



# Utilization of nutritional resources and energy budgets for populations of the hydrothermal vent polychaete *Paralvinella sulfincola* on Axial Volcano, Juan de Fuca Ridge (Northeast Pacific)

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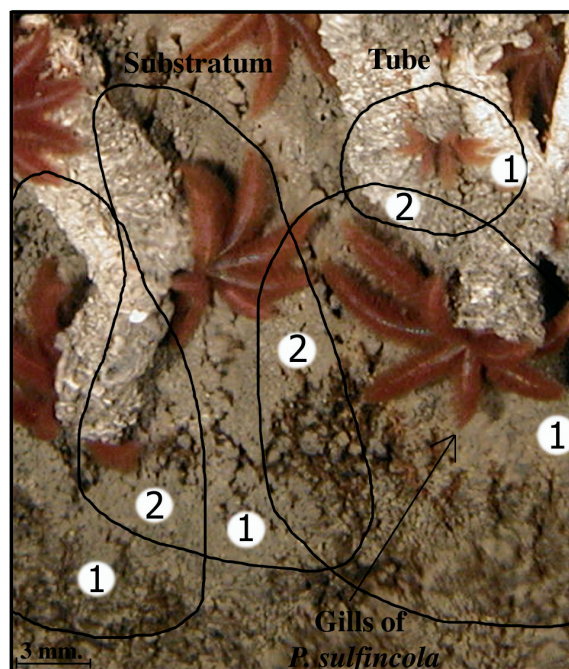
## Introduction

The nutritional resources available to deposit and suspension feeding animals at deep-sea hydrothermal vents have been little studied or systematically quantified (Juniper, 1994), despite the fact that grazing and detritivorous species can constitute the major portion of the biomass and organism abundance at vent sites (Sarrazin et al., 1999). Most of the particulate organic matter ingested by these vent organisms is presumed to be of autochthonous origin, produced by chemoautotrophic microorganisms (Karl, 1995). Consumer organisms may directly graze on microbial mats and biofilms, or ingest accumulated detritus within vent faunal assemblages.

Quantitative confirmation of the capacity of vent chemosynthesis to support non-symbiotic animal consumers requires comparison of the availability and production of particulate organic matter with the requirements of consumer populations. This is a challenging task in a milieu where faunal communities and particulate food resources are spatially heterogeneous at decimeter scales (Sarrazin et al., 1997), and where all sampling and manipulation must be performed by submersible. In this study, we examined food resources and consumer requirements in a mono-specific macrofaunal community where consumer biomass, feeding area, and food concentration could be constrained by a combination of biological sampling and image analysis.

*Paralvinella sulfincola* Desbruyères & Laubier, 1993, is one of the first metazoans to colonize newly formed mineral substrata on hydrothermal vent sulphide edifices of the Juan de Fuca Ridge (Northeast Pacific) (Juniper, 1994). Its populations are often found on surfaces exposed to intense hydrothermal fluid flow and frequently form a front between tolerable physicochemical conditions and bare surfaces where conditions are too severe for colonization (Sarrazin et al., 1997). This polychaete is a deposit feeder, ingesting

particles on mineral surfaces near its tube entrance (Juniper, 1994; Grelon, 2001). Territorial behaviour in *P. sulfincola*, documented by Grelon (2001), limits individual feeding areas to a definable zone around the tube entrance (Fig. 1). Within the area exploited by *P. sulfincola*, bacterial cells and non-living detritus are the most plausible major sources of organic matter (Juniper, 1994). We present here preliminary quantitative data on organic carbon and nitrogen in the



**Figure 1.** Limits of the *Paralvinella sulfincola* feeding area at High Rise site (Endeavour Segment, Juan de Fuca Ridge): (1) Area occupied by one worm; (2) Area occupied by two worms.

worm's feeding area, and a first order estimation of organic matter ingestion through analyses of rates of particle capture and particle size. We compare available nutritional resources in the feeding area to the rate of particle capture by the polychaete, and then construct a preliminary model of carbon consumption and requirements for an average-sized *P. sulfincola* adult in the ASHES vent field (Axial volcano, Juan de Fuca Ridge).

## Material and methods

### Sampling

Biological samples and video imagery were collected from the ASHES and CASM hydrothermal fields, located in the crater of Axial Volcano, on the Juan de Fuca Ridge. Samples were collected during four NeMO (New Millennium Observatory) cruises between 1998 and 2001 using the remotely operated vehicle ROPOS. Images were acquired with the submersible's onboard 3-CCD camera. Polychaetes, tubes and associated substrata were collected with the ROPOS suction sampler tool and from a piece of sulphide brought to the surface in the ROPOS "biobox". Freshly sampled material was frozen at  $-80^{\circ}\text{C}$  on the ship. Images were recorded on S-VHS and digital (Mini-DV) tapes. Still video frames for analyses of feeding area were digitized from analogue recordings using a computer equipped with a video capture card, or imported directly into analysis software from digital video.

### Food availability

Available food resources were determined from analysis of total organic carbon and nitrogen in worm tubes and samples of substratum from the worms' feeding area. Mean "activity area" was determined by Grelon (2001) from video recordings of worm movements for these same *P. sulfincola* populations. The activity area is comprised of both substratum and tube surfaces. Depending on the density of *P. sulfincola*, part or all of the tube (Fig. 1) is included in each worm's activity area. For the purpose of this study, we assumed that the tube, secreted by the worm, did not serve as a food resource. Individual feeding area was thus calculated to represent the total activity area minus the area occupied by one tube, calculated using equations of Grelon (2001). Twenty-one tubes, five samples of substratum and three polychaetes were analysed, in duplicate, for carbon and nitrogen. Total carbon and nitrogen analyses were performed on a CE Instruments CN 2500 analyser. For the substratum, specific gravity was determined by weighing the mass of substratum displacing  $1\text{ cm}^3$  of water. All dry weights were determined after freeze-drying for 48 hours.

### Particle capture

The size of particles consumed by the polychaete was estimated from close-up video sequences of individual worms capturing (and presumably later ingesting) particles. Scale was determined by comparing particle diameter in digitized images to the length of extended gill filaments, which are directly proportional to the polychaete's wet weight. The wet weight of the average sized adult worm, 110 mg, was determined from data from the three *P. sulfincola* populations sampled by Grelon (2001). Grelon's (2001) allometric relationship between gill

filament length and wet weight was used to scale gill filaments and estimate particle diameter.

Both energetic requirements and resource availability were determined for an average sized adult worm using data from *P. sulfincola* populations sampled by Grelon (2001).

### Energetic requirements

To construct a preliminary model of carbon consumption and requirements for an average polychaete, energetic (organic carbon) requirements were determined using the following equation (Odum, 1971):

$$(1) \text{ Total energy required (mgC polychaete}^{-1} \text{ day}^{-1}) = R + G + \text{Tb} + \text{Repr}$$

where : R = energy required for respiration

G = energy required for growth

Tb = energy required for tube building (annual replacement of tube)

Repr = energy required for reproduction (not determined)

The energetic requirements for respiration were calculated from the allometric relationship (equation 2 below) between body size and respiration determined experimentally at  $15^{\circ}\text{C}$  by Nielsen et al. (1995) for *Nereis virens* (Sars). Respiration rates of several hydrothermal-vent species have been found to be reported to be similar to those of active shallow water species of the same class (Childress & Mickel, 1985) :

$$(2) R_m = 704W^{1.0}$$

where : M = metabolic rate ( $\mu\text{l O}_2\text{ h}^{-1}$ )

W = body dry weight (g)

Metabolic rate was then converted to carbon requirements using a factor of  $1\ \mu\text{l O}_2 = 0.482\ \mu\text{g C}$ , determined by Cammen (1980) for *Nereis succinea* (Frey & Leuckart).

Energy requirements for growth were derived from analysis of the population structure of three *P. sulfincola* populations in the ASHES vent field in Grelon (2001). Differences in mean body wet weight between the two largest sized cohorts in each of the two populations were assumed to represent annual net growth increments. The largest-sized cohort was not statistically definable in the third population, likely due to the smaller sample size (Grelon, 2001). Wet weight growth increments were converted to organic carbon based on total carbon content of dried worm tissues ( $n=3$ ) and an empirically determined wet weight/dry weight relationship for *P. sulfincola* (Grelon, 2001).

Organic carbon contained in sampled tubes from these same populations was used to estimate energy requirements for tube building, assuming that individual worms secreted a new tube annually. Observations (Grelon, 2001) indicate that the worms can abandon their tubes, migrate and build new tubes more frequently than once per year, but we chose a more conservative estimate of one tube per year.

## Results and Discussion

### Organic matter analysis (Table 1)

The tube, composed of mucus and secreted by the worm (Juniper, 1994), had a much higher carbon content (2.16%) than the sampled mineral substratum (0.12%) (Table 1). Both C/N ratios are close to the theoretical ratio of microbial cells of 4.0; although the mucopolysaccharides that form the tube can also be rich in nitrogen and give C/N values in the 4 to 5 range (Juniper, 1994).

**Table 1.** Percentage of carbon and carbon/nitrogen ratio in tubes and substratum samples for an average-sized adult *P. sulfincola* in the ASHES vent field (Axial Volcano, Juan de Fuca Ridge) (mean  $\pm$  standard deviation).

	Number of samples	%C	C/N
Tubes	21	2.16 $\pm$ 1.04	4.17 $\pm$ 0.20
Substratum	5	0.12 $\pm$ 0.02	3.43 $\pm$ 0.20
<i>P. sulfincola</i> tissues	3	37.36 $\pm$ 1.80	4.54 $\pm$ 0.10

#### Food availability (Table 2)

Grelon (2001) determined that *P. sulfincola* aggressively defends an activity area around its tube entrance, on the order of 488.7 mm<sup>2</sup> (Fig. 1), of which 377.0 mm<sup>2</sup> consists of substratum not covered by the worm's tube (i.e. the worm's feeding area). The thickness of the surface layer of substratum accessible to *P. sulfincola* is not known. Juniper (1994) observed that *P. sulfincola* affected sulfide chimney surface mineralogy down to at least 2 mm depth. This latter thickness was chosen for the purpose of our calculations of the total volume of the feeding area. Based on our analysis of substratum carbon content and specific gravity (1.52), the food resources available in their feeding area would be 1.37 mgC per polychaete. This is equivalent to 1.2 mgC g<sup>-1</sup> of substratum, within the range found by Smith (1989) for deep-sea sediment (0.9 to 6.8 mgC g<sup>-1</sup>).

**Table 2.** Energy requirements and resources for an average-sized adult *P. sulfincola* in the ASHES vent field (Axial Volcano, Juan de Fuca Ridge) (Value expressed in mgC polychaete<sup>-1</sup> day<sup>-1</sup> apart for food availability in mgC polychaete area<sup>-1</sup>).

Requirements		Resources	
Respiration (mgC polychaete <sup>-1</sup> d <sup>-1</sup> )	1.48 x 10 <sup>-1</sup>	Particle ingestion (mgC polychaete <sup>-1</sup> d <sup>-1</sup> )	8.79 x 10 <sup>-2</sup>
Growth (mgC polychaete <sup>-1</sup> d <sup>-1</sup> )	2.79 x 10 <sup>-2</sup>	Food availability in feeding area (mgC polychaete area <sup>-1</sup> )	1.37
Tube construction (mgC polychaete <sup>-1</sup> d <sup>-1</sup> )	1.14 x 10 <sup>-2</sup>		
<b>Total</b>	<b>1.87 x 10<sup>-1</sup></b>		

#### Particle capture

In our video observations, worms were seen capturing particles with their oral tentacles. We documented the capture of four particles by three individual worms. Subsequent calculations are based on the assumption that all of this collected material was later ingested by the worm.

Particle diameter was approximately 0.3 times the length of the gill filaments, yielding an average diameter of 0.80 mm (equation 1) and a volume of 0.27 mm<sup>3</sup>. Smaller particles not visible in video imagery may also have been captured by the observed polychaetes.

Behaviour observations revealed that, on average, *P. sulfincola* left their tubes to explore the substratum 2.5 times during 10 minutes of observation (Grelon, 2001). Not every exploration resulted in the capture of a particle, and during some outings, polychaetes captured more than one particle. To simplify calculations, we first assumed that individual *P. sulfincola* captured 0.5 particles per exploration, equivalent to 1.25 particles per 10 minute

period or 180 particles per day per worm. At this rate, the average worm would turn over all particulate matter in its feeding area every 15.51 days. Since feeding areas of neighbouring polychaetes overlap by a mean of nearly 50% (Grelon, 2001), this turnover time should be considered as a maximum value.

This rate of ingestion is comparable to other deposit feeding invertebrates. At 180 particles d<sup>-1</sup>, *P. sulfincola* captures 73.2 mg of substratum daily, equivalent to 0.66 times their average individual wet weight, per day. This is somewhat lower than the typical rate of sediment ingestion by other studied deposit feeders (1x the wet weight daily) reviewed by Lopez & Levinton (1987). Based on the analysed carbon content of the two potential food resources, this rate of particle capture would provide the worms with 8.79 x 10<sup>-2</sup> mgC polychaete<sup>-1</sup> d<sup>-1</sup>.

#### Energetic requirements (Table 2)

Using the Nielsen et al. (1995) equation (2) and a mean individual wet weight of 110 mg (Grelon 2001), respiration by *P. sulfincola* would require the metabolism of 1.48 x 10<sup>-1</sup> mgC polychaete<sup>-1</sup> d<sup>-1</sup>. Similar results (not shown) are obtained using the general allometric equation of Lavigne (1982) relating basal metabolic rate to body size in poikilotherms. Respiration represents the major portion of the energetic requirement of most animal species, including *P. sulfincola* (Table 2).

Net growth for the study populations was calculated to be 4.5 x 10<sup>-1</sup> mg wet weight d<sup>-1</sup> per individual, equivalent to 2.79 x 10<sup>-2</sup> mgC polychaete<sup>-1</sup> d<sup>-1</sup> at 37.36% C in *P. sulfincola* tissues (Table 1). This is equivalent to an individual growth increment of 0.41% wet body weight per day, comparable to the range of 0.4 to 5.6% daily body weight increments determined experimentally for the polychaete *Nereis virens* by Nielsen et al. (1995).

Tube dry weight was 193 mg, with a mean carbon content of 2.16%, giving 4.17 mgC per tube. Building a new tube every year would thus require that the worm secrete 1.14 x 10<sup>-2</sup> mgC d<sup>-1</sup> in the form of tube binding mucous.

#### Energy budget

In our energy budget calculations, carbon assimilated was assumed to be equivalent to the carbon contained in the captured particles. But between particle capture and carbon assimilation, there are two major unknowns: selectivity prior to ingestion and assimilation efficiency for ingested material. Examined *P. sulfincola* guts contained filamentous bacteria, mucus, sulphide grains and diatoms debris (Juniper, 1994), suggesting little selectivity. However, we have observed some particle reworking following the worm's return to the tube entrance and prior to particle disappearance (= ingestion). We thus cannot exclude the possibility of particle sorting before ingestion. Assimilation efficiency is generally quite high for deposit feeders, ranging from 40 to almost 100% of ingested organic matter (reviewed in Cammen, 1980). As the C/N ratio of the particulate material feeding area of the *P. sulfincola* population is close to the theoretical value of microbial cells and to the value for *P. sulfincola* tissues (4.4) (Table 1), it is reasonable to assume a high assimilation efficiency in this case. We used the average assimilation efficiency of 57% estimated for heterotrophic microbes ingested by detritivores and deposit feeders (Cammen, 1980). At this

efficiency, only 26.7% of the total carbon requirement would be met by particle ingestion. Even at 100% assimilation efficiency, only 47.0% of the worm's total carbon requirement would be met. This difference may be due to the fact that the substratum samples analysed in the laboratory did not correspond to the real food resources available to *P. sulfincola* in its habitat, or to the existence of an unidentified food source, such as the surface of their own tubes, or to an overestimation of energy requirements. Since both growth and respiration requirements calculated for *P. sulfincola* are comparable to values determined experimentally for nereid polychaetes, we limit discussion to the possibility that available food resources were underestimated. We observed two cases of *P. sulfincola* capturing particles on their own or neighbouring tubes. This source of food may be important, especially at sites with a very high density of *P. sulfincola*, where much of the substratum is covered by tubes and tube aggregates (Grelon, 2001; pers. obs.). Moreover, the higher percentage of carbon in tube samples (2.16%) compared with the substratum (0.12%) (Table 1) and the fact that the external surface of *P. sulfincola* tubes has been shown to be heavily colonized by filamentous bacteria (Juniper, 1994), lead to the suggestion that this microbial growth may be the target of the worm's exploration and particle capture activities on tube surfaces.

We may have also underestimated the carbon content of the substratum. The sampled piece of sulphide chimney was manipulated by the submersible and subjected to jarring and vibrations prior to sampling for organic matter analysis. Adhering surface biofilms and microbial mats, a likely target of grazing by *P. sulfincola* may have been lost prior to analysis. Moreover, C. Levesque (pers. com.) found that the carbon content of the substratum for similar *P. sulfincola* habitats was 4 to 5x higher than reported here.

#### Productivity of the sites (Table 3).

Respiration and secondary production, represented by the energy budget of *P. sulfincola* (Table 2), must be supported by primary production. We used our data to consider the productivity of microbial food resources on the substratum required to at least balance carbon consumed by *P. sulfincola* populations. Carbon ingestion by *P. sulfincola* in its feeding area would have to be supported by a local primary productivity of 144.8 to 232.9 mgC m<sup>-2</sup> d<sup>-1</sup> (at 57% and 100% assimilation efficiency, respectively). Primary productivity required to support the worm's energy requirements is even higher, representing 496.8 mgC m<sup>-2</sup> d<sup>-1</sup>. These estimate overlap the upper range of primary productivity measured for photosynthetic microorganisms that colonize substrata surfaces in other marine habitats, such as epibenthic microalgae or sea ice algae (Table 3). This

**Table 3.** Estimated chemosynthetic primary productivity rate in *P. sulfincola* habitat compared to photosynthetic algal biofilms in other marine habitat (Values expressed in mgC m<sup>-2</sup> day<sup>-1</sup>).

Site characteristics	Reference	Primary production (mgC m <sup>-2</sup> d <sup>-1</sup> )
<i>P. sulfincola</i> habitat	This study	> 144.8 - 496.8
Ice algal production	Vézina et al., 1997	38.4
Microbenthic algae in estuaries	Roux et al., 2002	80.0 - 243.0

requirement for high primary productivity is not surprising, given the high biomass of the vent fauna, compared to other marine ecosystems (Sarrazin & Juniper, 1999).

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