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Distributional and biological aspects of copepods at hydrothermal vents on the Juan de Fuca Ridge, north-east Pacific ocean

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The abundance patterns of copepods on the Juan de Fuca Ridge was examined. One species was studied in detail. Twelve non-parasitic species are recorded from the Juan de Fuca, but only three dirivultid species and some unidentified harpacticoids are abundant in collections. Densities are estimated at 0.5 copepod cm^{-2} on vestimentiferan tubes to over 8 cm^{-2} on chimney surfaces. *Aphotopontius forcipatus* is most abundant at new vents and *Benthoxynus spiculifer* is most abundant at mature vents. Vents with reduced or undetectable fluid flow have higher diversity of copepod fauna.

The life cycle of the siphonostome *Stygiopontius quadrispinosus* begins with a centrolecithal egg brooded singly or doubly on the female. Hatching and naupliar stages are unknown in benthic samples. The pre-adult stage (copepodite V) recruits to the vent habitat. Pre-adult males attach to pre-adult females and fertilize at the final copepodite VI moult. As the sex ratio is highly skewed in favour of females, males probably inseminate many females and there may be mate competition in populations where males are rare. Reproduction is probably continuous or semi-continuous. Abundance is greatest on sulphide edifices near the points of hot water egress. This copepod co-occurs with the alvinellid polychaete *Paralvinella sulfincola*.

INTRODUCTION

Copepods are a major constituent of benthopelagic zooplankton samples in the deep sea both in diversity and abundance (Wishner, 1980). Copepod taxa represented at vents are different from those in soft-bottom abyssal environments (Dinet et al., 1988). Vent copepods belong almost exclusively to two orders, the Poecilostomatoida and Siphonostomatoida (Humes & Segonzac, 1998) and constitute a significant proportion of vent species diversity and endemism (Humes, 1999; Heptner & Ivanenko, 2002). Seventy-four endemic vent copepod species are currently described and these species are 17% of all vent species (Tunnicliffe et al., 1998). On the Juan de Fuca Ridge where vent species richness is only about 80 species (V. Tunnicliffe, personal observation), copepod species represent 15% of the fauna and 50% of these species are endemic to this ridge (Humes, 1991).

Worldwide distribution of vent and seep copepods as well as biogeographic patterns are well-known (Humes, 1991; Humes & Segonzac, 1998; Heptner & Ivanenko, 2002). Copepods at eastern Pacific vents are, for the most part, different from those on the Mid-Atlantic Ridge in taxonomic association and richness. In the eastern Pacific, about 50 species are known compared with 12 species found on the Mid-Atlantic Ridge (Humes & Segonzac, 1998). Scant information is available about the distribution of copepods among vents on a single ridge. This paper presents the distribution of copepods from the Juan de Fuca, in the north-eastern Pacific. In addition, we examine the ecology and reproductive biology of one Juan de Fuca species, *Stygiopontius quadrispinosus* (Humes, 1987) (Siphonostomatoida: Dirivultidae). The genus *Stygiopontius*, with 22 species, is found worldwide and is the most speciose hydrothermal vent genus (Tunnicliffe et al., 1998). Humes (1987) described *S. quadrispinosus* as the type species for this new genus of dirivultid from hydrothermal vents based on specimens from the Juan de Fuca Ridge. Our investigation of *S. quadrispinosus* is the first time the population biology of a vent or seep copepod has been examined.

MATERIALS AND METHODS

Study site

The Juan de Fuca Ridge is in the north-east Pacific at the junction of the Pacific and Juan de Fuca plates (Embley et al., 1990). Average depth is 2300 m. The ridge is 525 km long, has an axis trending N020°E, and has seven principal segments (Baker & Hammond, 1992). Our data set comes from the north Cleft, Axial, and Endeavour segments. Cleft is the 80 km-long southernmost discrete segment of the Juan de Fuca. The north Cleft vents lie between 44°50′N to 45°02′N, average depth is 2200 m. This segment established new vents after an eruption in 1986. Tsurumi & Tunnicliffe (2001) describe the vent assemblages in this expanse of diffuse flows punctuated by only a few high temperature edifices. Axial lies 113 km north-north-east on the central segment of the ridge at 45°58′N 130°02′W. The summit of Axial has a well-defined, three-sided caldera at 1500 m with three

Table 1. *Number of samples in different habitat types. Only samples with 50 or more individuals are included. For habitat age comparisons, only mature vent samples from Axial were used to minimize any geographic effect on the results.*

		Temperature		Age		
Segment	Total samples	High	Low	New	Mature	Old
Axial	33	9	23	8	21	3*
Cleft	3	1	2	0	not used	0
Endeavour	8	1	6	0	not used	1
Total	44	11	31	8	21	4

*, includes one sample from CoAxial segment adjacent to Axial.

active hydrothermal systems. The vent communities do not vary markedly among these sites except for fauna at new vents established in the eastern caldera after an extrusive eruption in 1998. Endeavour segment lies 220 km north at 47°57′N 129°06′W. Our samples are from Main and High Rise vent fields, two complex areas of diffuse venting around large high temperature structures.

Sample collection

Samples were taken by submersible from July to September between 1988 and 1999 on basalt and sulphide substrata. Manipulators grabbed one or two samples of tubeworms or sulphide projections, plus associated biota, and placed these in closable boxes. Copepods could be washed from the tubeworms during the transfer from manipulator to sample box. Alternatively, a suction system drew animals into a jar with a fine mesh (63 μm) over the out-take valve. This technique was used mostly at new vents where vestimentiferans had not yet colonized. On Endeavour, sulphide chimneys with vigorous high temperature flow often have flanges with reflecting pools of trapped hydrothermal fluid on the bottom of the projection (Delaney et al., 1992). The sample from Crypto vent was a flange with a reflecting pool. Temperature was measured on and around the sampled area before the flange was broken from the chimney and carried to the surface wrapped in a blanket.

Low temperature habitats can be on basalt or sulphide. Sampled areas have relatively low fluid flux and temperatures around 20°C. High temperature habitats are defined as areas directly surrounding high temperature fluid orifices on sulphide chimneys. These habitats are distinguished visually by vigorous flows and high abundances of the alvinellid polychaete, *Paralvinella sulfincola* (Desbruyères & Laubier, 1993).

Sample processing and analysis

Samples, fixed in 7% seawater formalin at sea, were sieved through a 1-mm mesh. The residue of all Axial and Endeavour samples and one north Cleft sample was sieved through a 63-μm mesh. All copepods were separated from both size fractions. The Crypto sample was treated differently: fauna was hand picked from 6.45 cm^2 squares in a grid overlaid on the flange and stored separately (total surface area of flange was 0.2 m^2). Eighty-six manipulator grabs and suction samples were examined. To ensure a minimum amount of comparability between habitats, we used samples containing 50 or more copepods for habitat comparisons (Table 1).

Table 2. *Per cent relative abundance of copepod species in vent samples from Axial, north Cleft, and Endeavour segments of Juan de Fuca Ridge. Per cent relative abundance calculations are for the entire sample. All siphonostomes are Family Dirivultidae.*

Order	Taxon	Authority	Axial (N=68)	Cleft (N=9)	Endeavour (N=9)
Calanoida	mixed*	F. Ferrari, personal communication	1.1	0.1	3.2
Cyclopoida	*Barathricola rimensis*	Humes, 1999	<0.1	0	0.6
Harpacticoida	*Uptionyx verenae*	Conroy-Dalton & Huys, 2000	0	0	0.2
Harpacticoida	Fam. Tisbidae, sp. unkn.	S. Conroy-Dalton, personal communication	0.6	1.0	0.6
Harpacticoida	mixed†	S. Conroy-Dalton, personal communication	4.9	59.3	29.2
Misophrioida	*Misophriopsis longicauda*	Humes, 1999	0.2	0.1	0.3
Siphonostomatoida	*Aphotopontius forcipatus*	Humes, 1987	5.8	2.8	14.0
Siphonostomatoida	*Benthoxynus spiculifer*	Humes, 1984	54.0	14.7	8.0
Siphonostomatoida	*Humesipontius arthuri*	Ivanenko & Ferrari, in press	<0.1	0	0
Siphonostomatoida	*Stygiopontius quadrispinosus*	Humes, 1987	33.3	22.0	44.0
		Total individuals	**26622**	**3875**	**3568**

*, mostly *Clausocalanus* sp. †, includes Families Ameiridae, Diosaccidae, Ectinosomidae, Thalestridae, and Tisbidae.

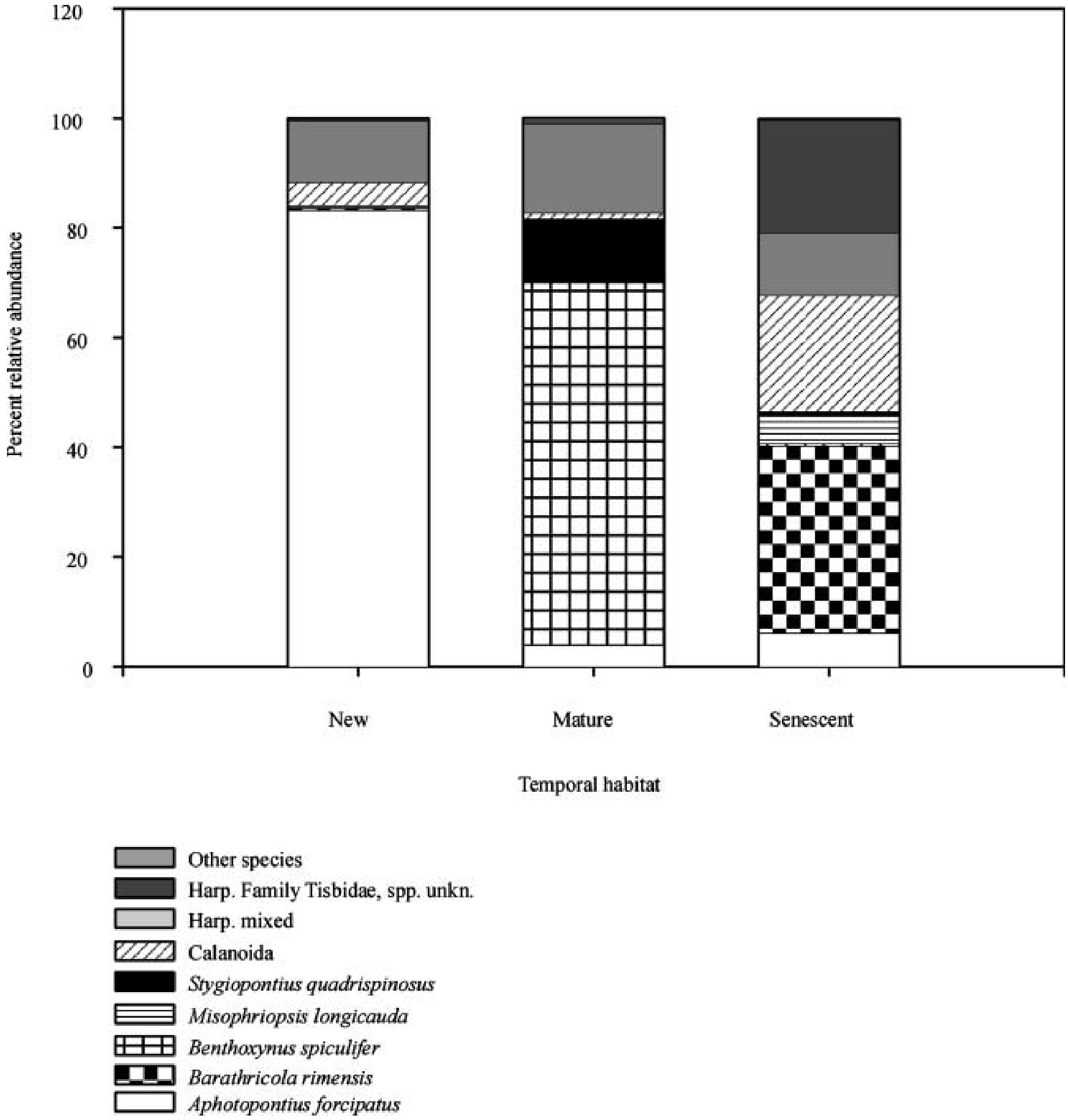

Figure 1. Juan de Fuca copepod distribution in habitats representing different stages of venting activity. 'New' are newly erupted vents sampled less than two years after inception (N=8). 'Mature' are samples from active vents older than two years (N=21). 'Senescent' are samples from inactive vents characterized visually and by no temperature or chemical anomalies (N=4).

Table 3. *Female and male* Stygiopontius quadrispinosus *lengths (mm) from Endeavour, Cleft, and Axial segments of the Juan de Fuca Ridge. Porkchop is a sulphide flange on Hell Vent.*

	Female			Male		
Site	Mean	SD	Range	Mean	SD	Range
Endeavour						
Crypto	0.711	0.047	0.531–0.811	0.599	0.043	0.468–0.695
Cleft						
Fountain	0.680	0.036	0.577–0.733	0.580	0.068	0.468–0.702
Monolith B	0.650	0.048	0.348–0.733	0.556	0.058	0.384–0.714
Axial						
Porkchop	0.772	0.034	0.650–0.900	0.650	0.048	0.600–0.730
T&S	0.731	0.046	0.608–0.855	0.594	0.083	0.513–0.703

Specimens for measurement were examined to the nearest 0.5 μm using a microscope ocular micrometer. Total length was measured along the dorsal longitudinal axis from rostrum to the last urosomal segment. Caudal rami and setae were excluded from body length measurements as many specimens lacked these structures. Size frequency histograms of male and female lengths of *Stygiopontius quadrispinosus* were plotted using 0.04-mm

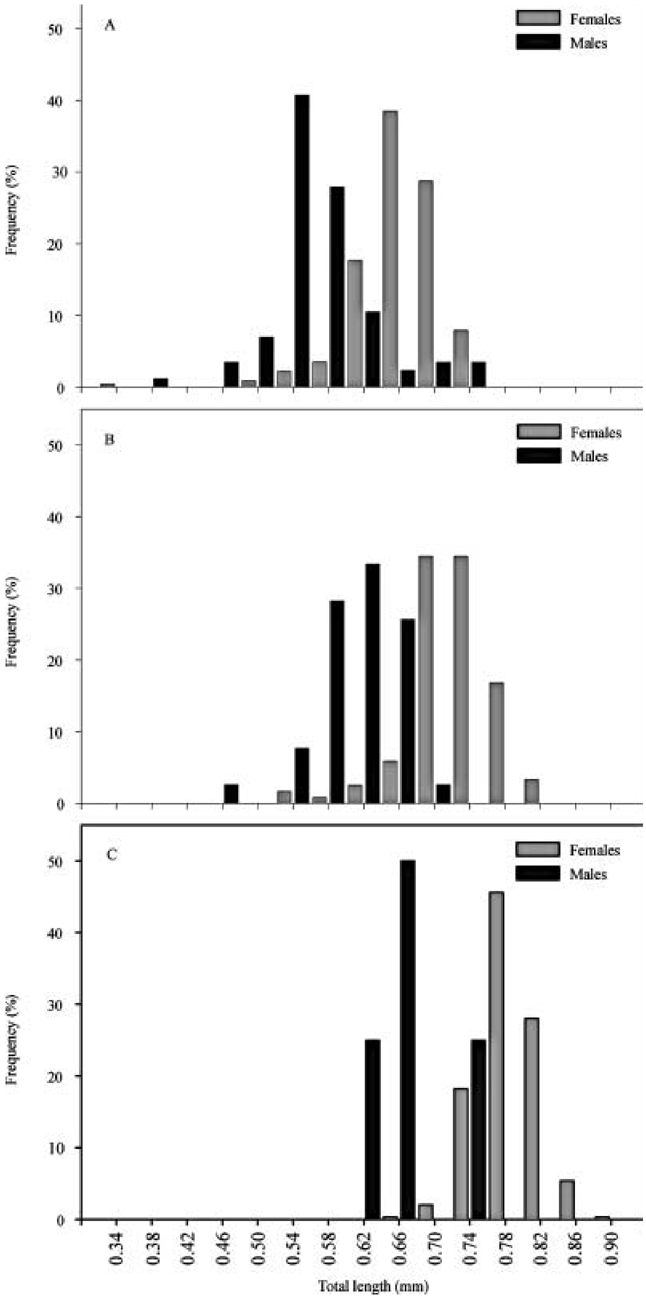

Figure 2. Size frequency distribution of males and females from selected samples. Frequency is the per cent of animals in each size range. (A) Monolith B Vent (N=313); (B) Crypto Vent (N=158); (C) Porkchop Flange, Hell Vent (N=300).

bins and probability paper analysis detected modal peaks and provided an interpretation of the mode of reproduction (Cassie, 1954; Cerrato, 1980). Cumulative binomial probabilities were calculated to examine the probabilities of finding male- or female-biased sex ratios in a population where the sex ratio is presumably 0.5.

Taxonomy

We have worked with several systematists to verify the identifications (Table 2). Most of the recently described species from Juan de Fuca vents were isolated from our collections. Examples of taxon groups were sent to specialists to ensure correct identification. Identification of the harpacticoid species by a specialist in these families is not yet completed.

Statistics

Mann–Whitney *U*-tests for non-normal data were used to compare *Stygiopontius quadrispinosus* length measurements at different vents. Principal components analysis was used to examine covariation of seven macrofaunal species and *S. quadrispinosus* among grid squares on the Crypto flange. *Paralvinella sulfincola* abundances were tested against other flange fauna using Pearson's correlation. All statistical tests were done in SAS and SPSS except for sex ratio probabilities calculated in Microsoft Excel using the binomial probability distribution.

RESULTS

Copepod fauna

Copepods in all samples appear to be free-living and belong to five orders with siphonostomes being most common (Table 2). One species of siphonostome, *Collocherides brychius*, whose type locality is on north Cleft (Humes, 1999), was not found in these samples. An additional species known from the Juan de Fuca is described from Middle Valley segment only: *Amphicrossus altalis* (Poecilostomatoida; Humes & Huys, 1992). Three taxa cannot yet be isolated to species. Calanoida are mostly *Clausocalanus lividus* (Frost & Fleminger, 1968), a non-vent species (F. Ferrari, personal communication). The 'mixed' Harpacticoida are nearly all Diosaccidae with rare occurrences of four other families: Ameridae, Ectinosomidae, Thalestridae, and Tisbidae (S. Conroy-Dalton, personal communication).

Copepod abundance is highly variable; in one sample almost 10,000 specimens occurred among 39,800 other animals. Of the three most common siphonostome species (Table 2), *Stygiopontius quadrispinosus* is the most abundant species for Endeavour and Cleft and second in abundance to *Benthoxynus spiculifer* (Humes, 1984) on Axial. Several species are very uncommon. The high abundance of mixed Harpacticoida at Cleft and Endeavour is due to one low temperature sample on each segment. Eleven samples came from 'high flow' habitats near chimney orifices where *Stygiopontius quadrispinosus* occurs at nearly 80% relative abundance; remaining individuals were mostly *Benthoxynus spiculifer*. In low flow basalt and sulphide habitats (N=31), species abundance becomes more even, *S. quadrispinosus* numbers are greatly reduced (~10%), and *B. spiculifer* is the dominant species at about 60%; harpacticoids and *Aphotopontius forcipatus* (Humes, 1987) are more common than *S. quadrispinosus*.

We encountered several different types of tubeworm bush communities with characteristics relating both to flow vigour and to apparent age from inception. Copepod dominance changes with the temporal stage of the community (Figure 1). At vents within nine months of inception on new lavas, *Aphotopontius forcipatus* is the most abundant species, with more than 80% relative abundance; other siphonostomes are nearly absent. In 'mature' tubeworm assemblages, *Benthoxynus spiculifer* becomes most abundant and the species abundances are more even than for new vents. These samples were highly variable, both in setting and in copepod fauna. There were, however, several collections that targeted vents where flow could not be seen nor temperature anomalies detected by probes; in these old and senescing assemblages, species abundances become much more even, and *B. spiculifer* and *Stygiopontius quadrispinosus* are almost nonexistent. *Aphotopontius forcipatus* increases slightly in abundance from mature assemblages, but harpacticoid and calanoid copepods are about 30% abundant; these species may not be specific to vents. The most abundant copepod species in senescent assemblages in our data set is the cyclopoid *Barathricola rimensis* (Humes, 1999) because of its high abundance in one of the samples (CoAxial 1996). This species is in low numbers in a few of the active vent samples as well.

It is difficult to derive meaningful quantitative numbers on copepod densities. For a rough estimate, we measured the surface area of the vestimentiferan worms in several collections. The tubeworm, *Ridgeia piscesae* (Jones, 1985), probably represents the major grazing/shelter surface for copepods in low temperature environments. We assumed all tubeworm surfaces were colonized. Surface areas ranged between 1200 and 30,000 cm^2. Upper density estimates are about 0.5 copepod cm^{-2}. With very close submersible video inspection, copepods can be seen crawling on vestimentiferan surfaces.

Stygiopontius quadrispinosus

The siphonostome *Stygiopontius quadrispinosus* occurs at all vent sites sampled. It is most abundant on sulphide chimneys in collections near high fluid flow. We retrieved seven samples with enough individuals for assessment of population characteristics. One structure, Monolith on Cleft segment, was sampled in three locations of increasing proximity to smokers at the top. For initial analyses, all specimens from the Crypto flange are combined.

Size distribution

The average length of females is 0.685 mm and that of males is 0.587 mm. A flange sampled on Axial (Porkchop flange at Hell Vent) has the largest females reaching a maximum of 0.900 mm; males in the Hell Vent population were larger than other samples. At all vents, females are significantly longer than males (Mann–Whitney *U*, two-tailed, $P<0.001$) (Table 3). Pairwise tests among populations at different vents show significant size differences among females (Mann–Whitney *U*, two-tailed, $P<0.001$). Hell Vent females are significantly larger than females at all other sites. The male sample size is large enough to test for differences among Monolith B, Fountain, and Crypto: males at the Crypto vent are significantly larger than males at Monolith B ($P<0.001$) and populations are from different ridge segments.

As copepods display incremental growth through exoskeleton moulting, distinct breaks in plots of total length vs cumulative frequency distributions can be detected (Cassie, 1954). Probability paper analysis of females and males from Crypto and Monolith B populations revealed a single break indicating a separation between two age classes: copepodite stage V (pre-adults) and copepodite stage VI (adults). The size of pre-adult females ranged up to 0.640 mm and males up to 0.550 mm. Pre-adults represent about 10% of all specimens. All samples examined contain very few (i.e. about 0.2% in Axial samples) to no early copepodite stages which are distinguished by size. Population size structure for *Stygiopontius quadrispinosus* on Axial, Cleft, and Endeavour is shown in Figure 2. Size frequency histograms for each sample are unimodal for each sex.

Sex ratio

The sex ratio of *Stygiopontius quadrispinosus* is strongly female-biased (Table 4). The overall female to male ratio is 7.6:1 and the probability of sampling this proportion in a species where the sexes are equally represented is almost zero. The ratio in our populations is, however, highly variable, from no males present to nearly an equal number. Table 4 compares these values to two other common dirivultids. *Aphotopontius forcipatus* is also female-skewed with a ratio of 10.6:1. However, the third dirivultid species at Juan de Fuca vents, *Benthoxynus spiculifer*, has a sex ratio of 1.5:1.

Reproduction

Four mating pairs of *Stygiopontius quadrispinosus* were located in the Monolith B collection, the males and females clasped together in preparedness for mating. Total lengths for these individuals indicated they were all copepodite stage V pre-adults. The male clasps the genital segment of the female with his geniculate antennae. Eggs are brooded. Females carry one or two large brood sacs, each containing one centrolecithal egg. Humes (1987) describes the egg sac to be $231\times154\ \mu\mathrm{m}$; our specimens have eggs ranging in length from 160 to 190 μm, and in width, from 100 to 140 μm. All collections contain oviferous females. The proportion of females in our collections bearing eggs ranged from 9.5 to 37.5%. All oviferous females and one female with an attached spermatophore were within the size range of our presumptive copepodite stage VI adult size-class.

Density

The measured specimens from Crypto vent on Endeavour segment are a subsample of fauna picked from a flange measuring 0.2 m^2 on top and bottom surfaces. Over 1000 copepods were found in 93 grid squares overlaid on the flange surfaces. It is fairly likely that some copepods were missed during processing. *Stygiopontius quadrispinosus* was the only species present. Minimum density estimates are: 1.4 individuals cm^{-2} on the top, and 1.8 individuals cm^{-2} on the bottom. The pooled fluid on the underside of the flange had temperatures in excess of 260°C. The edge demarcating this fluid was clearly visible on the flange upon collection. The highest density of copepods, 8.7 individuals cm^{-2} occurred within 4 cm of the pool where a 255°C measurement was made. Spatial distribution of males and females was similar: there was neither clumping of sexes nor of oviferous females over the flange surface.

Species associations

A principal components analysis examined the co-variation of seven macrofaunal species and *Stygiopontius quadrispinosus* among the 147 grid squares on the flange. The first two axes accounted for 76% of the variation and identified four major groupings of species. *Stygiopontius quadrispinosus* was abundant in two groupings: either with the alvinellid polychaete, *Paralvinella sulfincola* or with

Table 4. *Sex ratio of female to male* Stygiopontius quadrispinosus, Aphotopontius forcipatus *and* Benthoxynus spiculifer. P*-values are calculated using the bionomial probability distribution based on a 1:1 sex ratio.*

Sample	Females	Males	Total	Sex ratio (F/M)	p. male	*P*-value
Stygiopontius quadrispinosus						
Crypto	119	39	158	3.051	0.247	0.000
Fountain	77	16	93	4.813	0.172	0.000
Hell 1	72	0	72	72:0	0.000	0.000
Hell 2	147	4	151	36.75	0.026	0.000
Hell 3 (Porkchop flange)	296	5	301	59.20	0.017	0.000
Hillock 1	92	0	92	92:0	0.000	0.000
Hillock 2	58	0	58	58:0	0.000	0.000
T&S	270	4	274	67.50	0.015	0.000
Base of T&S	188	19	207	9.895	0.092	0.000
Monolith A	45	12	57	3.750	0.211	0.000
Monolith B	225	88	313	2.557	0.281	0.000
Monolith C	36	27	63	1.333	0.429	0.314
Total	**1625**	**214**	**1839**	**7.593**	**0.116**	**0.000**
Aphotopontius forcipatus						
Hatfield	60	13	73	4.615	0.178	0.000
Joystick	63	23	86	2.739	0.267	0.000
Marker 108	53	0	53	53:0	0.000	0.000
Marker 113 1	487	10	497	48.70	0.020	0.000
Marker 113 2	111	4	115	27.75	0.035	0.000
Nascent	113	1	134	133.0	0.007	0.000
Old Flow	47	10	57	4.700	0.175	0.000
Snail 1	35	35	70	1.000	0.500	1.100
Snail 2	88	7	95	12.57	0.074	0.000
Total	**1077**	**103**	**1180**	**10.55**	**0.087**	**0.000**
Benthoxynus spiculifer						
Bouquet 2	488	470	958	1.038	0.491	0.583
Goblin	939	513	1452	1.830	0.353	0.000
Hairdo	43	13	56	3.308	0.232	0.000
Hatfield	5829	3934	9763	1.482	0.403	0.000
Inferno 1	368	397	765	0.927	0.519	1.723
Inferno 2	451	430	881	1.049	0.488	0.500
ROPOS/ISCA	47	17	64	2.765	0.266	0.000
ISCA	48	21	69	2.286	0.304	0.002
T&S	86	123	209	0.699	0.589	1.992
Total	**8299**	**5518**	**13817**	**1.504**	**0.399**	**0.021**

Table 5. *Summary of global distribution for genera and species found on the Juan de Fuca Ridge. Information from Humes & Segonzac (1998).*

Taxon	Total number of species	North-east Pacific	East Pacific	Atlantic	West Pacific
Aphotopontius	12	Yes	Yes	Yes	No
A. forcipatus		Yes	No	Yes	No
Benthoxynus	2	Yes	Yes	No	No
B. spiculifer		Yes	No	No	No
Stygiopontius	22	Yes	Yes	Yes	Yes
S. quadrispinosus		Yes	No	No	No

this polychaete plus *P. palmiformis* (Desbruyères & Laubier, 1986), *Lepetodrilus fucensis* (McLean, 1988), and *Depressigyra globulus* (Waren & Bouchet, 1989) (the latter two are gastropods). The abundance of the vestimentiferan *Ridgeia piscesae* and this copepod were negatively correlated. Near sites of flange edge accretion and hot water egress, *S. quadrispinosus* and *P. sulfincola* co-occurred in high abundance. To test this relationship on a broad distributional scale, we also looked at total *P. sulfincola* abundances in eight samples from north Cleft; the correlation with *S. quadrispinosus* is positive ($r^2=0.556$; $P<0.021$).

Table 6. *Summary of species and habitat information for the seven vent siphonostomes on the Juan de Fuca Ridge.*

	Amphicrossus altalis^{1}	*Aphotopontius forcipatus*	*Barathricola rimensis*	*Benthoxynus spiculifer*	*Collecherides brychius*^{2}	*Misophriopsis longicauda*	*Stygiopontius quadrispinosus**
Colour	?	?	?	Red	?	?	Red
Food	?	Particulates?	Particulates?	Particulates?	Particulates?	Particulates?	Bacteria
Free-living	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Habitat							
temperature	Low?	Low	Low	Low	Low	Low	High
vent activity	?	New	Senescent	Mature	Mature?	Senescent	Mature
substratum	Sediment	Hard: basalt? Vestimentiferan tubes?	Hard	Hard: Vestimentiferan tubes?	Hard	Hard	Hard: sulphide
Recruitment	?	?	?	?	?	?	Continuous
Sex ratio (F/M)	?	10.6	2.9	1.5	?	4	7.6
Average size (mm):							
Female	2.44 (2.41–2.46)	0.77 (0.70–0.86)	0.73 (0.67–0.79)	1.68 (1.61–1.79)	0.57 (0.55–0.58)	1.86 (1.80–1.94)	0.85 (0.81–0.90)
Male	2.06 (1.98–2.13)	0.87 (0.80–0.94)	0.52 (0.47–0.57)	1.03 (0.97–1.09)	0.50 (0.50–0.51)	1.39 (1.28–1.45)	0.67 (0.63–0.72)

*, length measurements are from Humes (1987) and include caudal rami. Humes' length measurements of *Stygiopontius quadrispinosus* are used to make measurements comparable to other species in the table. Information from authorities in Table 2, this study, ^{1}, Humes & Huys (1992), and ^{2}, Humes (1999).

DISCUSSION

Global distributions of the three common Juan de Fuca genera and species of dirivultids are given in Table 5. At Juan de Fuca vents, the overall diversity of copepods, like other taxa, is low, but species are widespread. A single copepod species tends to dominate each sample although multiple species are usually present. Copepod data from other ridges are not available for comparison with our findings.

Habitat type and vent age appear to determine which copepod species are most abundant in our samples. *Aphotopontius forcipatus* is a pioneer species that is most common at vents recently created after an eruption. It is apparently replaced in older, low temperature assemblages by *Benthoxynus spiculifer*. At high temperature vent communities on sulphide chimneys, *Stygiopontius quadrispinosus* is very abundant. Humes (1990) reports over 15,000 individuals from a Gorda Ridge sample. As fluid circulation slows and venting wanes, diversity in senescing assemblages increases and many deep-sea species appear. Species composition shifts and dirivultids are replaced by harpacticoids, calanoids, and misophrioids. These assemblage groupings match those described by Jollivet (1996) for a vent site on the East Pacific Rise where differentiation of copepods among habitats was recorded.

Reasons for the taxon shifts in different habitat conditions may include differential colonization success, resource competition, and physiological tolerances to higher sulphide and temperature conditions. Epipelagic copepods are limited in their distribution by narrow physiological tolerances (Mauchline, 1998) and this may be the case with vent copepods. The blood of the dirivultid *Benthoxynus spiculifer* contains haemoglobin (Hourdez et al., 2000) and we note that *Stygiopontius* is also red. The high concentration of haemoglobin in vent copepods likely supports aerobic respiration in low-oxygen conditions (Hourdez et al., 2000; Sell, 2000).

Siphonostomes are classified as parasitic or associated (Huys & Boxshall, 1991); while some dirivultids are ectoparasites on vestimentiferans (Humes, 1999), the three abundant dirivultids on the Juan de Fuca are free-living. There may be a dependence on other species at earlier copepodite life stages; an unknown species deposits eggs inside the common Juan de Fuca vent limpet (V. Tunnicliffe, personal observation). *Stygiopontius quadrispinosus* lacks parasitic modification of mouth and body parts, and its mouth parts' design suggests that it feeds on particulate matter (Humes, 1991). Bacteria with partly lysed cell walls are found in its foregut (Dinet et al., 1988). It likely roams the sulphide surfaces near high temperature flows where autotrophic microbes grow very rapidly. *Stygiopontius quadrispinosus* is one of the few species at Juan de Fuca vents with a clear preference for the most extreme habitat near smokers.

Table 6 summarizes the information available for the seven vent siphonostomes on the Juan de Fuca. All species are considered free-living and lack specialized mouth parts that might indicate a parasitic feeding mode. Food source is unknown for all but *Stygiopontius quadrispinosus*. Other than *S. quadrispinosus*, most species appear to colonize low temperature habitat at a variety of temporal stages. All but *Amphicrossus altalis* inhabit hard substratum. Hard substratum (basalt or sulphide) is the main vent habitat on the Juan de Fuca. *Stygiopontius quadrispinosus* habitat preference is on sulphide edifices near points of hot water egress and is associated with *Paralvinella sulfincola*, a species also common to high temperate habitats. Tolerance to high temperature through respiratory adaptations may allow this species to inhabit areas unavailable to other species. Sister species of *S. quadrispinosus* elsewhere may have a similar adaptation. On the Mid-Atlantic Ridge, *S. pectinatus* associates with the shrimp *Rimicaris exoculata* (Williams & Rona, 1986) at areas of high temperature fluid flow and *S. sentifer* (Humes, 1987) on the East Pacific Rise is associated with the polychaete *Alvinella pompejana* (Desbruyères & Laubier, 1980) on high temperature chimneys (Humes, 1987). *Alvinella pompejana* is an ecological analogue to *P. sulfincola*. *Stygiopontius quadrispinosus* may form part of the diet of *P. sulfincola*, a deposit feeder on surfaces around and on its tube.

Adult sizes among *Stygiopontius quadrispinosus* populations varied by up to 15%. These differences may be a response to environmental conditions, population genetic characteristics, or differential recruitment success of cohorts. The fact that females collected only 2 m apart on Monolith are significantly different in length suggests that this variation may be a population's response to immediate environmental conditions, rather than characteristic of a population's genotype. Food availability affects the size of some epipelagic copepods (Ashjian & Wishner, 1993). Thermochemical properties of the vent fluid could also influence growth rate by affecting the allocation of energy to maintenance of exoskeleton over growth.

The normal curve of size distribution of *Stygiopontius quadrispinosus* suggests that their reproduction is likely continuous or semi-continuous. A predominance of females (as seen in female-skewed sex ratios for *S. quadrispinosus*) suggests continuous reproduction (Mauchline, 1972). The variable presence of oviferous females in all collections is consistent with reproduction that is not, for the most part, synchronous. The small number of eggs carried by siphonostomes means that fertilized eggs are presumably extruded often to produce the large numbers of adults seen at vents (Humes, 1987). Juveniles are rare in all samples and absent in the samples used to measure *Stygiopontius* length. The smallest copepod sampled was 0.350 mm which is consistent with Humes' (1991) record of vent collections with mostly adults and occasional late stage copepodites and is consistent with our presumptive copepodite stage V pre-adult class. He suggests that dispersal is early in the life cycle, perhaps as nauplii or early copepodites. Ivanenko (1998) reports copepodite stages I–V of three species of dirivultids in the plankton over a vent and concludes that the development of subadult stages of these dirivultids occurs in the plankton. This plankton also contained subadult calanoids, planktonic poecilostomatids, and some adult dirivultids. The same may be true for *S. quadrispinosus*. Subadult stages and postlarval dispersal of vent shrimp on the Mid-Atlantic Ridge occurs in the plume (Herring & Dixon, 1998). In contrast, Dinet et al. (1988) find large numbers of nauplii in the top two centimetres of Guaymas Basin hydrothermal sediments where nauplii are 18–48% of the copepod fraction. Although nauplii are not identified to order, almost all of the adult copepods in their samples are harpacticoids.

Female-biased sex ratios are common among deep-sea copepods (Mednikov, 1961; Mauchline, 1972; Wishner, 1980). Many *Stygiopontius* species descriptions are based solely on female specimens because no males were found (Humes, 1987, 1989, 1990). In over 7000 specimens of *S. pectinatus* (Humes, 1987), only females are known (Humes, 1996). Explanations for the observed female bias include: (1) sex ratio is 1:1, but males and females are in different locations and males are under sampled; (2) sex ratios are equal at birth, but the mortality rates differ; and (3) habitat conditions induce preferential formation or survival of females. While the first is possible, it is unlikely; a wide range of samples does not produce large numbers of the 'missing' males. In two samples, males outnumber females. Both samples are from high temperature habitats and nothing distinguishes these collections from other samples. Secondly, the presence of two samples with male-biased sex ratios means that we cannot exclude differential mortality rates. Males may die shortly after mating and females may be able to fertilize multiple clutches from one mating event. Finally, several environmental factors such as temperature, pressure, salinity, food supply, predation, chemical agents, and population density can affect copepod sex ratio (Vacquier, 1961; Hicks & Coull, 1983). Temperature effects on sex ratio are known in an intertidal harpacticoid (M. Voordouw, personal communication) and *S. quadrispinosus* on smokers may be similarly affected. However, *Aphotopontius forcipatus*, is female-biased in low temperature habitats that are eventually colonized by *Benthoxynus spiculifer* which has no sex-ratio bias.

Further work at more sites on the Juan de Fuca, especially the sedimented segment, could expand our knowledge of Juan de Fuca copepod habitat preferences. Comparable distributional and diversity data on copepods from other ridge systems are needed. Another future focus will be to determine the locations for naupliar and copepodite development by examining the hyperbenthos and plankton in the vent plumes.

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