



Population biology of two pycnogonid species (Ammonotheidae) at hydrothermal vents in the northeast Pacific

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Introduction

Little is known about the biology of the less conspicuous hydrothermal vent species. Studies on the evolution and ecology of this habitat remain dependent on understanding the basic biology of important component organisms. That requirement fuelled this study on pycnogonids or "sea spiders". These animals are often abundant in vent collections from the northeast Pacific and observers have noted them in high densities near high temperature vents.

Class Pycnogonida is a marine arthropod group found throughout the ocean. Although they are chelicerates, they only superficially resemble true spiders of the order Araneae. They typically have four pairs of multiarticulate legs but some genera have up to six pairs. Their distinguishing features include the much reduced abdomen and a large proboscis used for feeding. During mating, the eggs are transferred to the male who carries the eggs in masses attached to ovigers held under the segmented trunk. The protonymphon larvae is often parasitic on invertebrates (Arnaud & Bamber, 1987).

Vent pycnogonids are known from the northeast Pacific, western Pacific and Atlantic vents. Child (1987) describes the two species studied here: *Ammonothea verena* Child, 1987 and *Sericosura venticola* Child, 1987 of the family Ammonotheidae. Both species are eyeless and similar in appearance. They are distinguished most readily by the number of palp segments. There is nothing reported about the population structure of these sea spiders nor how they fit into the food web of the hot vent habitat. "Another question begging an answer, in relation to hydrothermal vent-associated pycnogonids, concerns the nature of food available to them." (Child, 1987, p. 900). Most pycnogonids, are fluid feeders on sessile invertebrates and have intracellular digestion.

The objective of this study was to determine i) if the niches of the two species can be readily identified, ii) if populations at the same site show stable structure, and iii) if there are unusual features of reproduction or feeding that can be deduced from collected specimens.

Methods

The collections of pycnogonids used for this study were grab samples obtained using manned and remote submersibles; after sorting, specimens were moved from 7% formalin to 70% ethanol. All but one collection was a haphazard selection designed only to subsample all fauna. The S&M (=Smoke and Mirrors) 1996 sample was a suction collection that targeted the mass of pycnogonids seen in Figure 1a. Over 900 specimens were examined from all parts of Explorer and Juan de Fuca Ridges. Population data were selected from the six collections that returned more than 40 individuals (Table 1).

Sexual maturity and gender were determined where possible and the number of egg masses borne by the males was noted. As the original description of *Sericosura venticola* did not include a female, our data do not separate the sexes. However, we believe the females can be differentiated by a reduced setose condition and few to no setae on the ovigers. Total body length was measured from the dorsal anterior edge of the cephalon to the junction of the last pair of lateral processes. For three males from the S&M 1994 collection, the diameter of egg masses and number of eggs per mass were determined.

Results

Ammonothea verena is known from all the major vent sites on the Explorer, Juan de Fuca and Gorda Ridges; it occurs in



Figure 1. Pycnogonida (sea spiders) at a vent on Juan de Fuca Ridge, northeast Pacific.

a. A mass of spiders at the base of a venting chimney on Endeavour Segment, the majority of which constitute the S&M 1996 collection in Table 1. Image is about 30 cm across.

b. A mating pair of *Ammothea verenae* retrieved from the spider mass in A; the darker more setose male is on top and the long frontal proboscis flanked by feeding palp is central on both specimens. 1 cm from top to bottom.

c. Underside of a male *Ammothea verenae* depicting numerous egg masses attached to the ventral ovigers.

over half of the ca.75 vents that we have sampled over 15 years. In contrast, *Sericosura venticola* was collected from but three vents within 50 m of each other on Endeavour Segment; samples from other vents at this site returned only *A. verenae*. *Sericosura venticola* was collected first in 1984 (Child, 1987) then a decade later at S&M vent in three successive years (Table 1).

Sericosura venticola always occurred with *Ammothea verenae*, never representing more than 50% of all pycnogonids present (e.g. Table 1). Visual observations suggest that pycnogonids prefer the peripheral areas of vents. They occur more commonly near or on smoker chimneys where our largest samples were derived. Pycnogonids can be extremely abundant in small patches. Individually, they are not easy to see but they will form

'masses' of several hundred (Figure 1a), where spiders are crawling over each other.

Image, video and in situ examinations show these animals to be slow moving and often inactive; they occur most frequently on hard substrata rather than on sediment or on worm tubes. Three individuals seen on a large bacterial mat were themselves completely covered in bacterial growth, suggesting a sedentary existence. Many individuals from chimney habitats had integuments covered in sulphide minerals often giving a golden or black coloration; nearly 90% of the 1994 S&M individuals were discoloured. We could determine no prey species from association or behaviour. Several individuals of both species had filamentous bacteria extending from the proboscis.

Table 1. Six collections of pycnogonids from Juan de Fuca Ridge that returned more than 40 individuals. A 'vent' is a single major fluid site that may occupy several square meters area. Determination of adult females of *Sericosura venticola* was not always clear thus the adult category was left gender undetermined.

Vent	Site	Year	<i>Ammothea verenae</i>			<i>Sericosura venticola</i>		
			number	juvenile/ adult	male female	% males ovigerous	number	juvenile/ adult
S&M	Endeavour	1994	87	2.95	1.22	90.0	36	0.5
S&M	Endeavour	1995	64	0.14	1.28	75.0	54	0.38
S&M	Endeavour	1996	269	0.23	2.16	81.9	17	1.25
Grotto	Endeavour	1991	42	1.00	0.75	56.0	0	-
Church	CoAxial	1995	307	6.13	1.14	0.0	0	-
Mkr22	Cleft	1990	59	4.80	1.49	66.7	0	-

There is a significant difference in adult body size between the two species, with *Ammothea verenae* being the larger species (one-tailed t-test, $p < .01$). Figure 2 illustrates the differences in adult sizes at one vent, S&M on Endeavour Segment. There is little overlap between species among adults in the 3.5 mm size class.

Juveniles and adults were found together in all samples in varying proportions. Three *Ammothea verenae* samples in Table 1 are dominated by juveniles. The Church Vent sample was not only predominantly juveniles (86% of specimens), but contained a myriad of released larvae less than 200 μm in size. A clear shift in population structure occurs in the S&M samples illustrated in Figure 2. An ANOVA test confirmed that the population structure differed from year to year ($F = 28.4$, $p < 0.001$). There was no significant difference between the body size of males and females (t-test; $p > 0.05$) for any of the collections.

A mating pair remained entwined upon collection: the male was on top with its ovigers wrapped around the female, ready to receive eggs (Figure 1b). Four egg masses were already attached to the male, perhaps from a previous encounter. The majority of males collected had egg masses attached to the ovigers (Figure 1c); the exception was Church Vent (Table 1). The number of masses on *Ammothea verenae* males ranged from 1 to 26 (averaging around 8) while *Sericosura venticola* carried between 1 and 5 egg masses. Within each mass on *A. verenae*, the number of eggs ranged from 61 to 1275; correlation between the egg mass size and egg number was significant ($r^2 = .258$, $P < 0.05$; Pearson's correlation). Eggs within different masses on the same male were at markedly different stages of development. Larval stages present in some egg masses were the protonymphon larvae typical of pycnogonids. The average fecundity (number of eggs plus larvae) of the three *A. verenae* males from the 1994 S&M sample was estimated at nearly 4000.

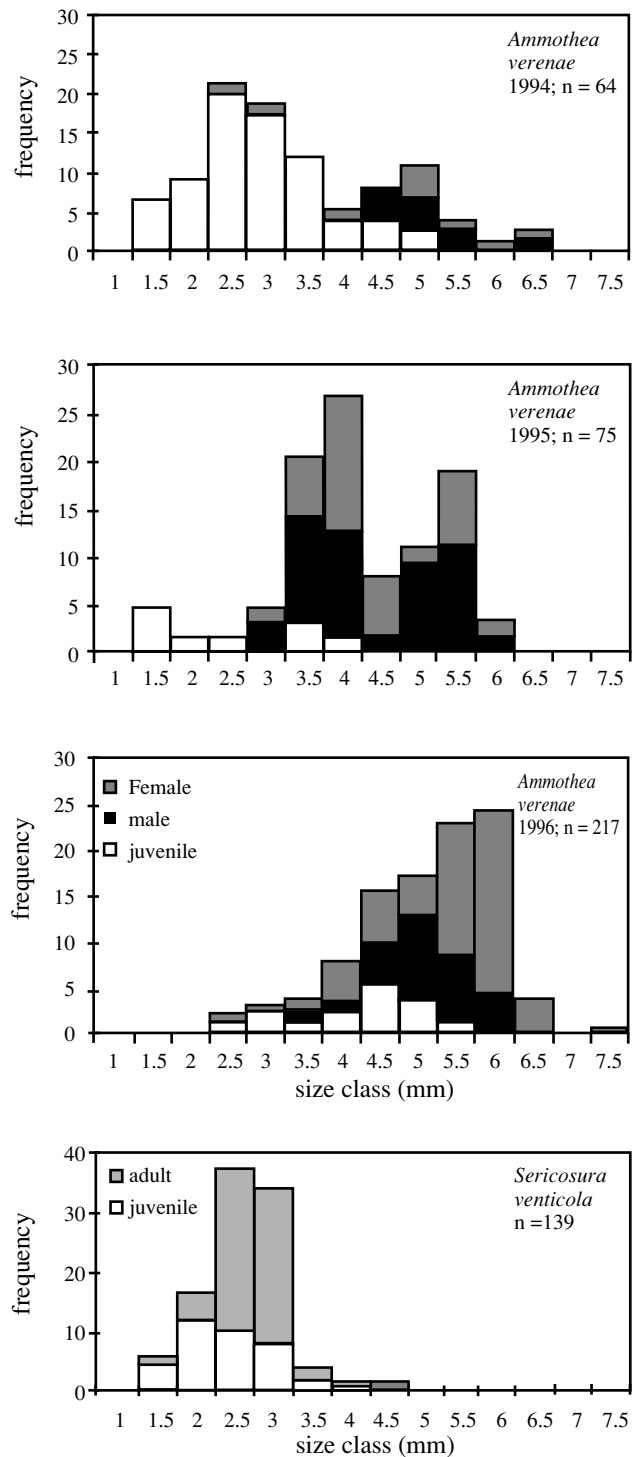


Figure 2. Size frequency histograms of pycnogonids from S&M vent. Top three histograms represent collections of *Ammothea verenae* in three successive years from the base of S&M vent. Bottom histogram is *Sericosura venticola*; three years of individuals were combined. Adult body size in the two species is markedly different. Representation by juvenile *A. verenae* shifts from 1994 to 1995.

Discussion

The pycnogonid species from Juan de Fuca Ridge have very different geographic distributions. The wide, versus restricted, distributions of the two species is difficult to explain without knowing more about the larval development habitat requirements. We may be seeing the result of long-term selection in which a competitive dominant is able to establish more rapidly at relatively ephemeral sites (such as Cleft and CoAxial). The two species differ in body size as adults and thus may exploit the physical environment differently. They were found most commonly in lower hydrothermal flow conditions. Sarrazin et al. (1997) made a detailed survey of the S&M structure and identified pycnogonids as most abundant in 'community VI' that predominates at the base of the structure farthest from the high temperature smokers. However, they also document the changes in venting and shifting communities in the years 1991 to 1995. The preferred habitat, on chimneys, is a dynamic one that may influence the population structure observed from year to year.

Population structure and age class varied across the collections sampled. Although increased sampling effort may eliminate such differences, the marked differences invite further examination to test for possible recruitment cycles, at least in *Ammothea verенаe*. One viable interpretation of the differential juvenile/adult proportions is pulsed recruitment. Mkr22 Vent, Cleft Segment is a young vent, likely initiated by an eruption four years previously (Embley & Chadwick, 1994): juveniles form over 80% of the collection. In 1994, a chimney sampled about 10 m from Church Vent returned only five adult pycnogonids; the abundance of juveniles and larvae in the 1995 sample indicates a recent recruitment event.

The rapidity with which the population structure may shift is illustrated in Figure 2. The same site, sampled in three consecutive years, yielded different populations. This result represents either a sampling artefact or an ageing population. It could be the former because the 1996 collection deliberately targeted the spider mass seen in Figure 1. One interpretation of this grouping is a mating event that attracts adults. The low proportion of both juveniles and *Sericosura venticola* may support this conjecture. Also anomalous in this collection is the high proportion of males which may stay through multiple matings.

Pycnogonids are brooders but a single male may produce a large number of offspring in "slow release" as eggs mature at different times. This strategy suits variable conditions on

a venting chimney. Little is known about the protonymphon larvae; they are rarely observed in meiofauna collections. Most pycnogonid larvae spend a parasitic stage in an invertebrate host but free-living development is possible (Arnaud & Bamber, 1987). The presence of abundant *Ammothea verенаe* larvae in one sample suggests a pulsed recruitment event either directly from nearby adults or as a "bulk delivery" from the plankton. Child (1987) notes the unusually small egg size of both species and suggests that they may have shorter embryonic and protonymphon stages with increased numbers of juvenile stages; as the complete life history of few pycnogonids is known, the significance of such a development pattern is unclear.

The role of these pycnogonids in the vent community remains uncertain. Their local abundance indicates a potentially important impact as a predator. Most pycnogonid species are fluid feeders on invertebrates with bryozoans, coelenterates and sponges as preferred prey (Arnaud & Bamber, 1987); none of these groups occur on Juan de Fuca chimney vents. Neither we nor Child (1987) could determine a prey species from observation in life or on stomach contents. The most obvious deduction of grazers on filamentous bacteria is at odds with the basic biology of the group but not without possibility.

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