1 Biodiversity and trophic ecology of hydrothermal vent fauna associated with

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# tubeworm assemblages on the Juan de Fuca Ridge

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### 25 Abstract

26 Hydrothermal vent sites along the Juan de Fuca Ridge in the north-east Pacific host dense 27 populations of *Ridgeia piscesae* tubeworms that promote habitat heterogeneity and local 28 diversity. A detailed description of the biodiversity and community structure is needed to 29 help understand the ecological processes that underlie the distribution and dynamics of 30 deep-sea vent communities. Here, we assessed the composition, abundance, diversity and 31 trophic structure of six tubeworm samples, corresponding to different successional stages, 32 collected on the Grotto hydrothermal edifice (Main Endeavour Field, Juan de Fuca Ridge) at 33 2196 m depth. Including R. piscesae, a total of 36 macrofaunal taxa were identified to the 34 species level. Although polychaetes made up the most diverse taxon, faunal densities were 35 dominated by gastropods. Most tubeworm aggregations were numerically dominated by the 36 gastropods Lepetodrilus fucensis and Depressigyra globulus and polychaete Amphisamytha 37 carldarei. The highest diversities were found in tubeworm aggregations characterized by the 38 longest tubes (18.5 ± 3.3 cm). The high biomass of grazers and high resource partitioning at 39 small scale illustrates the importance of the diversity of free-living microbial communities in 40 the maintenance of the food webs. Although symbiont-bearing invertebrates R. piscesae 41 represented a large part of the total biomass, the low number of specialized predators on 42 this potential food source suggests that its primary role lies in community structuring. Vent 43 food webs did not appear to be organized through predator-prey relationships. For example, 44 although trophic structure complexity increased with ecological successional stages, showing 45 a higher number of predators in the last stages, the food web structure itself did not change 46 across assemblages. We suggest that environmental gradients provided by the biogenic structure of tubeworm bushes generate a multitude of ecological niches and contribute to 47 48 the partitioning of nutritional resources, releasing communities from competition pressure 49 for resources, thus allowing species co-existence.

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51 Keywords: Juan de Fuca Ridge; hydrothermal vents; Ridgeia piscesae; community structure;
52 diversity; stable isotopes; food webs; successional stages

# 53 **1. Introduction**

54 Deep-sea hydrothermal vents occur along mid-ocean ridges and back-arc spreading centres, 55 which are characterized by strong volcanic and tectonic activity. The resulting hydrothermal 56 fluid fosters dense communities of highly specialized fauna that colonize the steep physical 57 and chemical gradients created by the mixing of hot vent fluids with cold seawater. These 58 communities are distributed according to species' physiological tolerance (Childress and 59 Fisher, 1992; Luther et al., 2001), resource availability (De Busserolles et al., 2009; Levesque 60 et al., 2003) and biotic interactions (Lenihan et al., 2008; Micheli et al., 2002; Mullineaux et 61 al., 2000, 2003). Although the fauna are highly dissimilar between oceanic basins (Bachraty 62 et al., 2009; Moalic et al., 2011), hydrothermal communities throughout the world share 63 some ecological similarities including a food web based on chemosynthesis (Childress and 64 Fisher, 1992), low species diversity compared with adjacent deep-sea and coastal benthic 65 communities (Van Dover and Trask, 2000; Tunnicliffe, 1991), high levels of endemism 66 (Ramirez-Llodra et al., 2007), and elevated biomass associated with the presence of large 67 invertebrate species.

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69 The high spatial heterogeneity of environmental conditions in vent ecosystems is amplified 70 by stochastic and periodic temporal variation in hydrothermal activity, influencing the 71 composition (Sarrazin et al., 1999), structure (Marcus et al., 2009; Sarrazin et al., 1997; 72 Tsurumi and Tunnicliffe, 2001) and dynamics (Lelièvre et al., 2017; Nedoncelle et al., 2013, 73 2015; Sarrazin et al., 2014) of faunal communities. In addition, the complexity of vent 74 habitats is increased by engineer species, whose presence strongly contributes to the 75 modification of the physical (temperature, hydrodynamics processes) and chemical 76 (hydrogen sulfide, methane, oxygen, metals and other reduced chemicals) properties of the 77 environment either by creating three-dimensional biogenic structures (autogenic species) or 78 through their biological activity (allogeneic species) (Jones et al., 1994, 1997). Habitat 79 provisioning and modification by engineer species increases the number of potential 80 ecological niches and, consequently, influences species distribution and contributes to an 81 increase in local diversity (Dreyer et al., 2005; Govenar and Fisher, 2007; Urcuyo et al., 82 2003). Engineer species promote local diversity through various ecological mechanisms 83 (Bergquist et al., 2003), providing secondary substratum for colonization, a refuge from predation and unfavourable abiotic conditions and important food sources that enhance the
development of macro- and meiofaunal communities (Dreyer et al., 2005; Galkin and
Goroslavskaya, 2010; Gollner et al., 2006; Govenar et al., 2005, 2002; Govenar and Fisher,
2007; Turnipseed et al., 2003; Zekely et al., 2006).

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89 Hydrothermal vent food webs are mainly based on local microbial chemosynthesis (Childress 90 and Fisher, 1992), performed by free-living or/and symbiotic chemoautotrophic 91 microorganisms that utilize the chemical energy released by the oxidation of reduced 92 chemicals species (H<sub>2</sub>, H<sub>2</sub>S, CH<sub>4</sub>) present in the hydrothermal fluids (Childress and Fisher, 93 1992). Several electron donors (e.g. H<sub>2</sub>, H<sub>2</sub>S, CH<sub>4</sub>, NH<sub>4</sub><sup>+</sup>) and electron acceptors (e.g. O<sub>2</sub>, NO<sub>3</sub><sup>-</sup>, SO<sub>4</sub><sup>2-</sup>) can be used by these microorganisms as energy sources, converting inorganic carbon 94 95 (e.g. CO<sub>2</sub>) into simple carbohydrates (Fisher et al., 2007). Chemosynthetic primary 96 production is exported to the upper trophic levels through direct ingestion (primary 97 consumers), or through the presence of intra- or extracellular symbiosis. Upper trophic 98 levels (secondary consumers) are represented by local predators and scavengers feeding on 99 primary consumers and by abyssal species attracted by the profusion of food. Stable 100 isotopes analysis is an important and efficient tool in studying trophic ecology and offers 101 many advantages over traditional methods (behavioural observations, stomach content 102 analyses), providing time-integrated overview of animal's diet over a long timescale. 103 Nevertheless, the physiology of marine invertebrates is poorly documented, resulting to a 104 lack of precision on the turnover rate of organism's tissues and therefore, the rate at which a 105 consumer integrates the isotopic signal, leading to an uncertainty about trophic-step 106 fractionation (isotopic enrichment between preys and predators). Moreover, although 107 trophic inferences using stable isotopes require the characterization of basal sources, this 108 remains difficult in the hydrothermal environment due to sampling technological constraint. 109 Despite this, the emergence of isotopic methods has opened new perspectives in the 110 understanding of food-web functioning and the organization of species diversity within 111 these ecosystems around the globe (Bergquist et al., 2007; De Busserolles et al., 2009; Van 112 Dover, 2002; Erickson et al., 2009; Gaudron et al., 2012; Levesque et al., 2006; Levin et al., 113 2009; Limén et al., 2007; Portail et al., 2016; Soto, 2009; Sweetman et al., 2013). The carbon isotope composition ( $\delta^{13}$ C) is an indicator of the food assimilated and remains relatively 114 115 constant during trophic transfers (±1‰). The kinetics of enzymes involved in the

biosynthetic pathways of autotrophic organisms influence the carbon isotope ratio  $({}^{13}C/{}^{12}C)$ , 116 117 allowing the discrimination between the sources fuelling the community (Conway et al., 1994; Van Dover and Fry, 1989). Nitrogen isotope composition ( $\delta^{15}N$ ) provides information 118 119 on trophic levels and becomes enriched in heavy isotopes at an average rate of ± 3.4‰ at each trophic level (Michener and Lajtha, 2008). At the community scale,  $\delta^{13}$ C and  $\delta^{15}$ N 120 121 signatures of all species in the ecosystem are used to retrace carbon and nitrogen fluxes 122 along the trophic chain and, therefore, to reconstitute the food web (Levin and Michener, 123 2002). Despite the relatively low diversity of vent communities, ample evidence suggests 124 that hydrothermal food-web structure is complex (Bergquist et al., 2007; Portail et al., 2016) 125 including many trophic guilds (Bergquist et al., 2007; De Busserolles et al., 2009) and 126 multiple sources of primary production (Van Dover and Fry, 1994). The carbon signature  $(\delta^{13}C)$  of primary producers differs according to their carbon fixation pathways that 127 128 differentially fractionate inorganic carbon sources. Despite the fact that the nitrogen signature ( $\delta^{15}$ N) do not discriminate primary producers, the variability of  $\delta^{15}$ N signatures can 129 130 be associated to their origins and also, to local biogeochemical processes (Bourbonnais et 131 al., 2012; Portail et al., 2016). Moreover, due to its degradation in the water column, photosynthesis-derived organic matter is characterized by high  $\delta^{15}N$  values in comparison 132 133 with local vent microbial producers, which are associated with low or negative values 134 characteristic of local inorganic nitrogen sources (Conway et al., 1994).

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136 Active hydrothermal vents on the Juan de Fuca Ridge (north-east Pacific) are colonized by 137 populations of the siboglinid polychaete *Ridgeia piscesae* forming dense faunal assemblages 138 in areas of high to low fluid flux activity (Southward et al., 1995). Diverse heterotrophic faunal species inhabit these tubeworm bushes, with a dominance of polychaete and 139 140 gastropod species (Bergquist et al., 2007; Govenar et al., 2002; Marcus et al., 2009; Tsurumi 141 and Tunnicliffe, 2001, 2003). To date, few studies have described the communities 142 associated with the R. piscesae tubeworm assemblages of the Main Endeavour vent field, 143 either in terms of diversity (Bergquist et al., 2007; Sarrazin et al., 1997) or trophic ecology 144 (Bergquist et al., 2007). Six distinct faunal assemblages exhibiting patchy distributions have 145 been identified on the Smoke & Mirrors hydrothermal edifice, and appear to represent 146 different successional stages (Sarrazin et al., 1997). Since 2011, a camera installed on the 147 Ocean Networks Canada cabled observatory has been recording high-resolution imagery of a

148 R. piscesae tubeworm assemblage and its associated fauna on the active Grotto 149 hydrothermal edifice (Main Endeavour, Juan de Fuca Ridge). The processing of this data 150 provided new insights on the influence of astronomic and atmospheric forcing on vent 151 faunal dynamics (Cuvelier et al., 2014; Lelièvre et al., 2017), but thorough knowledge of the 152 faunal communities observed by the camera is still needed to understand and interpret the 153 temporal patterns and their underlying mechanisms. However, although video imagery is 154 useful for investigating the spatial distribution of communities (Cuvelier et al., 2011; Sarrazin 155 et al., 1997), species behaviour (Grelon et al., 2006; Matabos et al., 2015) and temporal 156 dynamics of a sub-set of species (Cuvelier et al., 2014; Lelièvre et al., 2017), direct sampling 157 is an essential and complementary approach for determining overall faunal composition, 158 abundance and species diversity and assess functioning (Cuvelier et al., 2012). In this 159 context, the objectives of the present study were: (i) to identify the composition and 160 structure of three faunal assemblages associated with *R. piscesae* tubeworm bushes on the 161 Grotto hydrothermal edifice, specifically with respect to density, biomass and species 162 diversity; (ii) to characterize the trophic structure of these biological communities and (iii) to 163 assess how diversity and trophic relationships vary over different successional stages.

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# 165 **2. Materials and Methods**

#### 166 **2.1. Geological setting**

167 The Juan de Fuca Ridge (JdFR) (Fig. 1a) is an intermediate spreading-rate ridge between the 168 Pacific and Juan de Fuca plates in the north-east Pacific Ocean. The Endeavour Segment 169 (47°57'N, 129°06'W) (Fig. 1b) constitutes a ~ 90 km long section of the JdFR, bounded to the 170 north by the Middle Valley and to the south by the Cobb Segment. It is characterized by a 171 500–1000 m wide axial valley whose walls reach up to 200 m in height (Delaney et al., 1992). 172 The five major vent fields – Sasquatch, Salty Dawg, High Rise, Main Endeavour Field (MEF) 173 and Mothra – found along the Endeavour axial valley are spaced regularly, about 2–3 km 174 apart.

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The MEF (Fig. 1c) is the most active of the five hydrothermal fields, with the presence of high-temperature (370-390°C), actively venting sulfide edifices and diffuse low-temperature (10-25°C) venting areas (Delaney et al., 1992; Kelley et al., 2012). This vent field is the

179 world's first hydrothermal marine protected area (Devey et al., 2007; Tunnicliffe and 180 Thomson, 1999) and was selected as a target site for the deep-sea cabled observatory Ocean 181 Networks Canada, providing unprecedented opportunities to better understand vent 182 ecology. Within the MEF, Grotto (47°56.958'N, 129°5.899'W, Fig. 1d) is an active 183 hydrothermal sulfide vent cluster (15 m long by 10 m wide by 10 m high) located at 2196 m 184 depth that forms an open cove to the north. This edifice is characterized by high short-term 185 variation in heat flux, but is stable across years (Xu et al., 2014). Like many other MEF 186 hydrothermal edifices, the site is largely colonized by dense assemblages of Ridgeia piscesae 187 (Polychaeta, Siboglinidae) with their associated fauna (Bergquist et al., 2007; Govenar et al., 188 2002; Sarrazin et al., 1997; Urcuyo et al., 2007).

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### **2.2. Faunal assemblage sampling**

191 Sampling took place during the ONC oceanographic cruises *Wiring the Abyss 2015 and 2016* 192 from 25 August to 14 September 2015 on the R/V Thomas G. Thompson, and from 10 May to 193 29 May 2016 on the E/V *Nautilus*, respectively. Using the remotely operated vehicles (ROVs) 194 Jason and Hercules, three samples of Ridgeia piscesae tubeworms and their associated fauna 195 were sampled each year at different locations on the Grotto hydrothermal edifice (n=6; S1 to 196 S6, Fig. 2). These samples corresponded to three distinct assemblages (assemblage III, 197 assemblage IV and assemblage V low-flow) according to Sarrazin et al. (1997). For each 198 sample, a checkerboard of 7 x 7 mm squares was first placed on each tubeworm sample to 199 estimate the surface area. Then, the first suction sample was taken to recover the mobile 200 fauna, followed by collection of tubeworms and their associated fauna, which were placed in 201 a BioBox using the ROV's mechanical arm. A final suction sample on the bare surface was 202 performed to recover the remaining fauna. The final sampled surface area was filmed with 203 the ROV camera to estimate its surface using imagery (see protocol in Sarrazin et al. 1997).

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## 205 2.3. Sample processing

206 2.3.1. Sample processing and identification

207 On board, all faunal samples were washed over stacked sieves (250  $\mu$ m and 63  $\mu$ m mesh 208 sizes). Macrofaunal specimens (>250  $\mu$ m) were preserved in 96 % ethanol and meiofauna 209 (250  $\mu$ m > x > 63  $\mu$ m) in 10 % seawater formalin. In the laboratory, bushes of *Ridgeia* 

210 piscesae were thoroughly disassembled and each tube was washed and sieved a second 211 time. All associated macrofaunal organisms were sorted, counted and identified to the 212 lowest possible taxonomic level. Specimens whose identification was unclear were sent to 213 experts for identification and/or description. Trophic guilds from the literature (symbiont 214 host, bacterivore, scavenger/detritivore or predator) were compiled for each vent species 215 (Table 1). For species with unknown diets, the compilation was based on trophic guilds 216 identified from closely related species (within the same family). These were then compared 217 to our isotopic results (see below).

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- 219 2.3.2 Habitat complexity and biomass

220 The *Ridgeia piscesae* tubes create a three-dimensional (3D) structure for other vent animals 221 to colonize. An estimation of the tubeworm surface area available for the fauna and the 222 volume for each sample provided a proxy for habitat complexity. Assuming that the tubes 223 are cylinders erected vertically, tubeworm surface area was estimated by measuring 224 lengthwise and crosswise (i.e. diameter) 10 % of the tubeworm tubes randomly selected. For 225 each tubeworm sample, species density is therefore expressed in number of individuals per square meter of tubeworm surface (ind  $m^{-2}$ ) to account for this 3D space (Marcus et al., 226 227 2009; Tsurumi and Tunnicliffe, 2001, 2003). Sampling volume was estimated by multiplying 228 the mean tube length by the sampled surface area and faunal density was also expressed as ind m<sup>-3</sup>. Biomass estimates were obtained from the total dry mass (DM) of a random sample 229 230 of a few individuals (3-10) for each species. DM of each species corresponds to the mean of 231 individual masses obtained after drying each individual at 80°C for 48 h, multiplied by the 232 abundance of each species.

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## 234 2.3.3. Stable isotope processing

Sample preparation for stable isotope analyses was specimen size-dependent. For large specimens, muscle tissue was dissected and used for stable isotope analyses. In the case of intermediate-size specimens, the gut content was removed before stable isotope analyses. For small species, entire individuals were analysed or pooled to reach the minimum required mass for isotopic analyses. Samples were freeze-dried and ground into a homogeneous powder using a ball mill or agate mortar. Approximately 1.3-1.4 mg of the powder was

241 measured in tin capsules for isotope analyses. For species containing carbonates (i.e. 242 gastropods, ostracods, amphipods, etc.), individuals were acidified to remove inorganic 243 carbon. Acidification was carried out by the addition of 0.1 M HCl. The samples were then 244 dried at 60°C for 24 h under a fume extractor to evaporate the acid. Five replicates per 245 species were analysed. Carbon and nitrogen isotope ratios were determined using a Thermo 246 Scientific FLASH EA 2000 elemental analyser coupled with a Thermo Scientific Delta V Plus 247 isotope ratio mass spectrometer. Values are expressed in  $\delta$  (‰) notation relative to Vienna 248 Pee Dee Belemnite and atmospheric N<sub>2</sub> as international standards for carbon and nitrogen, respectively, according to the formula:  $\delta^{13}$ C or  $\delta^{15}$ N = [(R<sub>sample</sub>/R<sub>standard</sub>)-1] x 10<sup>3</sup> (in ‰) where 249 R is  ${}^{13}C/{}^{12}C$  or  ${}^{15}N/{}^{14}N$ . Analytical precision based on repeated measurements of the same 250 sample was below 0.3‰ for both  $\delta^{13}$ C and  $\delta^{15}$ N. 251

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### 253 **2.4. Statistical analyses**

In the present study, *Ridgeia piscesae* was regarded as a habitat builder and thus discarded from all statistical analyses. Species-effort curves were computed for each faunal sample collected to assess the robustness of the sampling effort. Local diversity (i.e.  $\alpha$  diversity) was estimated for each tubeworm sample from several complementary indices (Gray, 2000) using the vegan package in R (Oksanen et al., 2017): species richness (S), exponential Shannon entropy (D), Simpson's (1- $\lambda$ ') indices of species diversity and Pielou's evenness index (J').

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# 262 **3. Results**

# **3.1. Species-effort curves, tubeworm structural complexity and diversity**

The rarefaction curves (excluding *Ridgeia piscesae*; Fig. 3) showed that, overall, the collected samples (S1 to S6) gave a fairly good representation of the species diversity on the Grotto hydrothermal edifice. In 2015, sample S2 (24 species) and S3 (31 species) rarefaction curves seemed to reach a plateau. S1 cumulated a total of 28 macrofaunal species. The samples from year 2016 exhibited lower species richness and did not reach an asymptote. Samples S4 and S5 had both a macrofaunal species richness of 19 species, while only 14 species were found in sample S6 (Fig. 3).

272 Tubeworm surface areas and volumes of the samples were used as proxies for habitat 273 complexity provided by the engineer species R. piscesae (Table 2). Samples S1 and S3 were 274 characterized by a similar degree of structural complexity, with tubeworm surface of 4.27 and 4.26 m<sup>2</sup>, respectively (Table 2). Sample S2 displayed a sampling area of less than half of 275 that of S1 and S3 reaching a total tubeworm surface area of 1.63 m<sup>2</sup>. Samples from 2016 276 277 were substantially smaller than those from 2015. Tubeworm surface areas varied between 0.1 and 0.57  $m^2$ . To resume, the tube surface areas of the different samples were as follow: 278 S1 > S3 > S2 > S5 > S6 > S4 (Table 2). Sample volumes were also strongly correlated ( $R^{2}_{adi}$  = 279 280 0.82; *p*-value = 0.008) to the tubeworm surface area for these Grotto samples and thus, can 281 be used as an easily measurable proxy to estimate habitat complexity.

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Alpha diversity measures showed that S4 displayed the lowest diversity (D = 2.605;  $1-\lambda' = 0.550$ ), followed by S6 (D = 3.998;  $1-\lambda' = 0.633$ ) and S5 (D = 4.348;  $1-\lambda' = 0.697$ ). The highest diversity values were observed S1 (D = 5.377;  $1-\lambda' = 0.728$ ), slightly lesser than S2 (D = 5.398;  $1-\lambda' = 0.749$ ) and S3 (Shannon D = 6.053;  $1-\lambda' = 0.778$ ). The S2 and S3 samples showed a more even distribution (J') of individuals among species than the other samples. In contrast, S4 had the lowest evenness (J'= 0.325) (Table 2). Species richness was significantly correlated with *R. piscesae* tube length (R<sup>2</sup><sub>adj</sub> = 0.62, *p-value* = 0.039).

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### **3.2.** Composition and structure of Grotto vent communities

292 The species list and abundances for each sample collected within the Grotto hydrothermal 293 edifice are provided in Table 3. A total of 148 005 individuals representing 35 macrofaunal 294 species (excluding *Ridgeia piscesae*) were identified in the six tubeworm bushes (S1 to S6) 295 sampled on the Grotto edifice. Overall, gastropods (5 species) and polychaetes (18 species) 296 respectively accounted for 69.5 ± 18.8 % and 16.3 ± 11.8 % of the total macrofaunal 297 abundance. The numerically most abundant species were the gastropods Lepetodrilus 298 fucensis and Depressigyra globulus as well as the polychaete Amphisamytha carldarei. The 299 highest macrofaunal densities were observed in samples S5 (59 450 ind m<sup>-2</sup>), S4  $(23784 \text{ ind m}^{-2})$ , S3  $(15452 \text{ ind m}^{-2})$  and S2  $(13748 \text{ ind m}^{-2})$ , whereas S1 and S6 had the 300 lowest densities with 7 212 ind  $m^{-2}$  and 6 518 ind  $m^{-2}$ , respectively. A high percentage (30 %) 301 302 of the species were only found in 1 or 2 samples.

304 More specifically, S1 was dominated by gastropod species such as L. fucensis, D. globulus 305 and Provanna variabilis (Table 3). High densities contrasted with low biomass were observed 306 for the ampharetid polychaete A. carldarei and the syllid polychaete Sphaerosyllis ridgensis. 307 S2 was also dominated by L. fucensis, D. globulus and A. carldarei, with, however, a high 308 proportion of ostracods Euphilomedes climax (Table 3). S3 was largely dominated by A. 309 carldarei and, to a lesser extent, was almost equally dominated by L. fucensis and D. 310 globulus. Polychaetes were also dominant, with the presence of S. ridgensis, the dorvilleid 311 Ophryotrocha globopalpata and the maldanid Nicomache venticola. There were high 312 densities of P. variabilis, the solenogaster Helicoradomenia juani, the halacarid 313 Copidognathus papillatus, the ostracod Xylocythere sp. nov. and the pycnogonid Sericosura 314 verenae (Table 3). S4 was dominated by L. fucensis and D. globulus and, to a lesser extent, by 315 the alvinellid polychaete Paralvinella palmiformis (Table 3). S5 was also dominated by L. 316 fucensis and D. globulus, followed by E. climax and P. variabilis (Table 3). Finally, S6 was also 317 dominated L. fucensis and D. globulus and, to a lesser extent, by A. carldarei and the 318 alvinellid polychaete Paralvinella pandorae (Table 3).

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# 320 **3.4.** $\delta^{13}$ C and $\delta^{15}$ N isotopic composition

321  $\delta^{13}$ C values of the vent fauna ranged from -33.4 to -11.8 ‰ among the different samples (Fig. 4). In more details,  $\delta^{13}$ C values ranged from -33.4 to -13.5 ‰ for S1, from -33.4 to 322 323 -15.4 ‰ for S2 and from -32.4 to -14.7 ‰ for S3. Samples from S4, S5 and S6 displayed 324 slightly narrower  $\delta^{13}$ C ranges, varying from -30.3 to -12.5 ‰, from -31.3 to -14.8 ‰ and from -32.3 to -11.8 ‰, respectively; most species were enriched in <sup>13</sup>C relative to the S1, S2 325 326 and S3 samples (Fig. 4). Overall, the gastropod Provanna variabilis (species #2) was the most 327 depleted in  ${}^{13}C$  with values around -32.2% (± 1.2 ‰). In contrast, Ridgeia piscesae siboglinids (species #1) showed the highest  $\delta^{13}$ C values, with constant values around 328  $-14.7 \ \%$  (± 1.0 %). The range of  $\delta^{15}$ N values in faunal assemblages varied between -8.5 and 329 330 9.4 ‰ (Fig. 4). Especially, S1 values ranged from 0.3 to 8.4 ‰, S2 from 0.4 to 9.2‰, S3 from -2.7 to 8.3‰, S4 from -1.3 to 8.7 ‰, S5 from -1.1 to 6.4 ‰ and S6 from -8.5 to 9.4 ‰ (Fig. 331 4). Generally, 15 species showed a  $\delta^{15}N > 5 \%$  in S1, S2 and S3 assemblages but only 4 332 species were over 5 ‰ in  $\delta^{15}$ N in S4, S5 and S6. In contrast to their  $\delta^{13}$ C values, *P. variabilis* 333 and *R. piscesae* displayed similar and relatively stable  $\delta^{15}N$  values among samples with 334 0.3 ‰ (± 0.8 ‰) and 1.5 ‰ (± 1.1 ‰), respectively. 335

### 337 **3.5. Biomass distribution in Grotto vent food webs**

338 The projection of the species isotopic ratios weighted by biomass is useful for estimating the 339 relative contributions of the different trophic pathways within the vent assemblages (Fig. 5). 340 In our study, there were similar patterns of biomass distribution in the six sampled 341 assemblages. In all six samples, the ecosystem engineering polychaete Ridgeia piscesae 342 (species #1) represented the highest proportion of biomass (69.3 ± 16 %). However, as it was 343 considered to be a structuring species of the ecosystem, it was not included in the following 344 biomass distribution analysis. With a total proportion of biomass ranging from 78.9 to 345 95.8 % (89.6 ± 6.8 %) across samples, gastropods seemed to play an important role in the 346 trophic food web of communities associated with the siboglinid tubeworms. The gastropod 347 biomass was dominated by Lepetodrilus fucensis (species #4), which accounted for 31.5 to 348 82.8 % (55.8 ± 18.3 %) of the total biomass. In addition to *L. fucensis*, the gastropods 349 Depressigyra globulus (species #3), Provanna variabilis (species #2) and Buccinum 350 thermophilum (species #5) showed relatively high proportions of biomass within the 351 different samples, ranging from 5.6 to 36.6 % (16.5 ± 13.8 %), 0.6 to 26.3 % (10.9 ± 9.8 %) 352 and 0 to 16.1 % (6.4 ± 6.8 %), respectively (Fig. 5). However, in some samples, other species 353 also significantly contributed to the total biomass. For example, in S3, the polychaete 354 Amphisamytha carldarei (species #7) contributed substantially (7.2%) to the total biomass. 355 Similarly, in S4, the polychaete Paralvinella palmiformis (species #13) contributed to 16.4 % 356 of the total biomass.

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## 358 **4. Discussion**

### 359 **4.1. Communities and diversity**

Hydrothermal ecosystems of the north-east Pacific are dominated by dense populations of tubeworms *Ridgeia piscesae*. In this study, a total of 36 macrofaunal species (including *R. piscesae*) were found in the six tubeworm bushes sampled on the Grotto edifice, which is consistent with previous community knowledge in the region (Bergquist et al., 2007). In this study, macrofaunal species richness was slightly lower than that observed at the Easter Island hydrothermal site on the Main Endeavour Field, where a total of 39 species had been identified in a single *R. piscesae* bush (Bergquist et al., 2007). Tsurumi and Tunnicliffe (2003)

367 reported the presence of 39 macrofaunal species in 25 collections from the Axial Segment 368 (JdFR), but lower values have been reported on other segments, with 24 species in 7 369 collections from the Cleft Segment (JdFR) and 19 species in 2 collections from the CoAxial 370 Segment (JdFR). These levels of diversity are lower than that found in *Riftia pachyptila* 371 bushes on the East Pacific Rise, where species richness in 8 collections reached 46 species 372 (Govenar et al., 2005). Macrofaunal diversity was also lower than those obtained in 373 ecosystem engineering mussel beds from Lucky Strike on the Mid-Atlantic Ridge, with 41 374 taxa identified (Sarrazin et al., 2015), or from the northern and southern East Pacific Rise, 375 with richnesses of 61 and 57 species, respectively (Van Dover, 2003). Variation between sites 376 and regions may be related to discrepancies in sampling effort and methodologies. 377 Alternatively, faunal dissimilarities between biogeographic regions may be closely related to 378 the geological context, species colonization history, connectivity to neighbouring basins, 379 presence of geographic barriers (transform faults, hydrodynamic processes, depths, etc.), 380 stability of hydrothermal activity, age of the vent system and distances between sites (Van 381 Dover et al., 2002).

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383 Tubeworm bushes sampled on the Grotto edifice were characterized by the dominance of a 384 few species such as Lepetodrilus fucensis, Depressigyra globulus and Amphisamytha 385 carldarei. Numerical dominance by a few species is a pattern that has also been reported 386 from other hydrothermal sites of the world oceans: Mid-Atlantic Ridge (Cuvelier et al., 2011; 387 Sarrazin et al., 2015), East Pacific Rise (Govenar et al., 2005), JdFR (Sarrazin and Juniper, 388 1999; Tsurumi and Tunnicliffe, 2001) and the southern East Pacific Rise (Matabos et al., 389 2011). Polychaetes were the most diverse taxa, representing half of the macrofaunal species 390 richness with 18 species. Similar results have been reported within R. piscesae bushes on 391 Easter Island, with the identification of 23 polychaete species (Bergquist et al., 2007). 392 Although the dominant species were similar among samples, variation between samples 393 involved mainly the relative abundance of the few dominant species and the identity of the 394 "rare" species. These variations may result from differences in sampling strategies between 395 years. The areas sampled in 2016 were smaller than in 2015 and a problem with the sampling boxes may have led to the loss of some individuals, even though not visible from 396 397 videos recorded by the submersible. Variation in species richness and diversity among 398 samples may also depend on the presence of environmental gradients, created by the

399 mixing between ambient seawater and hydrothermal effluents (Sarrazin et al., 1999). 400 Unfortunately, no environmental data were recorded with our samples. However, physical 401 and chemical conditions are known to change along the ecological succession gradient on 402 the MEF from newly opened habitat characterized by high temperature and sulfide 403 concentrations, colonized by the sulfide worm Paralvinella sulfincola, to mature 404 communities in low diffuse venting areas characterised by low temperatures and sulfide 405 concentrations and colonized by long skinny R. piscesae tubeworms (Sarrazin et al., 1997). 406 Tubeworm samples S1 and S3 were visually recognized as type V low-flow assemblages 407 (Sarrazin et al., 1997), an advanced stage in the ecological succession characterized by longer 408 tubes (18.5  $\pm$  3.3 cm) and thus a higher level of structural complexity. Both samples showed 409 the highest species richness, diversity and most complex food webs, suggesting a strong 410 influence of engineer species and the importance of biogenic structure in the diversification 411 and persistence of the local resident fauna. By increasing the number of micro-niches 412 available for vent species, the 3D structure of R. piscesae bushes helps to increase the 413 environmental heterogeneity and thereby promotes species richness and diversity at 414 assemblage scales (Jones et al., 1997; Tsurumi and Tunnicliffe, 2003). As mentioned by 415 several authors (Bergquist et al., 2003; Govenar et al., 2002; Tsurumi and Tunnicliffe, 2003), 416 various ecological mechanisms may explain the influence of R. piscesae tubeworms on local 417 diversity: new habitats generated by tubeworm bushes provide (i) a substratum for attachment and colonization; (ii) interstitial spaces among intertwined tubes, increasing 418 419 habitat gradients and therefore the number of ecological niches; (iii) a refuge to avoid 420 predators and to reduce the physiological stress related to abiotic conditions and (iv) a 421 control on the transport of hydrothermal vent flow and nutritional resource availability. 422 Samples S2 and S5, also identified as type V low-flow assemblages (Sarrazin et al., 1997), 423 presented shorter tube lengths than S1 and S3, which might explain the lower species 424 richness in these two samples. High densities of A. carldarei in R. piscesae tubeworm bushes 425 (up to 93.4 %) may be related to this ampharetid's tolerance to environmental conditions 426 and, therefore, to their ability to take advantage of a wide range of ecological niches 427 (McHugh and Tunnicliffe, 1994). Similar to L. fucensis, A. carldarei is characterized by early 428 maturity and high fecundity, contributing to the success of this species in vent habitats 429 (McHugh and Tunnicliffe, 1994). The dominance of gastropods L. fucensis and D. globulus as 430 well as the relatively high abundance of the Paralvinella polychaete species in samples S4

431 and S6 suggest that they belong to lower succession levels, corresponding to transitory 432 states between types III and IV assemblages described by Sarrazin et al. (1997). The latter 433 two samples were characterized by low species richness and diversities. We hypothesize 434 that the numerical dominance of gastropods negatively affected species diversity by 435 monopolizing space and nutritional resources and by potentially grazing new recruits, 436 therefore reducing the settlement of other vent species. As suggested by Sarrazin et al. 437 (2002), the development of tubeworm bushes along the successional dynamics leads to the 438 diversification of ecological and trophic niches which may increase the complexity of the 439 food web.

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### 441 **4.2.** Trophic structure of tubeworm assemblages

The *Ridgeia piscesae* tubeworm assemblages of the Grotto hydrothermal edifice harbour a relatively diverse heterotrophic fauna. The isotopic analyses conducted on the most dominant vent macrofaunal species within the bushes revealed a high degree of resemblance in trophic structure among the six faunal samples. In this study, the position of species in the food webs (trophic structure) was consistent with the ones reported in Bergquist et al. (2007), with however, less variability in carbon and nitrogen stable isotopes.

449 Hydrothermal food webs are generally based on two main energetic pathways: the transfer 450 of energy from symbionts to host invertebrates and the consumption of free-living microbial 451 production (Bergquist et al., 2007). In the present study, the contrasting isotope 452 compositions of the gastropods Provanna variabilis, Lepetodrilus fucensis and the polychaete 453 R. piscesae suggest a wide range of isotopically distinct, symbiotic and/or free-living microbial production available to primary consumers. The high  $\delta^{13}$ C values of *R. piscesae* 454 455 were associated with chemosynthetic endosymbiosis linked to thiotrophic symbionts (Hügler 456 and Sievert, 2011). Despite that R. piscesae contributed to 86 % of the total biomass, a low number of species displayed similar  $\delta^{13}$ C values, suggesting that specialist species deriving 457 458 the majority of their food sources from siboglinid tubeworms are rare. Similar observations, 459 where engineer species contribute to the community more as an habitat than as a food 460 source, have been reported in *R. piscesae* tubeworm bushes from the Easter Island vent site 461 (Bergquist et al., 2007) and in *Bathymodiolus azoricus* mussel bed assemblages on the Tour 462 Eiffel hydrothermal edifice (Lucky Strike, Mid-Atlantic Ridge) (De Busserolles et al., 2009).

463 The low degree of exploitation of this large biomass and potential food resource suggests that rather than playing a trophic role, R. piscesae would play a primarily structuring role in 464 vent ecosystems. Nevertheless, the  $\delta^{13}$ C and  $\delta^{15}$ N values of polynoids *Branchinotogluma* 465 466 tunnicliffeae and Lepidonotopodium piscesae were consistent with a predatory diet including 467 R. piscesae tubeworms. Moreover, the predation of tubeworms by polynoids is often 468 observed as shown here on a video sequence from the ecological observatory module 469 TEMPO-mini, deployed on the Grotto hydrothermal edifice (ONC observatory; Video S1). The 470 <sup>13</sup>C-depleted stable isotope compositions of *P. variabilis* suggest a possible symbiosis with 471 chemoautotrophic bacteria or reliance on feeding on a very specific free-living microbial 472 community that depends on a <sup>13</sup>C-depleted carbon source (Bergquist et al., 2007). To date, 473 no study has reported the presence of chemoautotrophic symbionts in P. variabilis, but 474 symbioses have been described for other species from the Provannidae family (Windoffer and Giere, 1997). With an intermediate  $\delta^{13}$ C composition between *R. piscesae* and *P.* 475 476 variabilis, L. fucensis gastropods seem to represent a major energetic pathway in these vent 477 communities. Food webs obtained in this study revealed that most vent species display a  $\delta^{13}$ C similar to *L. fucensis*, but with slightly higher  $\delta^{15}$ N values. Through its high densities, 478 479 large biomasses and its position at the base of the food webs, we suggest that L. fucensis 480 could play an important role in structuring vent communities. The wide-ranging feeding 481 strategies of this limpet may exert a high pressure on the availability of nutritional resources 482 for others vent species. Likewise, the range of feeding strategies open up more 483 opportunities for L. fucensis, allowing this limpet to take advantage of resources that other 484 species cannot. The four Paralvinella species observed in our samples, which are described 485 as suspension and/or deposit-feeders (Desbruyères and Laubier, 1986; Tunnicliffe et al., 1993), displayed low or negative  $\delta^{15}$ N values. These lowest  $\delta^{15}$ N values may be related to the 486 487 nutrition of a microbial pool based on local nitrogen sources. In fact, the ammonium 488 produced during the microbial degradation of organic matter appears to be usually <sup>15</sup>N-489 depleted (Lee and Childress, 1996). Amongst these Paralvinella species, Paralvinella 490 sulfincola, Paralvinella palmiformis and Paralvinella dela shared the same isotopic niche 491 while *P. pandorae* displays a distinct isotopic composition.

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Like in many vent food webs (Van Dover and Fry, 1994; Levesque et al., 2005; Limén et al.,
2007), Grotto primary consumers were dominated by grazers and deposit feeders (Table 1).

495 The high diversity, densities and biomass of bacterivores emphasize the importance of free-496 living bacteria in the establishment and maintenance of the structure of the vent food web 497 (Bergquist et al., 2007). The bacterivore guild was mainly represented by the gastropods P. 498 variabilis, Depressigyra globulus and L. fucensis and the polychaetes P. sulfincola, P. 499 palmiformis, P. pandorae and P. dela. Like Paralvinella grasslei and Paralvinella bactericola 500 at vent sites of the Guaymas Basin (Portail et al., 2016), the alvinellid species found at Grotto had comparable  $\delta^{13}$ C values but different  $\delta^{15}$ N signatures. Paralvinella pandorae showed a 501 502 depleted  $\delta^{15}N$  signature relative to other alvinellid species. A previous study of isotope 503 variability among three sympatric alvinellid species, P. palmiformis, P. sulfincola and P. *pandorae* on the JdFR reported that their differences in  $\delta^{15}N$  isotope composition could be 504 505 closely related to the presence of food-source partitioning and/or to spatial segregation 506 (Levesque et al., 2003). The comparatively small size of P. pandorae compared with other 507 alvinellid species (Desbruyères and Laubier, 1986; Tunnicliffe et al., 1993) may be linked to 508 the presence of interspecific competition for food resources and/or a diet based on an isotopically distinct microbial source. The wide range of  $\delta^{13}$ C signatures in bacterivores, 509 510 coupled with the high interspecific variability in the isotopic space, suggest a large, 511 diversified microbial pool in the hydrothermal ecosystem and high variability in isotope 512 ratios in dominant microbial taxa. Detritivore/scavenger species were observed at an 513 intermediate trophic level, between the bacterivore and predator feeding guilds. This guild 514 was represented by a low number of species including the gastropod Buccinum 515 thermophilum, the ampharetid Amphisamytha carldarei and the orbiniid Berkeleyia sp. nov. The predator-feeding guild was represented by the highest  $\delta^{15}N$  values. High predator 516 diversity was found in our vent assemblages, and was associated with a wide range of  $\delta^{13}$ C 517 518 values, covering the isotopic spectrum of lower trophic level consumers (i.e. bacterivores as 519 well as scavengers/detritivores). This guild of predators appears to be dominated by polychaetes, which tend to show the highest  $\delta^{15}$ N values. The syllid *Sphaerosyllis ridgensis*, 520 521 the polynoid Levensteiniella kincaidi and the hesionid Hesiospina sp. nov. displayed the 522 highest  $\delta^{15}$ N values, suggesting that they play a role of predators in the benthic food web. Similarly, the solenogaster *Helicoradomenia juani* consistently displayed higher  $\delta^{15}$ N values 523 524 than other molluscs, indicating a predator trophic position. The presence of Zoarcidae 525 eelpouts Pachycara gymninium and Oregoniidae spider crabs Macroregonia macrochira on 526 the Grotto edifice, not sampled but observed in the video recorded by the TEMPO-mini

527 ecological module, could also played a role of predator within the ecosystem. Except for the 528 polynoid *L. kincaidi*, whose isotopic variability seemed to reveal a nutrition based on highly 529 diversified food resources, stable isotope analyses conducted on predators revealed narrow ranges of  $\delta^{13}$ C and  $\delta^{15}$ N values at the species scale, suggesting the dominance of specialist-530 531 feeding strategies, as was the case for bacterivores. An accurate assessment of the isotopic 532 composition of food sources and a description of the meiofaunal communities would be 533 necessary to further increase our understanding of the functioning of these chemosynthetic 534 communities and their trophic structures.

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### 536 **4.3. Ecological niche partitioning**

537 Vent species on the Grotto hydrothermal edifice exhibit high isotopic heterogeneity that 538 reflects the complexity of vent ecological food webs. The distribution of species in the bi-539 dimensional isotopic space depends on their diets, environmental conditions and biotic 540 interactions, which together define the concept of species ecological niche (Newsome et al., 541 2007) or the realized species trophic niche (Bearhop et al., 2004). Here, the fact that most of 542 the isotopic space was occupied by isotopically distinct species shows that the available food resources are partitioned within the community. Although the  $\delta^{15}N$  variability among 543 544 primary consumers did hinder our inference of trophic levels based on nitrogen isotopes, these communities are unlikely to host more than three trophic levels, given the overall  $\delta^{15}N$ 545 546 ranges. Moreover, although predators were quite diverse, they only represented a minor 547 part of the biomass, suggesting that Grotto vent communities are mostly driven by bottom-548 up processes. Food webs of chemosynthetic ecosystems - such as hydrothermal vents and 549 cold seeps - do not appear to be structured along predator-prey relationships, but rather 550 through weak trophic relationships among co-occurring species (Levesque et al., 2006; 551 Portail et al., 2016). Habitat and/or trophic partitioning are important structuring processes 552 at the community scale (Levesque et al., 2003; Levin et al., 2013; Portail et al., 2016). Our 553 results corroborate with those from Axial Volcano in the JdFR (Levesque et al., 2006) and the 554 Guaymas basin (Portail et al., 2016), where habitat heterogeneity induces spatial partitioning 555 of trophic niches, leading to a spatial segregation of species and species coexistence 556 (Levesque et al., 2006). Although the observed isotope variability (standard deviations) in 557 Grotto vent species suggests the occurrence of both trophic specialists and generalists 558 within the assemblages, the majority of vent species exhibited low standard deviations,

559 suggesting a predominantly specialist feeding behaviour. As already shown in previous 560 studies of vent sites with alvinellids (Levesque et al., 2003) and sulfidic sediments at 561 methane seeps with dorvilleid polychaetes (Levin et al., 2013) in the north-east Pacific, food 562 partitioning may occur between different species of the same or related taxonomic family, 563 allowing species coexistence through occupation of distinct trophic niches. Our study 564 confirmed this pattern for alvinellid polychaetes of the genus Paralvinella (Levesque et al., 565 2006). Hydrothermal vent gastropods were numerically dominant in all Ridgeia piscesae 566 bushes collected on the Grotto edifice and their isotope compositions were fairly diverse. 567 Gastropods exhibit great diversity in feeding strategies, and as a result they are found in a 568 wide variety of niches where they exploit many food sources (Bates et al., 2005; Bates, 2007). The isotope composition of *Provanna variabilis* indicated low  $\delta^{13}$ C and  $\delta^{15}$ N values. 569 Lepetodrilus fucensis gastropods had higher  $\delta^{13}$ C and  $\delta^{15}$ N values than *P. variabilis* but a 570 similar range of  $\delta^{13}$ C as Clypeosectus curvus and Depressigyra globulus. However, these 571 572 latter two species occupy an upper position in the trophic structure of their communities. 573 The great ecological success of L. fucensis in vent habitats may be attributed to a 574 combination of several characteristics. First, this species is characterized by a broad trophic 575 plasticity that includes: (i) grazing on siboglinid tubeworms and hard substrata (Fretter, 576 1988), (ii) active suspension feeding (Bates, 2007) and (iii) harbouring filamentous bacterial 577 epibionts in its gills, which – via endocytosis – may contribute to the animal's nutritional 578 requirements (Bates, 2007; Fox et al., 2002). In addition, the early maturity, high fecundity, 579 and continuous gamete production of *L. fucensis* may help to maintain the large populations on the edifice (Kelly and Metaxas, 2007). Stacking behaviour near fluid emissions also 580 581 suggests that L. fucensis is an important competitor for space and food in the community 582 (Tsurumi and Tunnicliffe, 2003). L. elevatus, the ecological equivalent of L. fucensis on the 583 East Pacific Rise, is a prey for the vent zoarcid fish *Thermarces cerberus*; the reduced limpet 584 population promotes the successful settlement and growth of sessile benthic invertebrates 585 such as tubeworms (Micheli et al., 2002; Sancho et al., 2005). The potential absence of an 586 equivalent predator for L. fucensis and the biological characteristics detailed above may 587 explain its ecological success on the north-east Pacific vent sites. In contrast, the nutrition of 588 D. globulus is based on the grazing of organic matter only (Warén and Bouchet, 1989). 589 However, its small size allows it to exploit interstitial spaces that are not available to larger 590 fauna (Bates et al., 2005). Finally, P. variabilis was relatively less abundant than the other

two species, but appeared to exploit a different thermal niche than *L. fucensis* and *D. globulus* (Bates et al., 2005). On the other hand, the isotope composition of *Buccinum thermophilum* clearly differentiates that species from the other gastropods with higher  $\delta^{13}$ C signatures. Differences in the diets of co-occurring species may contribute to the high abundance and diversity of vent gastropods through niche partitioning (Govenar et al., 2015).

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598 Habitat specialization among co-occurring vent species may drive differences in their diets 599 (Govenar et al., 2015), facilitating species coexistence in heterogeneous habitats such as 600 hydrothermal ecosystems. We hypothesized that vent food webs display a small scale spatial 601 structure that is linked to the 3D architecture of the biogenic structures generated by 602 engineer species. This would promote high interspecific trophic segregation. The spatial 603 segregation of trophic niches by environmental gradients limits the occurrence of biotic 604 interactions such as predation and competition for resources between species sharing a 605 common spatial niche (Levesque et al., 2006). Vent food webs may therefore be structured 606 through the interplay between the availability and diversity of food sources and the abiotic 607 and biotic conditions structuring species distribution.

608

#### 609 **5. Conclusion**

610 This study provides the first characterization of the structure, species diversity and food web 611 structure of macrofaunal assemblages living in Ridgeia piscesae tubeworm bushes on the 612 Grotto hydrothermal edifice. Like many vent structures (Cuvelier et al., 2011; Sarrazin et al., 613 1997), the Grotto hydrothermal edifice is inhabited by a mosaic of habitats and faunal 614 assemblages that may represent different successional stages. Our results suggest that the 615 development of *R. piscesae* tubeworms introduces complexity and heterogeneity in the 616 hydrothermal environments and exerts a strong influence on ecosystem properties. The 617 structural complexity of these tubeworms enhances community diversity and thereby 618 increases the potential trophic interactions between vent species in the food web. 619 Environmental gradients provided by the interstitial spacing of intertwined tubeworms 620 generate a multitude of ecological niches and contribute to the partitioning of nutritional 621 resources, leading to the species coexistence. Habitat modifications incurred by R. piscesae bushes may thus directly stimulate the development of complex food webs. However, 622

despite the increasing complexity in the trophic structure along the ecological succession, the position of species in the isotopic space (trophic structure) did not change across assemblages. A thorough knowledge of hydrothermal biodiversity and ecological functioning of these remote ecosystems is necessary to determine their uniqueness and contribute to the protection and conservation of this natural heritage.

628

### 629 Author's contributions

630 M.M., J.S. and P.L. designed and supervised the research project. Y.L., J.M., T.D. and S.H.: 631 data acquisition and analyses. Y.L., M.M., J.S., G.S. and P.L. conceived the ideas and 632 contributed to the interpretation of the results. All authors contributed to the writing 633 process and revised the manuscript.

634

# 635 **Competing interests**

- 636 The authors declare that they have no conflict of interest.
- 637

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**Figure 1.** (a) Location of the Juan de Fuca Ridge system and the seven segments (yellow diamonds). (b) High-resolution bathymetric map of the Endeavour Segment, with the locations of the five main active vent fields (white triangle). (c) Location map of the Main Endeavour vent field indicating the positions of hydrothermal vent edifices (black diamonds). (d) Bathymetric map of the Grotto active hydrothermal edifice (47°56.958'N, 129°5.899'W). The 10 m high sulfide structure is located in the Main Endeavour vent field.



**Figure 2.** Hydrothermal samples collected on the Grotto edifice (Main Endeavour Field, Juan de Fuca Ridge) during *Ocean Networks Canada* oceanographic cruises *Wiring the Abyss 2015 and 2016*.



**Figure 3.** Rarefaction curves for species richness in the six vent samples (S1 to S6) collected on the Grotto hydrothermal edifice.





**Figure 4.** Stable isotope bi-plots showing vent consumers' isotope signatures (mean  $\delta^{13}$ C versus  $\delta^{15}$ N values ± standard deviation) for the six vent assemblages sampled on the Grotto hydrothermal edifice. Each vent species is designated by a number: 1 = Ridgeia piscesae; 2 = Provanna variabilis; 3 = Depressigyra globulus; 4 = Lepetodrilus fucensis; 5 = Buccinum thermophilum; 6 = Clypeosectus curvus; 7 = Amphisamytha carldarei; 8 = Branchinotogluma tunnicliffeae; 9 = Lepidonotopodium piscesae; 10 = Levensteiniella kincaidi; 11 = Nicomache venticola; 12 = Paralvinella sulfincola; 13 = Paralvinella palmiformis; 14 = Paralvinella pandorae; 15 = Paralvinella dela; 16 = Hesiospina sp. nov.; 17 = Sphaerosyllis ridgensis; 18 = Ophryotrocha globopalpata; 19 = Berkeleyia sp. nov.; 20 = Protomystides verenae; 21 = Sericosura sp.; 22 = Euphilomedes climax; 23 = Xylocythere sp. nov.; 24 = Copepoda; 25 = Copidognathus papillatus; 26 = Paralicella cf. vaporalis; 27 = Helicoradomenia juani. Known trophic guilds are distinguished by a colour code: pink: symbiont; green: bacterivores; blue: scavengers/detritivores; red: predators. For more information on the interpretation of guilds, please consult the web version of this paper.



**Figure 5.** Stable isotope bi-plots showing vent consumers' isotope signatures weighted by biomass per square meter of tubeworms (filled circles) for the six vent assemblages (S1 to S6) sampled on the Grotto hydrothermal edifice. Considered as a habitat, the biomass of *Ridgeia piscesae* (denoted by a triangle symbol) is not shown. Each vent species is designated by a number: 1 = *Ridgeia piscesae*; 2 = *Provanna variabilis*; 3 = *Depressigyra globulus*; 4 = *Lepetodrilus fucensis*; 5 = *Buccinum thermophilum*; 6 = *Clypeosectus curvus*; 7 = *Amphisamytha carldarei*; 8 = *Branchinotogluma tunnicliffeae*; 9 = *Lepidonotopodium piscesae*; 10 = *Levensteiniella kincaidi*; 11 = *Nicomache venticola*; 12 = *Paralvinella sulfincola*; 13 = *Paralvinella palmiformis*; 14 = *Paralvinella pandorae*; 15 = *Paralvinella dela*; 16 = *Hesiospina* sp. nov.; 20 = *Protomystides verenae*; 21 = *Sericosura* sp.; 22 = *Euphilomedes climax*; 23 = *Xylocythere* sp. nov.; 24 = Copepoda; 25 = *Copidognathus papillatus*; 26 = *Paralicella cf. vaporalis*; 27 = *Helicoradomenia juani*. For legibility, the biomass of *P. pandorae* in collection S6 is not shown.

Table 1. Trophic guild and nutritional modes of macrofaunal species associated with the *Ridgeia piscesae* tubeworm assemblages of the Grotto hydrothermal edifice (Main Endeavour Field, Juan de Fuca Ridge). An asterisk (\*) marks the original description of the species.

Species	Trophic guil - Nutritional mode	Reference(s)
Annelida		
Polychaeta		
Siboglinidae		
Ridgeia piscesae Maldanidae	Symbiotic	Jones,1985*; Southward et al., 1995; Bergquist et al., 2007; This study
Nicomache venticola Dorvilleidae	Bacterivore - Surface deposit feeder or grazer	Blake and Hilbig, 1990*; Bergquist et al., 2007; This study
<i>Ophryotrocha globopalpata</i> Orbiniidae	Predator	Blake and Hilbig, 1990*; Bergquist et al., 2007; This study
<i>Berkeleyia</i> sp. nov. Hesionidae	Scavenger/detritivore - Suspension feeder	Jumars et al., 2015; This study
Hesiospina sp. nov. <sup>(1)</sup>	Predator	Bonifácio et al., in preparation*; This study
Protomystides verenae	Predator	Blake and Hilbig, 1990*; Bergquist et al., 2007; This study
Branchinotogluma tunnicliffeae	Predator	Pettibone, 1988*; Bergquist et al., 2007; This study
Lenidonotonodium niscesae	Predator	- Pettibone 1988*: Levesque et al 2006: Bergquist et al 2007: This study
Levensteiniella kincaidi	Predator	Pettibone, 1985*; Bergquist et al., 2007; This study
Pholoe courtneyae	Predator	Blake, 1995*; Sweetman et al., 2013
Sphaerosyllis ridgensis	Predator	Blake and Hilbig, 1990*; Bergquist et al., 2007; This study
Alvinellidae Paralvinella dela	Bacterivore - Surface denosit feeder or grazer: suspension feeder	Detinova et al. 1988*. This study
Paralvinella palmiformis	Bacterivore - Surface deposit feeder or grazer; suspension feeder	Desbruyères and Laubier, 1986*; Desbruyères and Laubier, 1991; Levesque et al., 2003. This study
Paralvinella pandorae	Bacterivore - Surface deposit feeder or grazer; suspension feeder	Desbruyères and Laubier, 1986*; Desbruyères and Laubier, 1991; Levesque et al., 2003. This study
Paralvinella sulfincola	Bacterivore - Surface deposit feeder or grazer; suspension feeder	Tunnicliffe et al., 1993*; Levesque et al., 2003; This study
Amphisamytha carldarei	Scavenger/detritivore - Surface deposit feeder or grazer	Stiller et al., 2013*; McHugh and Tunnicliffe, 1994; Bergquist et al., 2007; This study
Ctenodrilidae Raricirrus sp.	Bacterivore - Surface deposit feeder or grazer	Jumars et al., 2015
Spionidae Prionospio sp.	Bacterivore - Surface deposit feeder or grazer	Jumars et al., 2015
Mollusca		
Aplacophora		
Simrothiellidae		
Helicoradomenia juani Gastropoda	Predator	Scheltema and Kuzirian, 1991*; Bergquist et al., 2007; This study
Buccinidae Buccinum thermophilum	Scavenger/detritivore - Surface deposit feeder or grazer	Harasewych and Kantor, 2002*; Martell et al., 2002; This study
Provannidae Provanna variabilis	Bacterivore - Surface deposit feeder or grazer	Warén and Bouchet, 1986*; Bergquist et al., 2007; This study
Depressigyra globulus	Bacterivore - Surface deposit feeder or grazer	Warén and Bouchet, 1989*; Bergquist et al., 2007; This study
Clypeosectudae Clypeosectus curvus	Predator	McLean, 1989*; Bergquist et al., 2007; This study
Lepetodrilidae	Symbiotic; Bacterivore - Surface deposit feeder or grazer;	McLean 1988*: Fox et al. 2002: Bates et al. 2007: Berequist et al. 2007: This study
Leperournus jucensis	suspension feeder	
Arthropoda		
Arachnida		
Conidoanathus nanillatus	Predator	Krantz 1982*· Bergquist et al 2007· This study
Amphinoda	redator	Kianiz, 1902 , Bergquist et al., 2007, This study
Alicellidae Paralicella cf. vaporalis		Barnard and Ingram 1990*
Calliopiidae		
Oradarea cf. walkeri Letpamphopus sp.	-	Shoemaker, 1930* -
Crustacea		
Philomedidae	Destaviuera Curface descrit feeder er grann	Karrishan 1001*. This study
Cytherudidae	Bacterivore - Surface deposit feeder of grazer	Komicker, 1991.; This study
<i>Xylocythere</i> sp. nov. <sup>(2)</sup>	Bacterivore - Surface deposit feeder or grazer	Tanaka et al., in preparation*; Maddocks and Steinceck, 1987; This study
Ammotheidae		
Sericosura verenae	Bacterivore - Surface deposit feeder or grazer	Child, 1987*; Bergquist et al., 2007; This study
Sericosura venticola	Bacterivore - Surface deposit feeder or grazer	Child, 1987*; Bergquist et al., 2007; This study
Sericosura cj. uissita	Dacterivore - Surface deposit reeder or grazer	chila, 2000 ; This study
Nemertea		
Unidentified	Predator	
Table advances		
Echinodermata		
opinuioiuae		

<sup>(1)</sup>This species refers to Hesiospina legendrei that is currently under description (Bonifácio et al., in preparation)
<sup>(2)</sup>This species refers to Xylocythere sarrazinae that is currently under description (Tanaka et al., in preparation)

**Table 2.** Univariate measures of macrofaunal community structure associated with *Ridgeia piscesae* tubeworm bushes on the Grotto edifice: Sample Surface Area (SSA), Tube Height (TH), Tube Diameter (TD), volume (V), species richness (S), exponential of Shannon entropy (D), Simpson's diversity index  $(1-\lambda')$  and Pielou's evenness (J').

Sample	SSA (m <sup>2</sup> )	TH (cm) ± sd	TD (cm) ± sd	TSA (m <sup>2</sup> )	V (m³)	S	D	1-λ'	J'
\$1	0.12	17.14 ± 6.83	4.72 ± 0.82	4.27	0.02	28	5.377	0.728	0.505
S2	0.06	5.32 ± 2.47	$2.24 \pm 0.42$	1.63	3.4×10 <sup>-3</sup>	24	5.398	0.749	0.531
S3	0.12	19.91 ± 9.31	5.48 ± 1.13	4.26	0.02	31	6.053	0.778	0.524
S4	0.02	7.15 ± 2.45	$2.48 \pm 0.57$	0.57	1.1×10 <sup>-3</sup>	19	2.605	0.55	0.325
<b>S</b> 5	0.02	3.46 ± 0.85	$1.91 \pm 0.34$	0.10	5.4×10 <sup>-4</sup>	19	4.348	0.697	0.499
S6	0.01	6.15 ± 2.80	$2.14 \pm 0.43$	0.18	7.5×10 <sup>-3</sup>	14	3.998	0.633	0.525

Table 3. Percentage abundance x 100 (% Ab.), faunal density (D. ind m <sup>3</sup> ), volume (V. ind m <sup>3</sup> ) and relative biomass x 100 (% Biom.) of the different macrofaunal taxa (>250 µm) identified in the 6 sampling units (S1 to S6) on the Grotto edifice. The taxa were identified to the lowest possible taxonomical level
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Enodos	S1 - Assemblage V low-flow			S2 - Assemblage V low-flow % Ab. D. (ind m <sup>-2</sup> ) V. (ind m <sup>-3</sup> ) % Biom.			S3 - Assemblage V low-flow				S4 - Assemblage IV % Ab. D. (ind m <sup>2</sup> ) V. (ind m <sup>3</sup> ) % Biom.				55	- Assembla	ge V low-flow	S6 - Assemblage III						
species	% Ab. D. (ind m <sup>-2</sup> ) V. (ind m <sup>-3</sup> ) % Biom.		% Ab. D. (ind m <sup>-2</sup> ) V. (ind m <sup>-3</sup> ) % Biom.				% Ab. D. (ind m <sup>-2</sup> ) V. (ind m <sup>-3</sup> ) % Biom.								% Ab. D. (ind m <sup>-2</sup> ) V. (ind m <sup>-3</sup> ) % Biom.									
Annelida																								
Polychaeta																								
Nicomache venticola	0.1	8	1604.5	0.2	0.1	14.1	7033.6	0.1	0.2	35.5	6363.3	1.1	0	0	0	0	0	0	0	0	0	0	0	0
Dorvilleidae	0.1	0	1004.5	0.2	0.1	14.1	7055.0	0.1	0.2	33.3	0505.5		0	0	0	0	0		0	Ū	0	0	0	0
Ophryotrocha globopalpata	0.1	4.2	849.5	< 0.1	0.1	9.8	4893	< 0.1	1.3	202	36241.1	< 0.1	< 0.1	1.8	934.6	< 0.1	< 0.1	10	1851.9	< 0.1	0	0	0	0
Orbiniidae																								
Berkeleyia sp. nov.	0	0	0	0	0	0	0	0	< 0.1	6.3	1137.8	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0
Hesionidae																								
Hesiospina sp. nov.	0.1	9.8	1982.1	< 0.1	0.1	10.4	5198.8	< 0.1	0.1	14.3	2570.6	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0
Phyllodocidae Protomustidas varanaa	-01	0.5	04.4	< 0.1	-01	0.6	205.9	- 0.1	-01	0.2	42.1	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0
Polynoidae	< 0.1	0.5	54.4	< 0.1	< 0.1	0.0	505.0	< 0.1	< 0.1	0.2	42.1	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0
Branchinotogluma tunnicliffeae	< 0.1	0.7	141.6	< 0.1	0.1	9.2	4587.2	< 0.1	< 0.1	2.6	463.6	< 0.1	0.2	47.4	25233.7	0.2	< 0.1	20	3703.7	< 0.1	0.3	16.4	400	< 0.1
Branchinotogluma sp.	0	0	0	0	0	0	0	0	0	0	0	0	< 0.1	1.8	934.6	< 0.1	0	0	0	0	0	0	0	0
Lepidonotopodium piscesae	0	0	0	0	< 0.1	1.2	611.6	< 0.1	< 0.1	3.8	674.3	< 0.1	0.2	43.9	23364.5	0.9	0.1	50.1	9259.3	0.2	0.2	10.9	266.7	0.1
Levensteiniella kincaidi	0.1	8.2	1651.7	0.1	0.1	10.4	5198.8	< 0.1	< 0.1	4	716.4	< 0.1	< 0.1	3.5	1869.2	< 0.1	< 0.1	20	3703.7	< 0.1	0	0	0	0
Sigalionidae																								
Photoe courtneyae	< 0.1	0.2	47.2	< 0.1	U	0	0	0	0	0	0	0	0	0	0	U	U	0	U	0	0	0	U	0
Sphaerosyllis ridaensis	3.6	257.6	51911 3	< 0.1	1	170.2	85015 3	< 0.1	17	262.6	47113.4	< 0.1	0	0	0	0	0.1	90.1	16666 7	< 0.1	0.1	5.5	133.3	< 0.1
Alvinellidae	5.0	257.0	51511.5	- 0.1	-	170.2	05015.5	- 0.1	1.7	202.0	47115.4	- 0.1	0	0	0	0	0.1	50.1	10000.7	- 0.1	0.1	5.5	155.5	. 0.1
Paralvinella dela	0	0	0	0	0	0	0	0	< 0.1	0.7	126.4	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0
Paralvinella palmiformis	0	0	0	0	0.1	10.4	5198.8	< 0.1	0.1	10.3	1854.2	0.1	3.3	726.4	386915.9	6.8	0.2	110.2	20370.4	0.8	0.7	43.6	1066.7	1.4
Paralvinella pandorae	< 0.1	0.7	141.6	< 0.1	< 0.1	2.5	1223.2	< 0.1	0.1	17.4	3118.4	< 0.1	0.1	17.6	9345.8	< 0.1	0.1	70.1	12963	< 0.1	5.4	354.3	8666.7	< 0.1
Paralvinella sulfincola	0	0	0	0	0	0	0	0	< 0.1	6.6	1179.9	0.1	0.6	122.8	65420.6	0.5	< 0.1	10	1851.9	< 0.1	0.2	10.9	266.7	0.1
Ampharetidae																								
Amphisamytha carldarei	26.8	1932.1	389334.6	0.5	24.5	3367.5	1681651.4	0.5	34.8	5378.8	964938.9	1.8	0.4	80.7	42990.7	< 0.1	5.1	3004.6	555555.6	0.2	7.4	479.6	11733.3	0.1
Paricirrus sp	< 0.1	0.2	47.2	< 0.1	0	0	0	0	< 0.1	1.0	227.1	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0
Spionidae	< 0.1	0.2	47.2	< 0.1	0	0	0	0	< 0.1	1.5	557.1	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0
Prionospio sp.	< 0.1	2.1	424.7	< 0.1	0	0	0	0	< 0.1	0.9	168.6	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0
Mollusca																								
Aplacophora																								
Simrotniellidae	2.7	262.7	E2120.2	< 0.1	2.4	461.1	220275.2	- 0.1	5.6	961.0	154614.4	0.14	0.1	17.6	0245.9	< 0.1	1.2	701.2	146206.2	< 0.1	2	120.9	2200	< 0.1
Gastropoda	5.7	205.7	33130.5	< 0.1	5.4	401.1	230273.2	< 0.1	5.0	001.9	134014.4	0.14	0.1	17.0	5545.0	< 0.1	1.5	/91.2	140290.5	< 0.1	2	150.0	5200	< 0.1
Buccinidae																								
Buccinum thermophilum	0.1	9.8	1982.1	3.2	0.1	18.4	9174.3	1.6	< 0.1	2.4	421.4	0.4	0	0	0	0	0.1	50.1	9259.3	5.8	0	0	0	0
Provannidae																								
Provanna variabilis	1.9	137	27607.4	2.2	1.6	224.8	112232.4	1.3	4.5	694.8	124652.3	6.8	0.3	61.4	32710.3	0.3	8.6	5117.8	946296.3	10	1.8	114.5	2800	0.4
Peltospiridae																								
Depressigyra globulus	10.8	779.9	157149.6	1.1	14.5	1986	991743.1	1.1	20.1	3105.4	557100.7	2.9	51.4	11294.7	6015887.9	13	44	26179.8	4840740.7	21	23.2	1515.1	37066.7	1.5
Chippeosectidae	0.5	24.7	6094.4	0.1	0.2	20.2	10091 7	< 0.1	< 0.1	6.9	1222.1	< 0.1	0	0	0	0	0.1	50.1	0250.2	< 0.1	0	0	0	0
Lepetodrilidae	0.5	54.7	0564.4	0.1	0.2	20.2	10091.7	< 0.1	< 0.1	0.0	1222.1	< 0.1	U	0	0	0	0.1	50.1	9239.5	< 0.1	0	0	0	0
Lepetodrilus fucensis	42.7	3083.1	621283.6	12.5	39.5	5429.4	2711315	10.1	22.8	3519.5	631394.9	11.5	43	9457.6	5037383.2	19.4	30.1	17907.2	3311111.1	18.1	55	3586.1	87733.3	18.2
Arthropoda																								
Arachnida																								
Halacaridae	4.0	240.6	70457.9	< 0.1	1.5	211.0	105910.4	- 0.1	4.0	75 4 7	125209.2	< 0.1	< 0.1		4672.0	< 0.1	< 0.1	60.1	11111 1	< 0.1	0	0	0	0
Amphinoda	4.5	549.0	70437.8	< 0.1	1.5	211.9	105810.4	< 0.1	4.5	/ 34./	155556.2	< 0.1	< 0.1	0.0	4072.9	< 0.1	< 0.1	00.1	11111.1	< 0.1	0	0	0	0
Alicellidae																								
Paralicella cf. vaporalis	< 0.1	1.6	330.3	< 0.1	< 0.1	6.1	3058.1	< 0.1	< 0.1	3.1	547.8	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0
Calliopiidae																								
Oradarea cf. walkeri	< 0.1	4.7	943.8	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Letpamphopus sp.	0	0	0	0	0	0	0	0	0	0	0	0	< 0.1	3.5	1869.2	< 0.1	0	0	0	0	0	0	0	0
Crustacea																								
Philomedidae																		5030.0					5000.0	
Euphilomedes climax	0.7	52	10476.6	< 0.1	10.9	1502.2	750152.9	0.1	0.2	23.3	41/1.9	< 0.1	0.3	70.2	37383.2	< 0.1	9.1	5378.2	994444.4	< 0.1	3.3	218	5333.3	< 0.1
Cytherudidae	2.0	206.9	41670.6	< 0.1	1.4	199	02665 6	< 0.1	2.7	412	74092.4	< 0.1	< 0.1	7	2729.2	< 0.1	0.2	170.2	21/191 5	< 0.1	0.1	5.5	122.2	< 0.1
Pycnogonida	2.9	200.8	410/0.0	~ 0.1	1.4	100	23003.0	~ 0.1	2.7	413	/**003.4	~ 0.1	< 0.1	/	3/30.3	~ 0.1	0.3	170.3	J1401.J	~ 0.1	0.1	3.3	133.3	~ 0.1
Ammotheidae																								
Sericosura verenae	0.6	42.6	8589.0	< 0.1	0.6	84.5	42201.8	0.5	0.7	113.5	20354	0.8	0.1	24.6	13084.1	0.2	0.6	360.6	66666.7	1.2	0.4	27.3	666.7	0.2
Sericosura venticola	0.2	15.2	3067.5	< 0.1	0.1	8	3975.5	0.5	< 0.1	1.9	337.1	0.8	< 0.1	1.8	934.6	< 0.1	0	0	0	0	0	0	0	0
Sericosura cf. dissita	0.1	5.6	1132.6	< 0.1	< 0.1	1.2	611.6	0.5	< 0.1	0.7	126.4	0.8	0	0	0	0	0	0	0	0	0	0	0	0
Nomorton																								
Inidentified	< 0.1	1 2	226.0	< 0.1	0	0	0	0	< 0.1	20	505 7	< 0.1	0	0	0	c	0	0	0	0	0	0	0	0
onachuneu	× 0.1	1.2	250.0	~ 0.1	0	J	U	U	< 0.1	2.0	303.7	~ 0.1	U	0	J	U	0	U	J	U	J	J	U	J
Echinodermata																								
Ophiuroidae	< 0.1	0.2	47.2	< 0.1	0	0	0	0	< 0.1	0.5	84.3	< 0.1	0	0	0	0	0	0	0	0	0	0	0	0