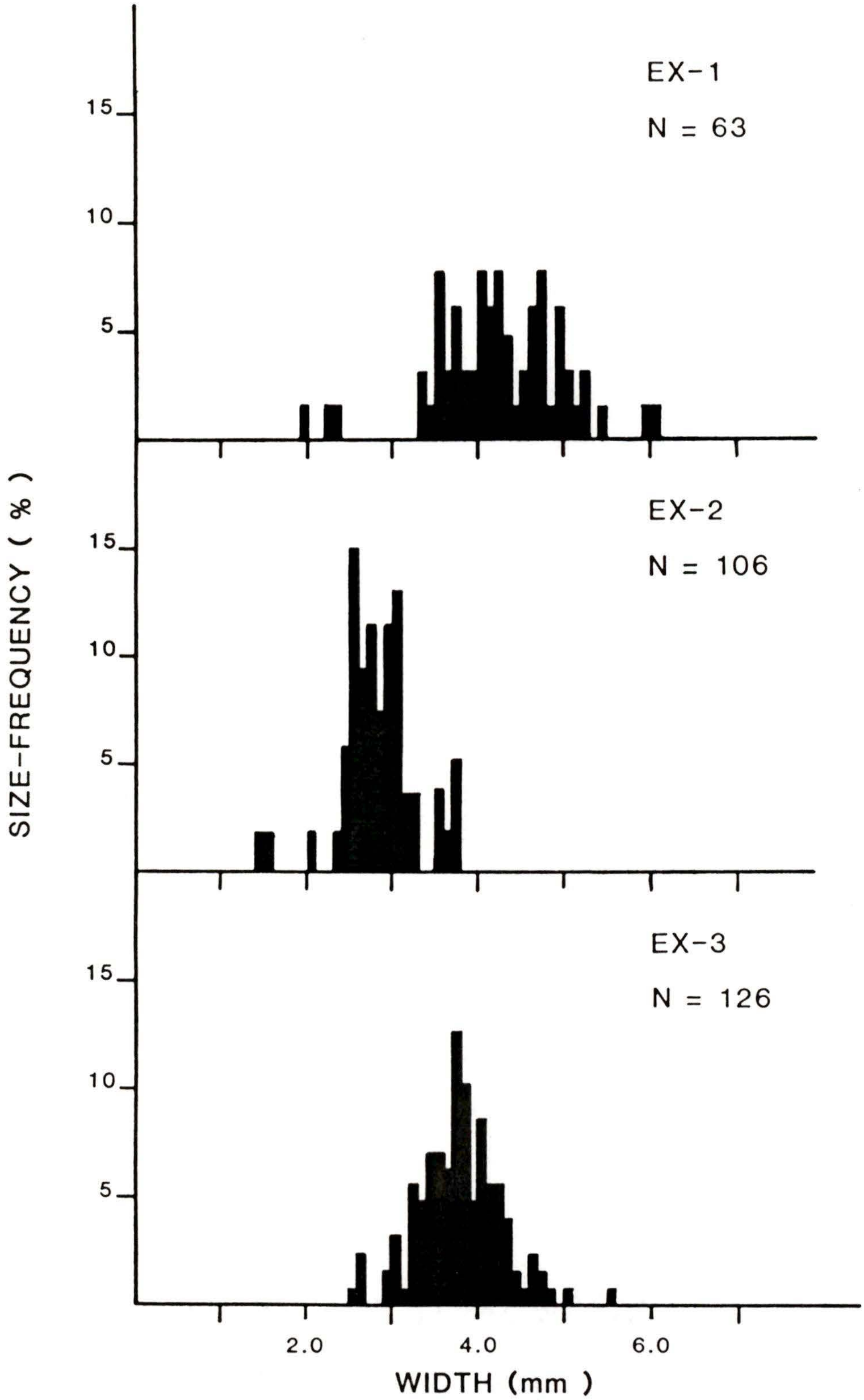
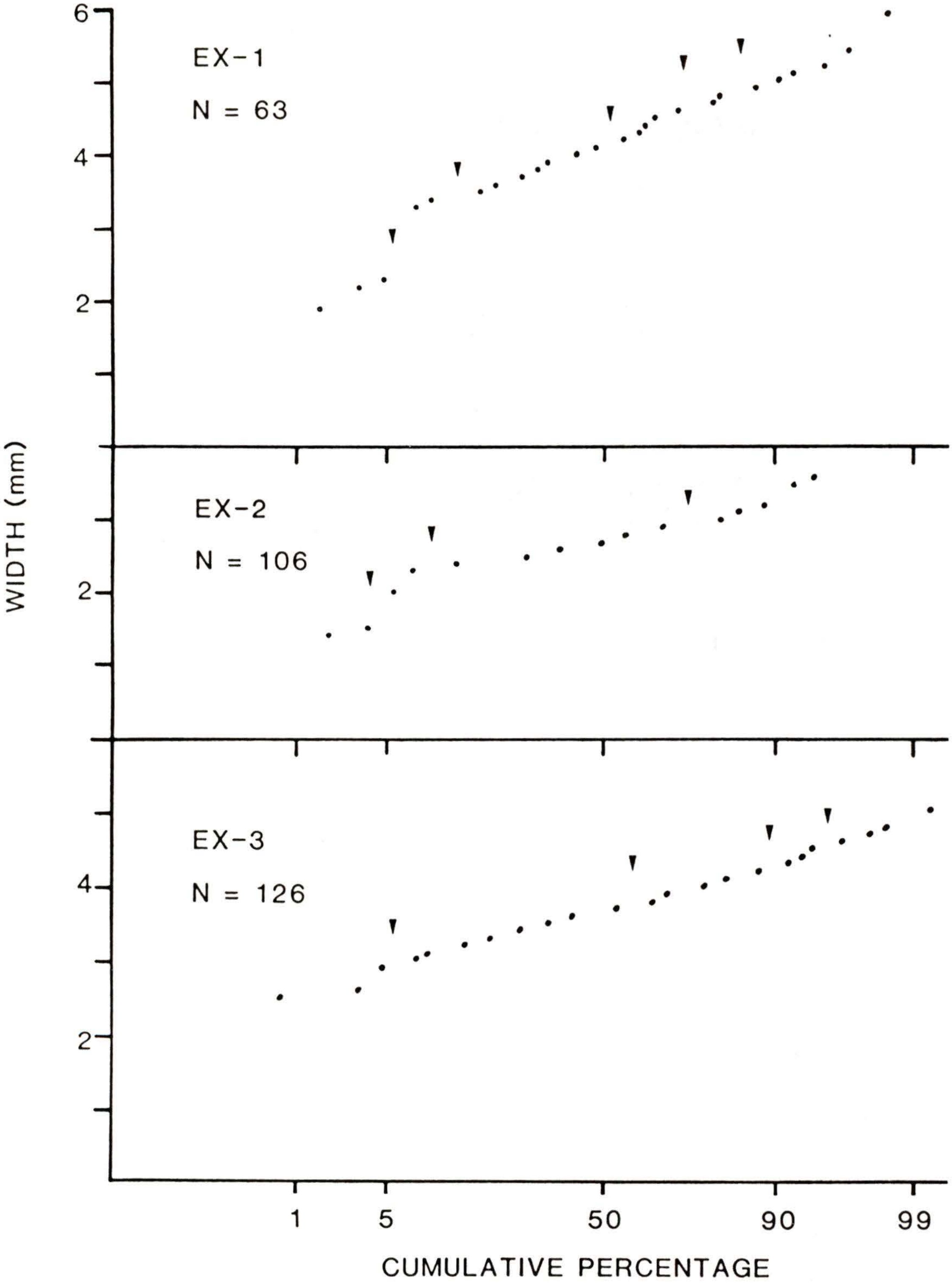

EX-1
N = 63
EX-2
N = 106
EX-3
N = 126
15
10
5
SIZE-FREQUENCY (%)
2.0
4.0
6.0
WIDTH (mm)

Figure 21: Probability paper analysis of widths for the Explorer Ridge samples of *Paralvinella palmiformis.*

Possible size class peak locations are marked with arrows.


EX-1
N = 63
EX-2
N = 106
EX-3
N = 126
WIDTH (mm)
6
4
2
2
4
2
1
5
50
90
99
CUMULATIVE PERCENTAGE

narrowest size range of all seven samples of *P. palmiformis*, 2.3mm; and EX-3 has a range of 3.0mm (Table 10).

All of the samples differ significantly from each other in their size distributions when analysed with the two-sample Kolmogorov-Smirnov test. Despite the differing distributions, there is no reason to suspect the existence of more than one size morph of *P. palmiformis* as a number of different size ranges, which form a continuum, is displayed by the seven samples studied.

Gametogenesis

P. palmiformis is gonochoric. Chi-squared tests reveal no significant differences from a 1:1 male:female ratio ($P<0.10$ - $P<0.90$). The gonads are located on the lateroventral sides of the worm in all except several anterior and posterior segments. Gametogenesis in this worm is similar to that of *P. pandorae*, with the gametes developing free in the coelom from an early stage. It also has two pairs of modified nephridia that function in sperm storage. Figure 22 illustrates diagrammatically the internal anatomy of male and female *P. palmiformis* as seen in histological sections.

In three subsamples of *P. palmiformis*, from END-2, END-3 and EX-2, very few or no gametogenic stages were observed in the thirty-six or more specimens examined from each vent. Of worms from the other four vents, only those of 2.0mm in width or greater have gametogenic stages present.

Female Specimens

Oogenesis in *P. palmiformis* closely resembles that in *P. pandorae* (Fig. 23). However, the maximum oocyte diameter recorded in *P. palmiformis* is larger, i.e., 220 µm. An ANOVA test showed that differences occur in mean oocyte size among vents ($F = 29.79$, $df = 3$, $P<0.0001$). The mean sizes for AX-1 and EX-1, and for END-1 and EX-3, are not significantly different from each other; all other pairs of sample means do differ significantly according to Tukey's range test (Table 12).

Percentage frequencies of coelomic oocyte diameter are shown in Figures 24 and 25. In each female specimen of *P. palmiformis* examined from the four sites, there is a similar wide range of oocyte sizes. The frequency distributions of oocyte sizes differ significantly from a normal distribution (Table 13), and all of the histograms constructed from END-1, EX-1 and EX-3 samples are skewed towards the right (Fig. 24 and Fig. 25). The AX-2 oocyte distribution does not demonstrate this strong skewness, rather it is composed of almost even proportions of oocytes in the early and intermediate stages of development (Fig.24).

ANOVA tests show that mean oocyte size differs 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 Tukey's range tests indicate that >60% of the individuals in each population do not differ significantly in their mean oocyte size ($P<0.25$).

The fecundity of *P. palmiformis* is estimated at a mean and standard deviation of $15.2 \times 10^3 \pm 9.9 \times 10^3 (n = 5)$.

Table 12: Oocyte size range, mean and standard deviation for four subsamples of *Paralvinella palmiformis* females.

n = number of oocytes in each sample. All pairs of samples, except those listed below, differ significantly in their mean oocyte size.

SAMPLE	n	OOCYTE SIZE RANGE (μm)	MEAN	S.D.
AX-2	428	10-220	70	39
END-1	351	10-160	56	30
EX-1	976	10-200	67	41
EX-3	1282	10-200	57	34
AX-2	Vs	EX-1	N.S.	
END-1	Vs	EX-3	N.S.	

Table 13: Results of tests of normality for the four oocyte size distributions of *Paralvinella palmiformis* females.

* = significantly different from a normal distribution at $\alpha = 0.05$.

SAMPLE	KOLMOGOROV STATISTIC		
AX-2	0.1017	*	P<0.01
END-1	0.1431	*	P<0.01
EX-1	0.1392	*	P<0.01
EX-3	0.1826	*	P<0.01

Male Specimens

Spermatogenesis in *P. palmiformis* appears to be similar to that in *P. pandorae* (Fig. 26). The three sperm developmental stages (spermatogonia, rosettes of spermatocytes, and sperm morulae) are represented in males from AX-2. However, spermatogonia and rosettes make up 95% of the noted stages, each composing almost 50% of the final total (Fig. 27). Sperm morulae represent only 4.6% of the spermatogenic stages present, and only one of the six males examined contain spermatozoa in the nephridia (Fig. 27).

In males from END-1, EX-1 and EX-3, only single or small clumps of spermatogonia were observed (Fig. 28). Larger rosettes of spermatocytes, which are composed of smaller and more condensed cells, were not present. Nor were there any morulae or detached spermatozoa.

Figure 22: A schematic drawing of the internal anatomy of male and female *Paralvinella palmiformis* based on histological sections.

bv = blood vessel,
bw = body wall,
c = coelom,
g = gut,
lm = longitudinal muscle,
nc = ventral nerve cord,
o = oocyte,
r = rosettes of spermatogonia,
s = secondary spermatogonia.

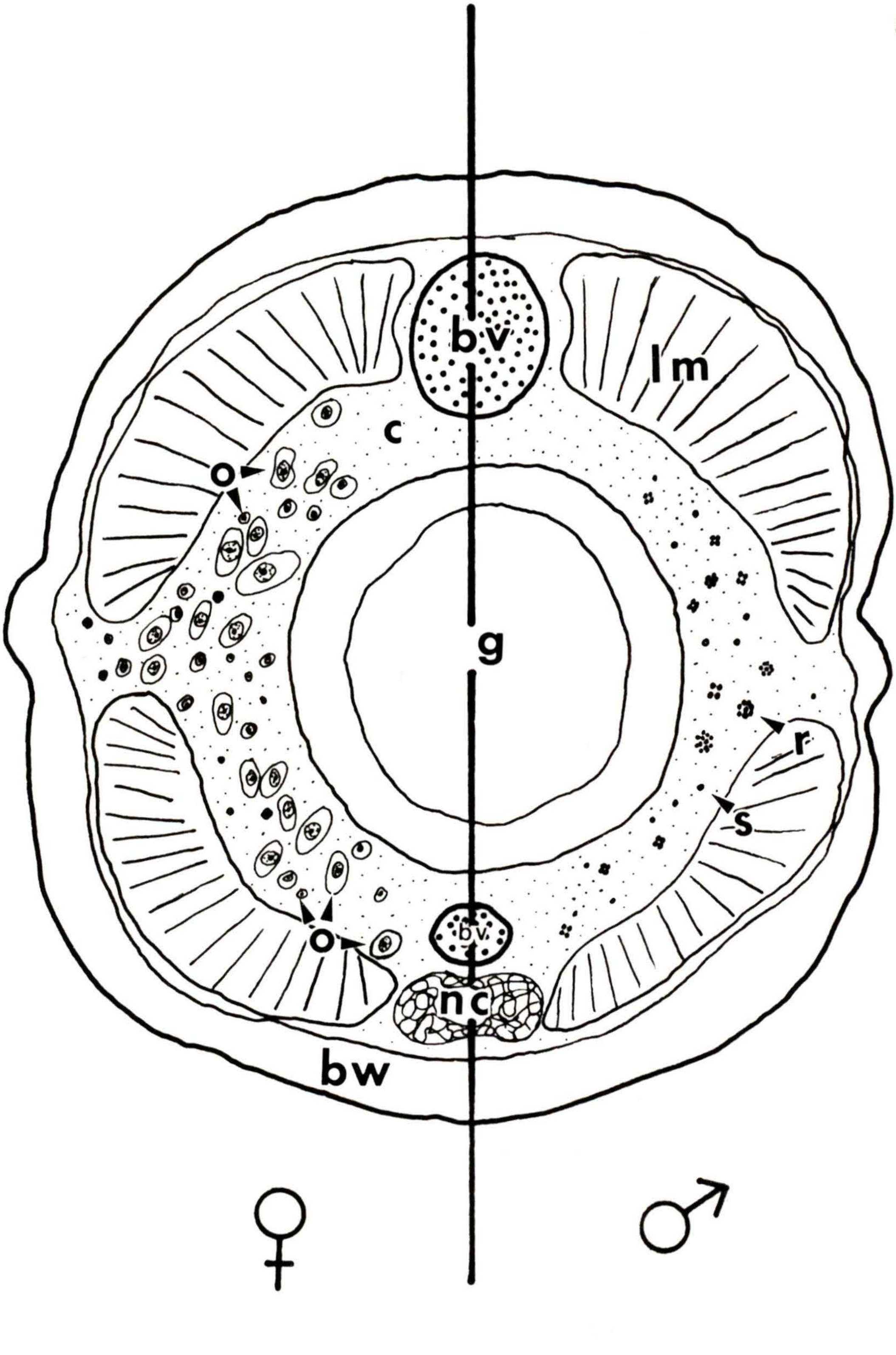

bv
lm
c
o
g
r
s
o
bv
nc
bw
♀
♂

Figure 23: Light micrographs of oogenesis in *Paralvinella palmiformis*.

(A) Longitudinal section through a AX-2 female showing irregularly-shaped oocytes developing in the coelom.

(B) An EX-3 female in cross section showing numerous small oocytes in the coelom.

(C) An oocyte in cross section showing the nucleus and nucleolus.

BW = body wall,
C = coelom,
LM = longitudinal muscle,
N = nucleus,
Nu = nucleolus,
O = oocyte.

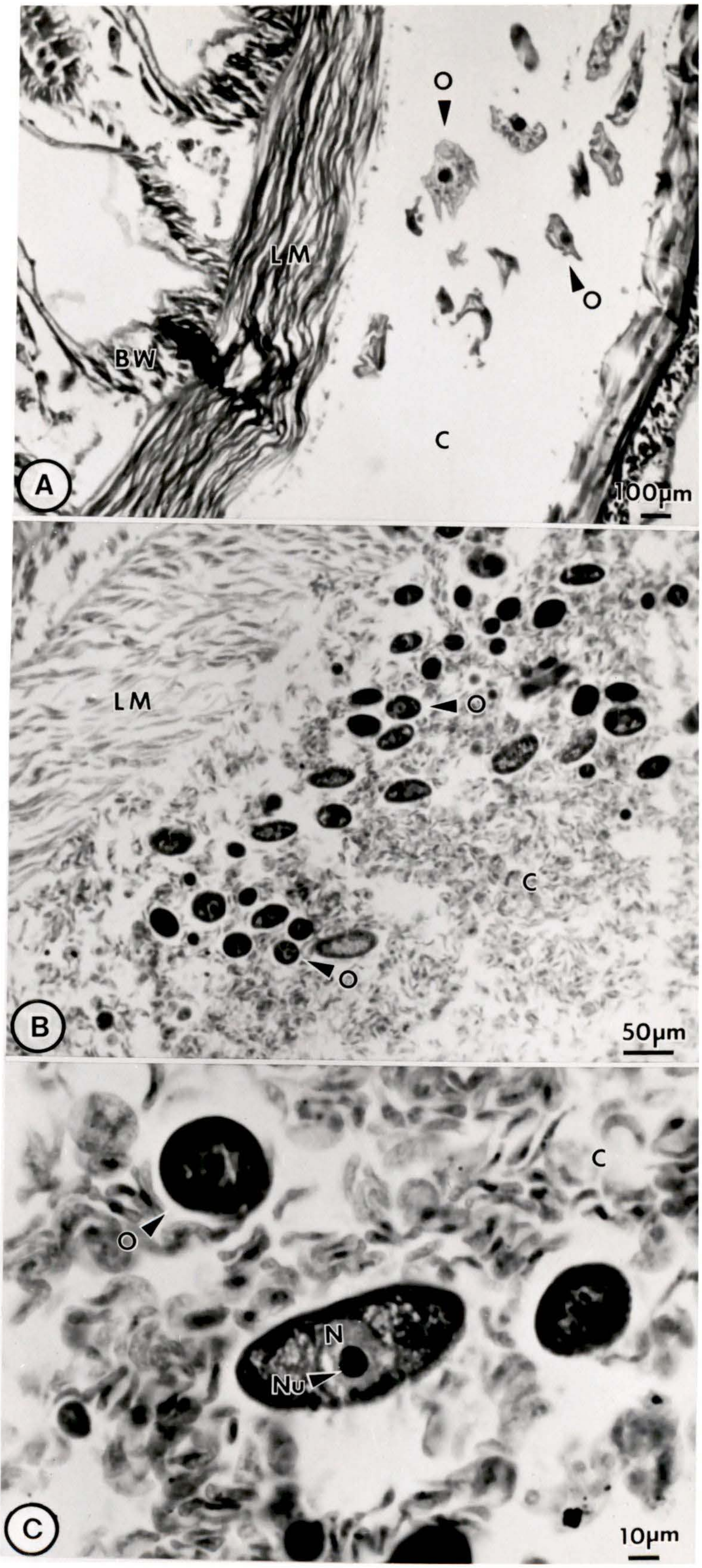

O
O
LM
BW
C
A
100μm
LM
O
O
C
B
50μm
C
O
N
Nu
C
10μm

Figure 24: Size-frequency histograms of maximum oocyte diameter for subsamples of *Paralvinella palmiformis* from AX-2 and END-1.

N = number of females in each subsample,
n = total number of oocytes measured.

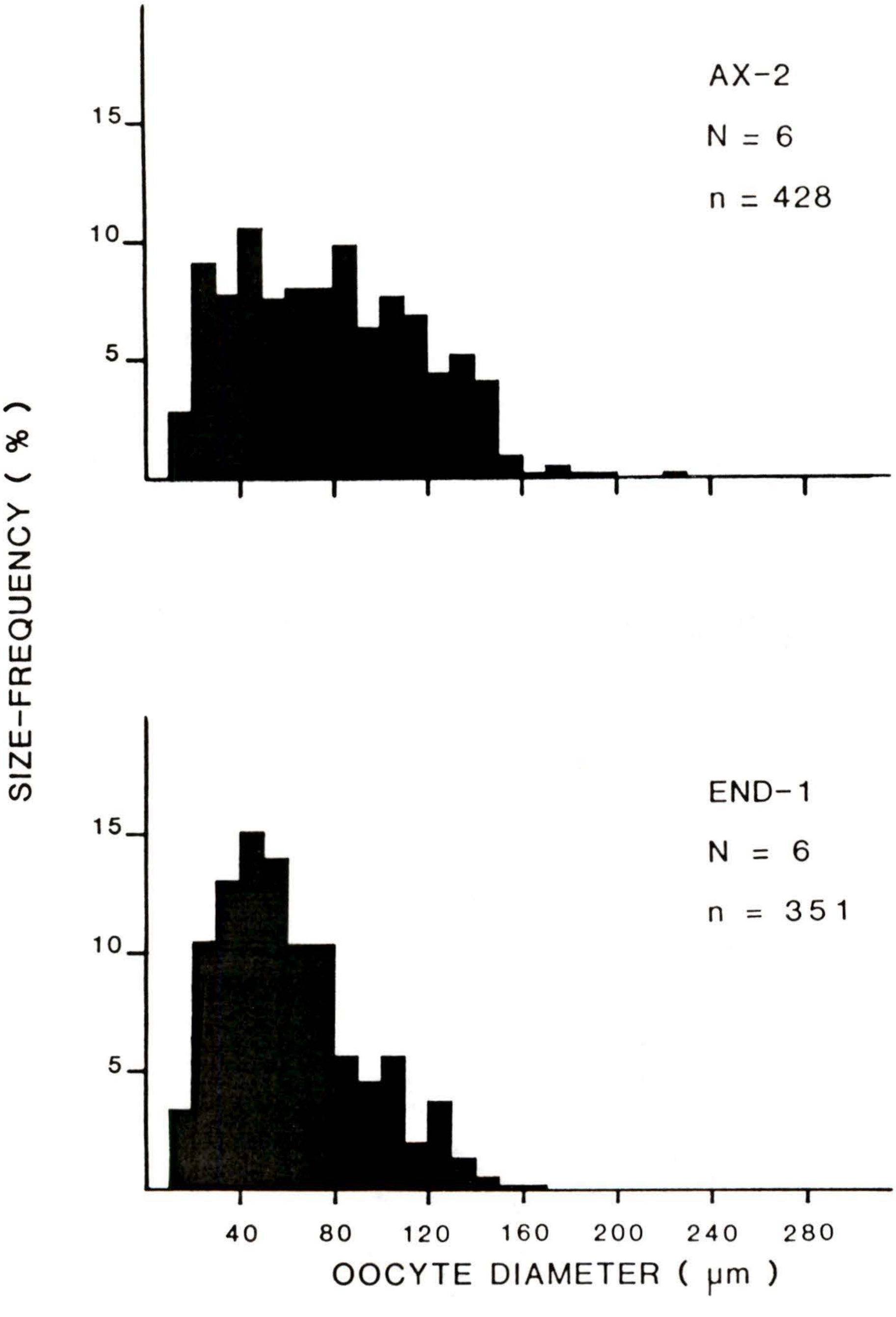

AX-2
N = 6
n = 428
END-1
N = 6
n = 351
15
10
5
SIZE-FREQUENCY (%)
40
80
120
160
200
240
280
OOCYTE DIAMETER (µm)

Figure 25: Size-frequency histograms of maximum oocyte diameter for subsamples of *Paralvinella palmiformis* from EX-1 and EX-3.

N = number of females in each subsample,
n = total number of oocytes measured.

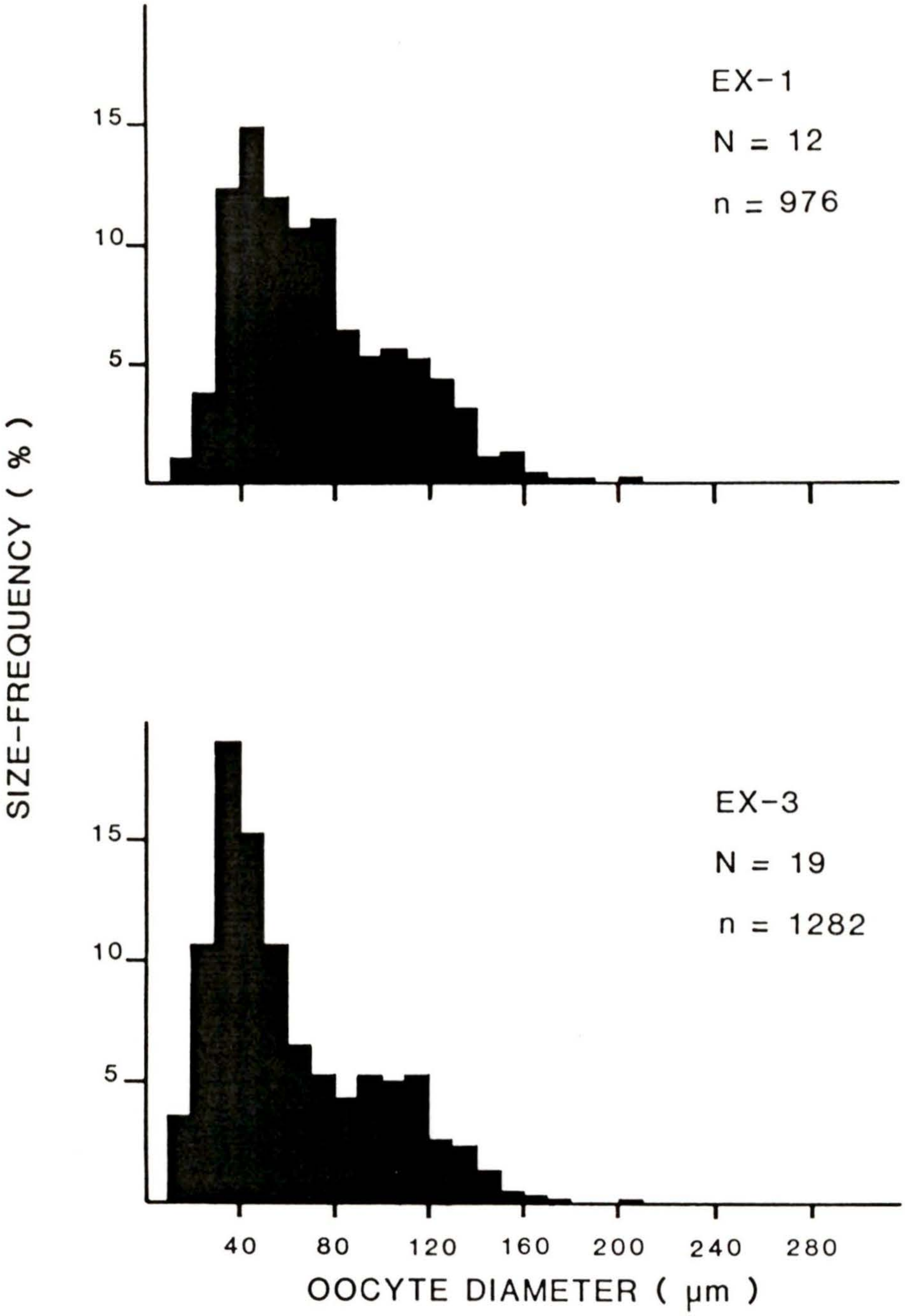

EX-1
N = 12
n = 976
EX-3
N = 19
n = 1282
15
10
5
SIZE-FREQUENCY (%)
40
80
120
160
200
240
280
OOCYTE DIAMETER (μm)

Figure 26: A section of an EX-3 male *Paralvinella palmiformis* showing early sperm development.

C = coelom,
LM = longitudinal muscle,
S = secondary spermatogonia.

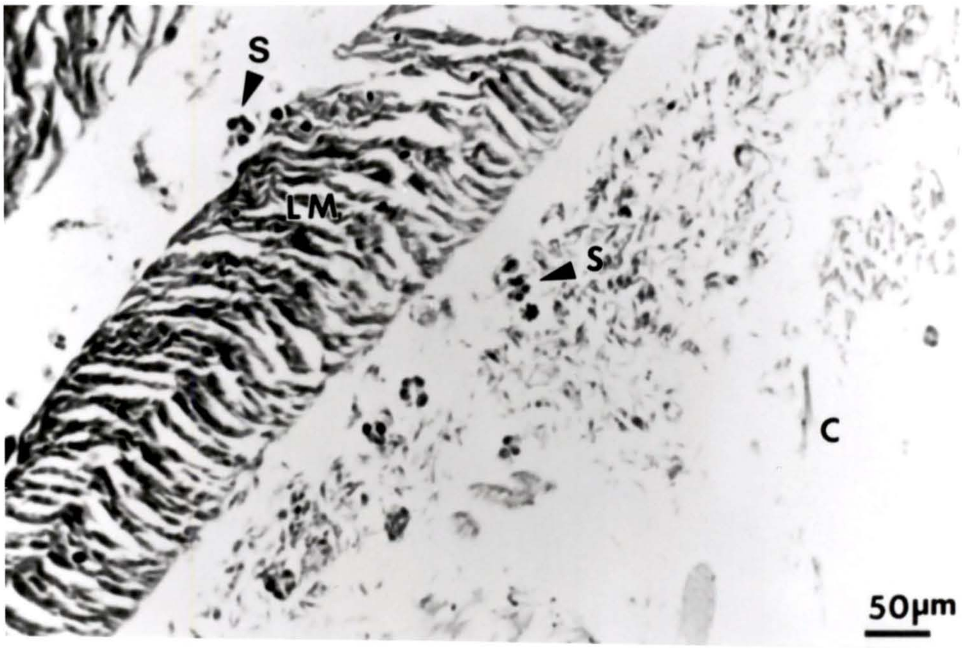

S
LM
S
C
50μm

Figure 27: Bar graphs representing the percent occurrence of the spermatogenic stages in the AX-1 subsample of male *Paralvinella palmiformis*

The shaded area of the pie chart denotes the percentage of males in which sperm was observed in the mixonephridia.

N = number of males in the subsample.

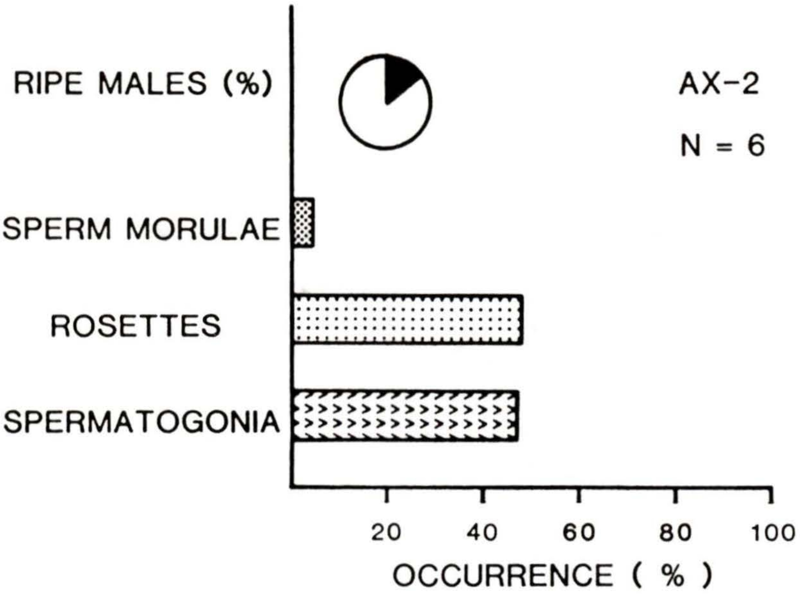
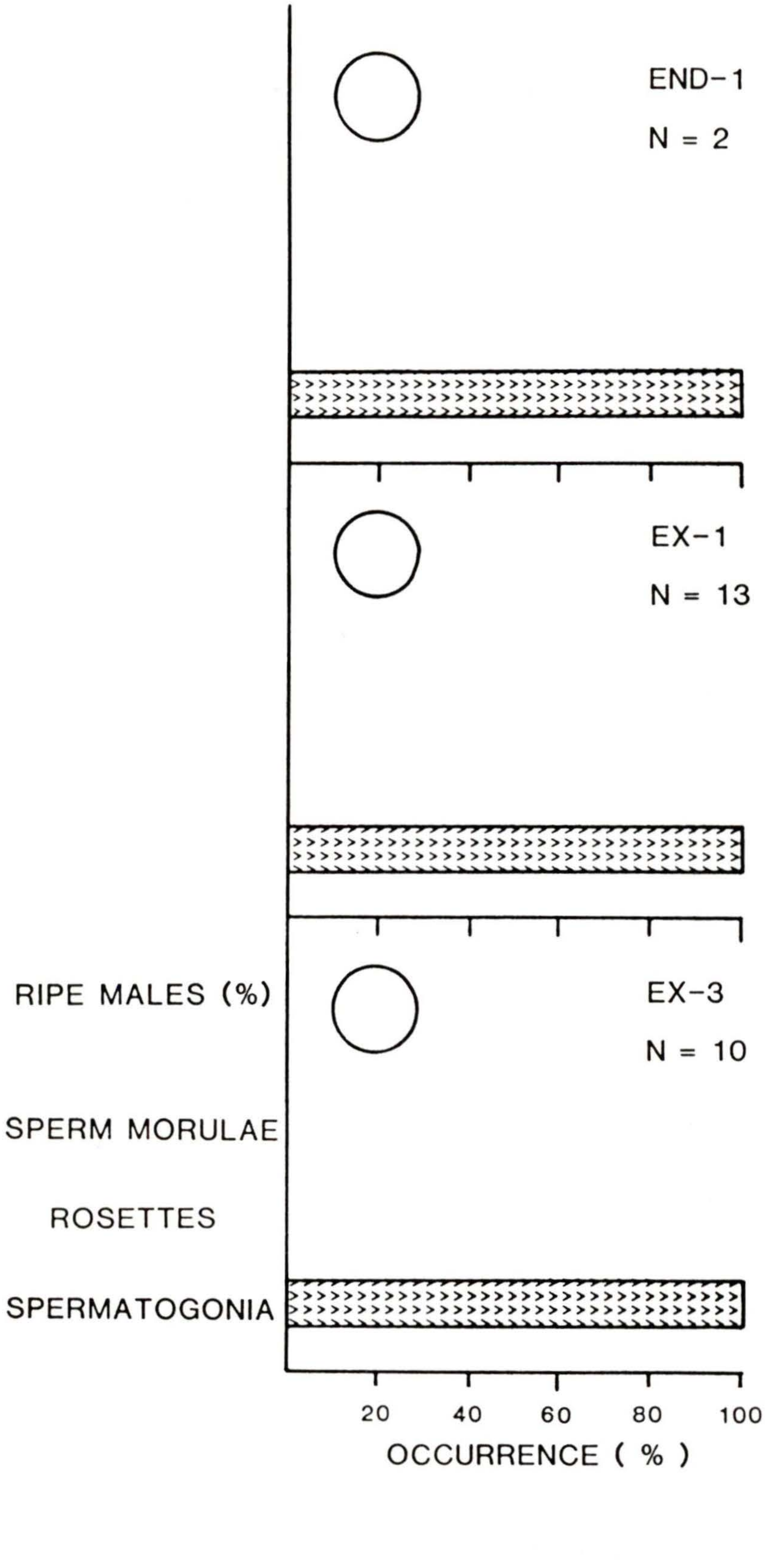

RIPE MALES (%)
AX-2
N = 6
SPERM MORULAE
ROSETTES
SPERMATOGONIA
20
40
60
80
100
OCCURRENCE (%)

Figure 28: Bar graphs illustrating the percent occurrence of the spermatogenic stages in subsamples of males of *Paralvinella palmiformis* from END-1, EX-1 and EX-3.

The empty pie charts denote the absence of males with spermatozoa in the modified nephridia.

N = number of males in each subsample.


END-1
N = 2
EX-1
N = 13
EX-3
N = 10
RIPE MALES (%)
SPERM MORULAE
ROSETTES
SPERMATOGONIA
20
40
60
80
100
OCCURRENCE (%)

Summary of Results

(I) *Paralvinella pandorae*

(a) It constructs a mucous sheath which is attached to vestimentiferan tubes. *P. p. pandorae* is found only at the four vent sites explored to date on the Juan de Fuca and Explorer Ridges, although the subspecies *P. p. irlandei* has been described from 13°N on East Pacific Rise. Abundance of *P. p. pandorae* at different vents on the Juan de Fuca Ridge and Explorer Ridge is variable.

(b) Mean width varies from 0.82mm to 1.55mm.

(c) Recruitment of juveniles does not seem to occur periodically or seasonally.

(d) Differences in size ranges occur at different vents. These differences do not appear to represent different morphs of the worm.

(e) The worm is gonochoric. Gametogenesis resembles that in other terebellids. There is a wide range of oocyte developmental stages in females from each population. Maximum oocyte diameter is 160 µm in cross section. All spermatogenic stages are well represented in males from each population. A high proportion of males in each population contain spermatozoa in paired mixonephridia.

(II) *Paralvinella palmiformis*

(a) It occurs naked, coiled around vestimentiferan tubes, or embedded in sulphide minerals. It is found only at the four vent sites explored to date on Juan de Fuca Ridge and Explorer Ridge. Abundance of the worm at different vents is variable.

(b) Mean width ranges from 1.74mm to 5.17mm.

(c) Juvenile recruitment appears to be discontinuous.

(d) Size range of the worm varies among different populations. It is unlikely that these variations represent different morphs of the worm.

(e) This polychaete is gonochoric. Gametogenesis is similar to that in *P. pandorae*. In representatives of three populations very few or no gametogenic stages are present. In the other populations oocyte size distributions are skewed to the right except in AX-2, where even proportions of early and intermediate stages are represented. Maximum oocyte size is 220 μm. Males from AX-2 contain even proportions of early and intermediate stages of spermatogenesis; one of six possesses spermatozoa. In the other populations, only spermatogonia are present in males.

DISCUSSION

Paralvinella pandorae and *Paralvinella palmiformis* are both found only at the four hydrothermally active sites explored to date on the Juan de Fuca and Explorer Ridge systems. However, the number of vents at which each species is found, and their abundance at each vent, varies substantially. *P. pandorae* is found at only eight of the twenty-one vents sampled, and *P. palmiformis* occurs at fifteen vents. It is highly unlikely that the absence of either species from a vent sample is due to sorting error, but it is difficult to rule out the possibility of biased sampling. *P. palmiformis*, being the larger and more colourful of the two species, may be sampled preferentially over *P. pandorae*, which is not easily visible at a vent. However, in this study it is assumed that the sampling technique provides a fairly accurate reflection of the distributional patterns of the worms.

On Endeavour Segment, *P. pandorae* is present at only one of the three vents used in this study. It is possible that END-3, where *P. pandorae* is abundant, is actually at a site different from that of END-1 and END-2. END-3 was sampled during a second cruise to the Endeavour Segment area and exact relocation of the original Endeavour site may not have occurred. Similarly, the exact location of EX-3 is not known in relation to the vents described by Tunnicliffe *et al.* (1986) from Explorer Ridge. If this is the case, then *P. pandorae* may be quite limited in its dispersability from one vent site to another one close by. It is interesting to note that *P. palmiformis* occurs at all of the three vents on Endeavour Segment.

Indeed the exclusive occurrence of *P. palmiformis* over *P. pandorae* at seven vents suggests it is the more widespread of the two species. This may be related to the versatility of *P. palmiformis* in its habit within the hydrothermal vent environment. It is found not only coiled around the tubes of vestimentiferans, but also associated with minerals within a metre or two from a vent. On a number of occasions, this species has been seen embedded in newly-formed mineral deposits within a few centimeters of hot (up to 330°C) fluid emissions (Tunnicliffe and Fontaine, in press; pers. obs.).

P. pandorae, on the other hand, always forms a mucous sheath attached to vestimentiferan tubes (pers. obs.). This restricted habit may be a cause of its limited distribution on Juan de Fuca Ridge and Explorer Ridge. Settlement at a vent which does not support a vestimentiferan population to act as a substratum would presumably result in complete post-settling mortality of the worm. Alternatively, settlement may not be induced in larvae drifting by a vent which did not support a vestimentiferan population. If settlement occurred at a vent with vestimentiferans, successful establishment of *P. pandorae* populations would be more likely. However, depletion of settling space at a suitable vent may be caused by the secretion of large amounts of mucus by *P. palmiformis* which, along with high densities of the limpet, *Lepetodrilus sp. nov.*, often smothers the tubes of vestimentiferans at low temperature vents (pers. obs.).

It is possible that a specific cue is required to stimulate settlement and metamorphosis in the larvae of both *P. pandorae* and *P. palmiformis*. Such cues have been demonstrated for many shallow-water invertebrates (Burke, 1983; Chia and Rice, 1978), and may be emitted by conspecifics, or the substratum. In alvinellids the cue could be particular hydrogen sulphide concentrations, as has been found for *Capitella* sp. 1 in shallow-water, sulphide-enriched habitats (Cuomo, 1985; Dubilier, 1986). The presence of vestimentiferans, or conspecifics may also serve as settling cues. Although there is no evidence for such phenomenona in vent species, it should not be ruled out as a means by which the demography of a species is influenced.

Considering the pattern of vent colonization by the two alvinellids in question, *P. palmiformis* alone may possess the ability to be the initial colonizer at a newly active vent. Because of *P. pandorae*'s apparent requirement for vestimentiferan tubes as a settling substratum, it would appear that it could only become established later in the history of a vent. This is not to say that *P. palmiformis* always inhabits a vent before *P. pandorae*. The occupation of a new vent by either species will depend primarily on the dispersal mechanisms of each worm, and also on the availability of suitable substratum. Unlike observations of *Alvinella* species (Desbruyères *et al.*, 1985), *Paralvinella* species do not seem capable of swimming. Both *P. pandorae* and *P. palmiformis* may have similar means of larval dispersal, although *P. palmiformis* has the additional potential for possible dispersal during the adult phase. In ship-board aquaria, *P. palmiformis* has been observed detaching itself from vestimentiferan tubes and subsequently coiling its tail end around any thin object with which it comes in contact (V. Tunnicliffe, pers. comm.). Indeed, this species has been observed coiled around the leg of a spider crab, *Macroregonia macrochira* (Tunnicliffe and Jensen, in press). Being capable of such motility may enhance the dispersal opportunities of *P. palmiformis* to different vents by passive mechanisms.

Paralvinella pandorae and *P. palmiformis* appear to utilize the same food source, i.e., dissolved and particulate organic matter. Presumably if one species has a well-established population at a vent, it may outcompete newly settling juveniles of the other species for food. Also, as has been reported for a number of shallow-water communities (Woodin, 1976; Wilson, 1980), adult-larval interactions can be important in structuring vent faunal assemblages. Adults of one alvinellid species may drastically increase larval mortality of a second by feeding on them. Such an interaction would imply that the first of the two species to become established at a vent would have a competitive advantage over the other. Of course, the building of a population by either species depends on a variety of factors, including the life-history strategy, predation pressures, intraspecific and interspecific competition, and the longevity of a vent.

Abiotic factors appear to be important in determining the distribution of alvinellids on Juan de Fuca and Explorer Ridges. Taking Explorer Ridge as an example, *P. palmiformis* is found only at warm (25^{o}C-85^{o}C) vents where hydrogen sulphide concentrations vary from 2.8 µmol to 60.9 µmol, and not at hot (286^{o}C-306^{o}C) vents, or vents where hydrogen sulphide concentrations are zero. At the three sites on Juan de Fuca Ridge, the only correlation between alvinellid distribution and physico-chemical parameters that is distinguishable is that they are only found when hydrogen sulphide is present and temperatures are below 100^{o}C.

From the distribution of *P. pandorae* and *P. palmiformis* among sites, both species appear to be capable of dispersal over a distance of up to 200km. This is the distance between Endeavour Segment and Explorer Ridge, which are separated by the Sovanco Transform fault; it is unlikely that there are active vents along the fault. However, neither species seems to have the ability to disperse over thousands of kilometers (minimum distance between southern-most vent site on Juan de Fuca Ridge and the northern-most site on East Pacific Rise). The absence of *P. pandorae* and *P. palmiformis* from vents south of Juan de Fuca Ridge is most probably related to inability to disperse rather than unsuitability of the vents there, because a number of other alvinellid species populate those sites. It has been proposed that, at some southern vents, the niche of *P. pandorae pandorae* is occupied by a second subspecies, *P. p. 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. p. irlandei* have been separated since the American Plate overrode the East Pacific Rise 28 million years ago (Desbruyères and Laubier, 1986). This isolation has led to the divergence of the two species due to limited dispersal capabilities that have prevented genetic exchange. 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.

In their demographics, *Paralvinella pandorae* and *Paralvinella palmiformis* seem to differ substantially. For *P. pandorae* all samples sizes are relatively large and therefore should give an accurate representation of population structure. The apparent absence of polymodality in two of the size-frequency histograms of this species may reflect continual low, or rarely-occurring recruitment to the populations studied, so that distinct peaks of juvenile input at defined intervals are not distinguishable. Similar interpretations have been made for the deep-sea holothurian, *Peniagone azorica*, for which histograms resembling those for *P. pandorae* were produced (Tyler *et al.*, 1985). Alternatively, each of the unimodal distributions may represent progeny of a single cohort, as has been hypothesized for *Kolga hyalina*, a deep-sea holothurian for which large samples yielded unimodal peaks in distribution (Billett and Hansen, 1982). However, when reproduction of *P. pandorae* is also taken into consideration (see later discussion), it is most probable that these populations of this worm experience continuous recruitment of juveniles. At AX-1, two possible peaks are evident in the size frequency histogram, which may indicate distinct recruitment events in this population. Such recruitment pulses may result from a clump of larvae settling at that vent simultaneously.

The small samples of *P. palmiformis* from several vents displayed numerous peaks in their size-frequency distributions. However, because of the small sample sizes it is inadvisable to extrapolate size classes from the peaks. Fortunately the very large sample of *P. palmiformis* retrieved from END-3 provides a histogram whose peaks provide strong evidence of discontinuous recruitment of juveniles to the population. This also lends credence to the occurrence of definite size classes in the other, smaller samples. As the conditions at each vent are not identical, it is not surprising that 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.

There appear to be at least five size classes in the END-3 population, although these cannot be interpreted as year classes as is often the case 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). *Bathymodiolus thermophilus*, the vent mussel found at Galapagos Rift vents, also exhibits a definite recruitment peak in its size-frequency distribution (Rhoads *et al.*, 1982).

The size range differences within *P. pandorae* populations, and *P. palmiformis* populations among the vents may reflect local habitat-induced variations in the populations. This phenomenon has been studied for a number of intertidal species which often experience fluctuations in local climatic features and chance factors that produce considerable variation in recruitment, growth, and maximum size in a population (Barnes, 1956; Southward and Crisp, 1956; Southward, 1967; Lewis and Bowman, 1975). Changes in hydrogen sulphide concentration, or food availability, or temperature at a vent could produce such effects. Alternatively, the different samples of each species may represent populations of varying ages. It is conceivable, for example, that the AX-1 sample of *P. pandorae* represents an older, longer established population than either that at END-3 or EX-3.

Although gametogenesis is similar in *Paralvinella pandorae* and *Paralvinella palmiformis*, there are obvious differences in the timing of events between the two species. Because of the presence of a wide range of gametogenic stages in the subsamples from all three vents, *P. pandorae* is thought to produce gametes continuously. Although ANOVA results imply a lack of synchrony of gametogenesis among individuals in each population, multiple range tests indicate that this result is accounted for by a small proportion of the individuals in each case. 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). Samples of these species taken at various times throughout the year yielded similar results to those for *P. pandorae* in this study. For both shallow-water polychaetes, it was postulated that suitable food is available all year round and therefore continuous reproduction has the advantage of avoiding excessive seasonal demands on the resources (Southward and Southward, 1958; Olive, 1970). This is potentially the case for *P. pandorae* also. However, this is only valid if both the adults and the larvae are capable of feeding effectively at the extremes to which they are exposed, e.g., highest or lowest hydrogen sulphide concentrations, or different temperatures.

As mentioned above, *P. pandorae* appears to breed continuously, and so may be considered an iteroparous species (Cole, 1954). From the information available, it is not possible to ascertain whether *P. pandorae* is a continuous breeder over an extended period, as defined by Bell (1976), or a semi-continuous breeder that releases a small number of mature gametes at frequent intervals (Olive and Clark, 1978). It is also possible that breeding occurs at a low level for extended times, but with maxima during certain defined periods, as has been reported for *Nephtys hombergi* (Olive, 1978; Oyenekan, 1986). Such maximum breeding peaks might explain the discernible recruitment peaks in the population at AX-1.

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 a 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* also spawns continuously (McLean, 1981).

With the continual production of gametes, the selection of mature oocytes and sperm from a heterogeneous pool of developing cells would be necessary to ensure that only ripe gametes are spawned. In the terebellid *Amphitrite ornata* a sorting mechanism exists on the coelomostome (Clark, 1979), and a similar form of regulation in *Cirratulus cirratus* has been observed (Olive, 1971). A detailed study of the mixonephridia of *P. pandorae* may reveal a similar mechanism.

If, as postulated, *P. pandorae* undergoes continuous or semi-continuous reproduction, then it seems most likely that the unimodal population structure of the species at two vents results from continuous or semi-continuous juvenile recruitment.

In *P. palmiformis* the total absence of developing gametes from three of the seven samples studied implies either (i) that those three populations had recently undergone a complete spawning of gametes, or (ii) that none of the members of the populations have reached adulthood, at which time gametogenesis would begin. Although these three samples possess the smallest maximum sizes of *P. palmiformis* from all seven sites, the latter of the two possibilities presented seems improbable, because developmental stages were observed in worms of 2.0mm in width and greater in the four other populations examined. The likelihood of complete spawning in a population is a strong indication that reproduction in *P. palmiformis* may be synchronized and discontinuous, i.e., *P. palmiformis* may differ from *P. pandorae* in its reproductive mode: it appears to be a periodic breeder. A discrete breeding cycle in *P. palmiformis* may be reflected as the numerous size class peaks of juvenile recruitment in the population structure of the species.

A degree of synchrony of gametogenesis in each population as a whole can be interpreted from the oocyte size distributions and staging of spermatogenic phases. In AX-2 worms, oocyte sizes and spermatogenic phases are split between early and intermediate stages. In the three other samples however, the oocyte size distributions are skewed to the left, and in males the only spermatogenic stages present are single secondary spermatogonia plus a small number of rosettes also composed of secondary spermatogonia. These three samples, END-1, EX-1 and EX-3, are, therefore, at the early stages of gametogenesis. At this early stage, gametogenesis appears to be synchronized between males and females in a population. Although ANOVA results indicate a lack of synchrony among individuals within each population, multiple range tests show that over half of the individuals in each population have the same mean oocyte size ($P<0.25$). This suggests that a large proportion of the individuals in each population are, in fact, synchronized in their gametogenesis.

Synchronized reproduction (gametogenesis and spawning) would be advantageous to *P. palmiformis*. The chances of fertilization increase when batches of mature male and female gametes are spawned simultaneously. Life-history studies on shallow-water terebellids have also found synchrony of reproduction (Hutchings, 1973; Christie, 1986). The means by which the coordination and synchronization of gamete maturation are achieved vary among different polychaetes. In *Melinna cristata*, Hutchings (1973) reported that the ovary exists in either a non-proliferative or a proliferative phase, depending on the time of year. Clark (1979) suggested that hormonal regulation of ovarian activity may control synchrony of oogenesis in *M. cristata*. In many other polychaetes with synchronized spawning, gated rhythms have been proposed as a method of control (Olive, 1984). For example, an increase in temperature may block the initiation of the final phase of oogenesis or spermatogenesis, whereas a decrease in temperature may activate that phase, as seen in *Streblospio benedictii* (Levin and Creed, 1986), some barnacle species (Patel and Crisp, 1960) and a sand crab (Efford, 1969).

Commonly the cycle of reproductive activity in Polychaeta is annual, but lunar or semi-lunar rhythms have also been observed in a number of worms (Hauenschild, 1960; Caspers, 1961) including the terebellid *Amphitrite ornata* (Scott, 1909). Evidence for seasonal currents in the deep-sea has been reported (Dickson *et al.*, 1982), and, at hot vents, a twice daily signal in phase with the semi-diurnal component of predicted surface elevation at hot vents has been observed (Johnson and Tunnicliffe, 1985; Childress, pers. comm.). These tidal pulses may influence the breeding cycle of *P. palmiformis*. However, because of the sparcity of information over extended time periods, it is impossible to invoke a single control mechanism for synchronized reproduction in this vent polychaete. Whatever the mechanism, it appears to function only in the case of *P. palmiformis*, an apparent periodic breeder, and does not affect the continuous breeding pattern of *P. pandorae*. Numerous deep-sea invertebrates have been found to exhibit a similar reproductive pattern to that hypothesized for *P. palmiformis* (Rokop, 1977; Tyler and Gage, 1980; Pearson and Gage, 1984; Tyler and Gage, 1984a; Van Praët and Ducheteau, 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 µm) are usually associated with planktotrophy in polychaetes, whilst larger eggs (> 150 µm) usually give rise to lecithotrophic larvae or brooded embryos (Hermans, 1979). Maximum oocyte diameter measures 165 µm in *P. pandorae*. If this dimension is corrected for tissue shrinkage during processing according to Baker (1963),[3] it is approximately 330 µm. *P. palmiformis* has a substantially larger maximum oocyte size of 220 µm, which, when corrected, approximates 440 µm in diameter. When these oocyte sizes are considered in relation to what is known about other, shallow-water, terebellids, the embryos of *P. pandorae* and *P. palmiformis* are most probably brooded (Marinescu, 1964; Eckelbarger, 1974; Zottoli, 1974; Cazaux, 1982; Clavier, 1984), or are free-swimming or crawling lecithotrophic larvae (Okuda, 1947; Nyholm, 1951; Guillou and Hily, 1983).

It is highly improbable that *P. pandorae* incubates its young because, despite the fact that thousands of worms have been removed from their sheaths, not one embryo has been found brooding there. In *P. palmiformis* it seems that brooding of young is not possible as it does not construct a tube. In both species therefore, a lecithotrophic mode of development can be expected.

It is unlikely that either species produces pelagic larvae that develop in surface waters, as wastage of larvae would undoubtedly ensue in the course of vertical transport of eggs and larvae through the water column. Further loss would result from transport to unsuitable settling areas. These factors must play a strong selective role in determining the life-history strategy of deep-sea vent fauna. Most probably both species have demersal lecithotrophic larval

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[3] Baker found that the volume of echinoderm eggs decreased by 48% following fixation in 4% formalin and embedding in paraffin. It is not known whether such shrinkage also occurs with polychaete eggs.

development. Large oocytes (> 200 µm) extracted from live *P. pandorae* and *P. palmiformis* are not buoyant, but rather they sink to the bottom of the container of surface seawater at 4°C in which they are held (pers. obs.). Assuming similar conditions in their natural environment, this suggests that the eggs would stay close to the bottom. However, surface seawater may be less dense than bottom water, especially water surrounding vents. Therefore, it is inadvisable to take this observation as evidence of demersal larval development in the two species.

In other terebellids studied to date, demersal larvae develop from eggs of 150-425 µm, and settle to metamorphose after three to several days (Okuda, 1947; Nyholm, 1951; Guillou and Hily, 1983). It would be erroneous to extrapolate too much from 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 larval longevity is increased (Pechenik, 1984). The length of larval life is normally limited by yolk supply (Lucas *et al.*, 1979; Pechenik *et al.*, 1979), although some lecithotrophs may be facultative plankton feeders (Perron and Carrier, 1981).

For many deep-sea species, extended larval life has been postulated as a means of dispersal over wide geographical areas (Sheltema, 1977). However, this hypothesis refers only to those larvae that develop in surface waters. Lutz *et al.*, (1980; 1984) have suggested that even 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 500m) throughout their free-swimming existence. Studies of deep-sea fouling off the Bahama Islands supports this hypothesis for deep-sea bivalves inhabiting ephemeral environments (Turner, 1965). Zottoli (1982), reporting on the biology of an ampharetid polychaete, *Decemunciger apalea*, from wood panels placed on the deep-sea floor, suggests that the numerous small eggs (150-170 µm) produced by the worm imply an r-selected life-history strategy. He also postulates, however, that *D. apalea* broods its embryos, a characteristic not associated with a high reproductive rate. *Amphisamytha galapagensis*, an ampharetid common at many vents in both the northeast and southeast Pacific, resembles *D. apalea* in its reproductive mode, with the exception that *A. galapagensis* is thought to have demersal larvae (Zottoli, 1983).

Paralvinella pandorae and *Paralvinella palmiformis* appear to have a demersal, lecithotrophic larval development in common. As the larvae swim in bottom waters or crawl along the bottom, they could repopulate vents. Bottom currents could carry them to other vent sites along the two ridge systems. The larger eggs of *P. palmiformis* may allow a longer pre-metamorphosis period which would provide it with higher chances of dispersal to new vents. This may, in part, explain the distributional differences between the two species.

The reproductive potential of both *P. pandorae* and *P. palmiformis* appears to be relatively low. Although *P. palmiformis* appears to have a lower fecundity than that of *P. pandorae*, it is not advisable to presume differences between the two species in this regard because of the inaccuracy of the method used to estimate this parameter. Nonetheless, both fecundity estimates are comparable to those for polychaete species that undergo non-planktotrophic larval development (Olive, 1970; Gibbs, 1971; Gremare and Olive, 1986).

The results of this study form the first detailed investigation of life-history patterns of hydrothermal vent polychaetes. Although the conclusions made from the study are sometimes necessarily speculative, they do provide preliminary information on the population structure and reproductive cycle of *P. pandorae* and *P. palmiformis*. For a complete knowledge of the life-cycles of these two hydrothermal vent polychaetes, a time-series of samples, from several vents, every month over a year or two is required. As the chances of this ever being possible are slim, perhaps the information resulting from this study could best be used to supplement future investigations that approach the subject from a different perspective. Genetic studies, through techniques such as starch-gel electrophoresis of proteins, on populations of both species from different vent sites may yield data on relative gene flow and levels of genetic variation. Such data, in conjunction with the results from this thesis, would allow more informed predictions of dispersal abilities of the two species. Electrophoretic techniques could also be used to determine the degree of genetic differentiation between northeast Pacific alvinellids and those occurring at vents on the East Pacific Rise. This information, along with the geological data available, could be used to develop a phylogenetic history of the Alvinellidae.

SUMMARY

The distributions of *Paralvinella pandorae* and *Paralvinella palmiformis* are limited to hydrothermal vents on Juan de Fuca Ridge and Explorer Ridge in the northeast Pacific. Variations in abundance of both species at different vents may result from competition for space and/or food. The absence of either species from a vent is possibly due to the inability to disperse to that vent, or to unsuitable settling substratum, or to inappropriate physico-chemical conditions at that vent. *P. palmiformis* occurs at twice as many vents as *P. pandorae*. This is attributed in part to the flexible habit of adult *P. palmiformis* which, unlike *P. pandorae*, does not depend solely on vestimentiferan tubes as a substratum. A possible longer larval life in *P. palmiformis* may also explain the distributional differences of the two species.

The restricted geographic distribution of both species appears to be due to dispersal limitations between vent fields in the northeast Pacific and those situated thousands of kilometers to the south. It is thought that *P. pandorae* and *P. palmiformis* have common ancestral roots in the southeastern Pacific, from which they diverged following the isolation of the Juan de Fuca Plate from the East Pacific Rise approximately 28 million years ago.

The population structures of *P. pandorae* and *P. palmiformis* appear to differ. Two *P. pandorae* populations show no evidence of discrete recruitment events, rather it seems that juvenile input is continuous, or semi-continuous; one

population appears to have experienced juvenile recruitment at intervals. *P. palmiformis*, on the other hand, displays definite size class peaks in all of its population structures. Recruitment in this species apparently occurs at periodic intervals, i.e., is discontinuous.

Observed variations in the size ranges of both species from different vents are thought to reflect local, habitat-induced variations in environmental conditions. In some cases, the presence of only very small specimens in a population may be due to the recent establishment of that population.

The pattern of gametogenesis in *P. pandorae* and *P. palmiformis* is similar, and follows that described for other terebellids. The presence of the full range of gametogenic stages, including spermatozoa in males, in all populations of *P. pandorae* examined, suggests continuous, or semi-continuous, iteroparous reproduction. *P. palmiformis* differs in that it appears to undergo discrete reproduction. The control of synchronization of gametogenesis and spawning in *P. palmiformis* is unknown.

Larval development, extrapolated from maximum oocyte size, is thought to be lecithotrophic and demersal in both species. Such larvae would provide for repopulation of a vent. The developmental rate of larvae may be quite slow at the ambient temperature of $2^{o}C$ around vents. Extended larval life would allow dispersal, possibly via bottom currents along the ridge systems, to other vents. The larger maximum oocyte size of *P. palmiformis* may indicate a longer larval developmental period than *P. pandorae*. Despite this, neither *P. palmiformis* nor *P. pandorae* appear capable of dispersal over the long distances to southeastern Pacific vents.

Neither *P. pandorae* nor *P. palmiformis* exhibit an extreme r-selected or K-selected life-history strategy. Neither species shows a high reproductive rate, rather they tend to be more K-selected in their life-history patterns. Both produce relatively small numbers of large, lecithotrophic larvae. However, *P. pandorae* appears to produce a continuous, or semi-continuous, stream of offspring, whereas *P. palmiformis* populations appear to spawn synchronously at the end of a defined breeding cycle.

These results are in agreement with the suggestions of Berg(1985), Turner *et al.* (1985) and Van Dover *et al.* (1985) that reproductive modes of vent species are mainly a function of phylogenetic constraints. As phlylogeny places adaptive constraints on reproductive strategies, especially mode of larval development (Strathmann, 1978a and b; Spight, 1979), the prediction of a particular life-history pattern at hydrothermal vents is not possible without considering the phylogeny of all the species that make up a vent community. Certainly, the life-histories of *P. pandorae* and *P. palmiformis* appear to be influenced more by the limitations of their evolutionary history than the selective pressures of the fluctuating, ephemeral environment which they inhabit. Nonetheless, their life-history strategies are apparently adequately adaptive for that environment.

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APPENDIX A

KEY TO VENT NAMES.

VENT	*NAME(S)*	*REFERENCE*
AX-1	Taylors Vent	1, 9
	Vent A	2
	AX-1	3
AX-2	Shepherds Vent	1, 9
	Vent B	2
AX-3	Lampheres Chimney	1
END-1	Lt.OBO	4, 6
END-2	Hole-in-the-ground	4, 6
END-3	A-1419	5, 7
END-4	Dual Smoker	4, 6
END-5	Skips Grotto	4, 6
EX-1	Pogo Peaks	1
	Vent 9	8
EX-2	Crab Vent	1
	Vent 17a	8

EX-3	Busted Thruster	1
EX-4	Gulatis Gusher	1
	Vent 12a	8
EX-5	Lunch Hour Vent	1
	Vent 12b	8
EX-6	Philosophers Vent	1
	Vent 1	8
EX-7	Oszusts Ogres	1
EX-8	Black and White Vent	1
	12d	8
EX-9	12c	8
EX-10	17b	8
SJdF-1	1A	10
SJdF-2	1B	10
SJdF-3	Plume	10

1 = University of Victoria specimen collection labels.

2 = Canadian American Seamount Expedition, 1985.

3 = Juniper *et al.*, 1986.

4 = Karsten *et al.*, 1984.

5 = Malahoff *et al.*, 1984.

6 = University of Washington specimen collection labels.

7 = Smithsonian Institute specimen collection labels.

8 = Tunnicliffe *et al.*, 1986.

9 = Desbruyères and Laubier, 1986.

10 = Tunnicliffe and Fontaine, in press.

VITA

Surname: McHugh

Given Names: Damhnait

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Date of Birth: 19.5.1961

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Honours and Awards:

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Title of Thesis

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