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Observations on parasitism in deep-sea hydrothermal vent and seep limpets

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ABSTRACT: Parasite burdens of shallow-water molluscs have been well documented, but little is known about parasite burdens of molluscs from deep-sea chemosynthetic environments (e.g. hydrothermal vents and seeps). Chemosynthetic habitats are characterized by high concentrations of reduced sulfur and, in the case of vents, high heavy metal concentrations. These compounds are noxious and even stress-inducing in some environments, but are part of the natural chemical milieu of vents and seeps. To examine parasite types and infection intensities in limpets from vents and seeps we documented parasite burdens in 4 limpet species from 4 hydrothermal vent fields (3 on the East Pacific Rise, 1 on the Mid-Atlantic Ridge) and 1 seep site (Florida Escarpment). Approximately 50% of all limpets examined were infected with 1 or more types of parasites. Limpet parasites were predominantly rickettsia-like inclusions in the digestive and gill epithelia. Limpets collected from the vent field on the Mid-Atlantic Ridge were free of parasites. We detected no histopathological effects that we could attribute to parasites.

KEY WORDS: Chemosynthetic ecosystems · Rickettsia · Community ecology · Parasite ecology · Mollusc

INTRODUCTION

Parasitic infections are common in aquatic communities, including those involving molluscs (Kim et al. 1998, Carballal et al. 2001, Poulin 2002). The effects of parasitic infection can be devastating to individual hosts and to host populations. Infections can impair growth, reproduction and the ability of the animal to compete for resources (Calvo-Ugarteburu & McQuaid 1998, Ward et al. 2004, this issue). Parasites can affect host population dynamics by influencing the outcome of predation and intra- and interspecific competition, thereby having an impact on the community structure and function of entire ecosystems. Although often overlooked by marine ecologists, interactions between parasites and hosts are as important as predation, facilitation and competition in structuring communities (Anderson 1978, Anderson & May 1978).

While parasites and their effects have been well documented for shallow-water communities, there are few studies of microparasites in the deep sea. Information on parasitism in chemosynthetic ecosystems, such as hydrothermal vents and cold seeps, is especially sparse. Hydrothermal vents and cold seeps provide an opportunity to study animals in extreme environments (Powell et al. 1999).

Deep-sea hydrothermal vents are characterized by high concentrations of hydrogen sulfide and heavy metals (reviewed in Van Dover 2000). Found along seafloor spreading centers, hydrothermal vents are home to diverse, chemosynthetically based ecosystems. Molluscs living at hydrothermal vents typically live at temperatures 1 to 20°C above the ambient 2 to 3°C of the surrounding seawater (Van Dover 2000). Sulfides and heavy metals in vent fluids bathing the animal communities are at levels that are normally toxic to aerobic organisms, but vent molluscs are adapted to these conditions (Cosson & Vivier 1997, Juniper & Tunnicliffe 1997, Sibuet & Olu 1998). Cold seeps are a second type of chemosynthetic environ-

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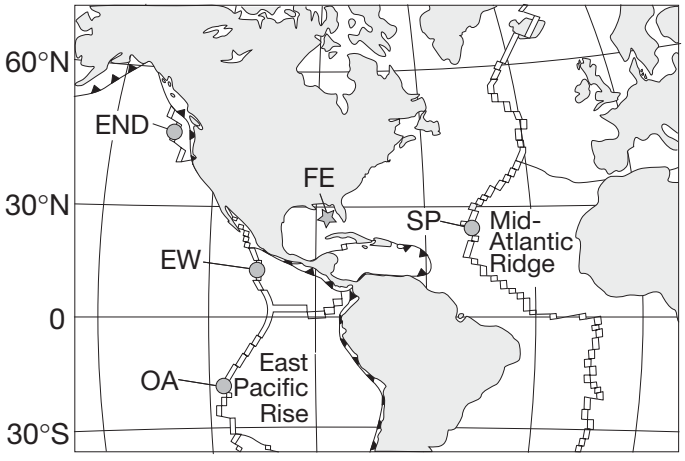

Fig. 1. Limpet collection sites. Grey circles: vents; grey star: seep. OA: Oasis, southern East Pacific Rise (17° 25.3′ S, 113° 12.3′ W, 2582 m; *Lepetodrilus elevatus* sampled in 1999); EW: East Wall, northern East Pacific Rise (9° 50.9′ N, 104° 17.5′ W, 2499 m; *L. elevatus* sampled in 1999). END: Endeavor, Juan de Fuca Ridge (47° 58.00′ N, 129° 05.50′ W, 2220 m; *L. fucensis* sampled in 1999). SP: Snake Pit, Mid-Atlantic Ridge (23° 22.1′ N, 44° 57.0′ W, 3490 m; *Pseudorimula midatlantica* sampled in 2001). FE: Florida Escarpment (26° 01.8′ N, 84° 54.9′ W, 3288 m; *Paralepetopsis floridensis* sampled in 2000)

ment found in the deep sea (see Sibuet & Olu 1998). Seeps occur in a variety of geological contexts, including brine seeps (e.g. Florida Escarpment seep; Paull et al. 1984), gas-hydrate seeps (e.g. Blake Ridge; Van Dover et al. 2003), and petroleum seeps (Gulf of Mexico; MacDonald et al. 1990).

Recently, 2 studies have focused on the parasite burdens of bathymodiolin mussels from chemosynthetic systems (Powell et al. 1999, Ward et al. 2004). Both studies documented parasites similar in morphology to those found in coastal molluscs. These types of parasites included rickettsia and chlamydia-like cellular inclusions and extracellular gill ciliates (Powell et al. 1999, Ward et al. 2004). Prevalence of some types of parasites, such as rickettsia- and chlamydia-like inclusions, was higher in deep-sea mussels than is typically observed in mussels from intertidal regions. Seep mussels were more heavily parasitized than vent mussels (Ward et al. 2004), possibly due to the greater stability of the seep environment compared to the hydrothermal vent environment (Sibuet & Olu 1998).

To extend our appreciation of parasite burdens in invertebrates in chemosynthetic environments, we chose to examine parasite burdens in deep-sea hydrothermal vent and seep limpets. Limpets, although small (typically <1 cm length), are common and abundant at vents and seeps, and often dominate the macrofaunal biomass. We studied 3 vent species (*Lepetodrilus elevatus* from 2 sites on the East Pacific Rise [EPR; sampled in 1999], *L. fucensis* from the Juan de Fuca Ridge [JDR; sampled in 1999], and *Pseudorimula midatlantica* from the Mid-Atlantic Ridge [MAR; sampled in 2001]) and 1 seep species (*Paralepetopsis floridensis* from the Florida Escarpment; sampled in 2000) (see Fig. 1 for sample locations). These species are the dominant limpet species at each site and represent 4 biogeographically distinct regions and 2 types of chemosynthetic habitats.

MATERIALS AND METHODS

All limpets for this study were collected using the research submersible 'Alvin'. Limpets were fixed in 10% buffered formalin for 24 h and stored in 70% ethanol. We selected 25 or 30 limpets of each species at random (except *Paralepetopsis floridensis*, for which only 8 specimens were selected), and numbered, measured (shell length ± 0.1 mm) and weighed (tissue wet weight ± 0.001 g) them.

Limpets were embedded in paraffin wax and sectioned (5 to 6 µm) longitudinally. Serial sections were stained with Gill's hematoxylin and eosin (H&E; Stevens 1990) for parasite identification. Infection prevalences (no. of host individuals infected with any parasite; Margolis et al. 1982) and intensities (no. of individuals of a particular parasite species in each infected host; Margolis et al. 1982) were determined quantitatively for each individual and the sex of each limpet was recorded. Individuals not infected with any parasites were excluded from the calculation of within-site mean infection intensities. Micrographs of parasites were taken using a Spot camera (Diagnostic Instruments); contrasts were adjusted using Adobe Photoshop (Adobe Systems).

Pearson's correlations and the non-parametric Kruskal-Wallis test where appropriate were undertaken using MINITAB software (Version 13.20, 2000). The multi-dimensional scaling (MDS) technique (PRIMER v5; Clarke & Gorley 2001) was used to examine differences between individuals based on parasite infection, using Bray-Curtis similarities calculated from the non-transformed infection intensities of parasites from each limpet, excluding individuals that were not infected with any parasites. The relative positions of individual points on MDS plots (unitless, 2D spaces) represent relative similarities of multivariate data for each limpet individual, derived from a parasite-abundance matrix. Analysis of similarity (ANOSIM subroutine of PRIMER v5) was used to determine significant differences between groups distinguished by MDS. ANOSIM provides R statistics: where $R > 0.75$, groups

are well-separated; where 0.75 > R > 0.5, groups are overlapping but clearly different; where R < 0.25, groups are not separable (Clarke & Gorley 2001). Factors contributing to these differences were determined from similarity percentages (SIMPER subroutine in PRIMER v5).

The limpet *Paralepetopsis floridensis* lacks gills. This character, plus the reduced sampling effort for *P. floridensis*, forced us to make descriptive rather than quantitative comparisons of parasite burdens between seep and vent limpets.

RESULTS

Parasite fauna

We identified 7 types of parasites in histological serial sections of *Lepetodrilus elevatus*, *L. fucensis*, *Pseudorimula midatlantica*, and *Paralepetopsis floridensis*. These 7 types can be placed into 3 groups: rickettsia-like gut and gill inclusions, gregarine protozoans, and bacterial gut inclusions (Table 1).

We identified 3 rickettsia-like gut inclusions infecting the cytoplasm of the host cell. The first, referred to hereafter as Digestive Rickettsia I (Fig. 2a), was found in the digestive epithelial cells of the stomach of *Lepetodrilus elevatus* from EPR vents. These basophilic inclusions were generally spherical in shape with an average diameter of 15 µm (n = 10). A membrane separated the inclusion from the host cell (Fig. 2b). Obvious tissue pathology was uncommon, although in some cases the inclusion could be seen breaking through the host cell membrane. Another rickettsia-like gut inclusion, referred to as Digestive Rickettsia II, was seen in epithelial cells of the digestive diverticula of *L. elevatus* from EPR vents (Fig. 2c). These inclusions had an average diameter of 12 µm (n = 10). Digestive Rickettsia II was characterized by an outer membrane and a grainy, almost filamentous internal structure (Fig. 2d), and were basophilic with H&E.

The rickettsia-like gill inclusion (referred to as Gill Rickettsia) was observed in the gill epithelial cells of *Lepetodrilus elevatus* (Fig. 2e) from the Oasis vent (southern EPR) and *L. fucensis* from the Endeavour

Table 1. *Lepetodrilus elevatus*, *L. fucensis*, *Pseudorimula midatlantica*, and *Paralepetopsis floridensis* infected by microparasites. Prevalences (as number of host individuals infected and % of total individuals) and mean infection intensity (SE) of parasite types and copepod infestation data. na: not applicable (n < 3); (n) = no. of limpets examined

Parasite type	Hydrothermal vent sites				Seep site
	East Wall *L.elevatus* (n = 30)	Oasis *L. elevatus* (n = 25)	Juan de Fuca *L. fucensis* (n = 25)	Snake Pit *P. midatlantica* (n = 25)	Florida Escarpment *P. floridensis* (n = 8)
Digestive Rickettsia I					
No. of limpets infected (%)	12 (40%)	4 (16%)	0	0	0
Mean infection intensity (±SE)	3.3 (1.3)	11.5 (9.2)	0	0	0
Digestive Rickettsia II					
No. of limpets infected (%)	3 (10%)	9 (36%)	0	0	0
Mean infection intensity (±SE)	1.7 (0.7)	10.2 (6.1)	0	0	0
Digestive Rickettsia III					
No. of limpets infected (%)	0	0	0	0	2 (25%)
Mean infection intensity (±SE)	0	0	0	0	1.5 (na)
Gill Rickettsia					
No. of limpets infected (%)	0	5 (20%)	5 (20%)	0	0
Mean infection intensity (±SE)	0	3.0 (1.5)	1.8 (0.4)	0	0
Gregarines					
No. of limpets infected (%)	0	2 (8%)	0	0	0
Mean infection intensity (±SE)	0	4.5 (na)	0	0	0
Bacterial Inclusion I					
No. of limpets infected (%)	10 (33%)	4 (16%)	0	0	2 (25%)
Mean infection intensity (±SE)	6.0 (1.6)	6.5 (1.6)	0	0	2 (na)
Bacterial Inclusion II					
No. of limpets infected (%)	0	6 (20%)	9 (36%)	0	0
Mean infection intensity (±SE)	0	56.4 (21.6)	34.8 (11.9)	0	0
Copepods					
No. of limpets infested (%)	0	1 (4%)	4 (16%)	1 (4%)	0
Infestation intensity (±SE)	0	1 (na)	1 (0.0)	1 (na)	0

vent. These inclusions were similar in size and morphology to Digestive Rickettsia I.

Gregarine protozoans were found only in *Lepetodrilus elevatus* from the Oasis vent. The gregarines averaged 123 µm (n = 9) in length and were aggregated in mantle tissues (Fig. 3a). The oocyst, located within the sporocyst (Fig. 3b) of each gregarine stained bright red or pink with H&E.

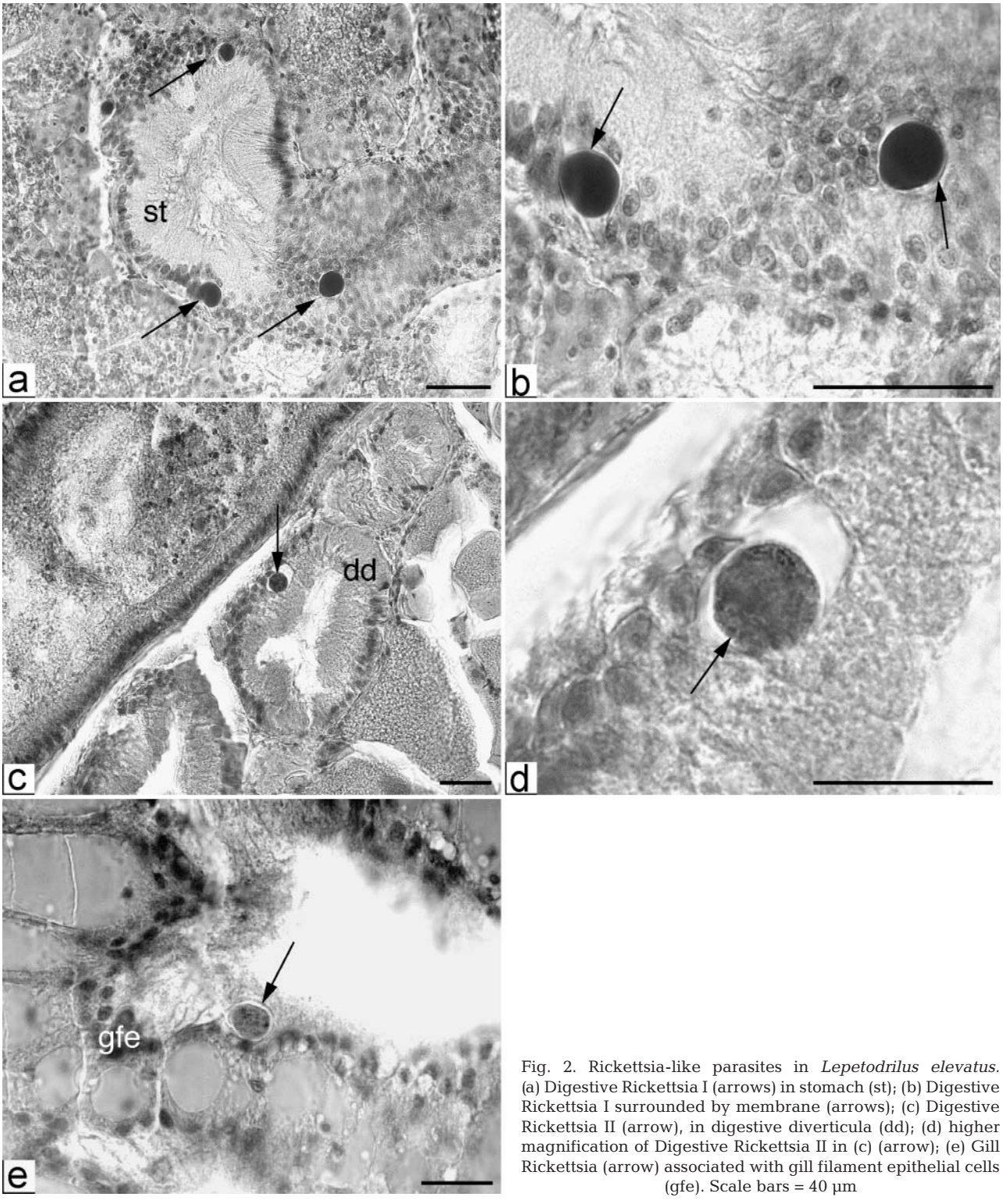

Fig. 2. Rickettsia-like parasites in *Lepetodrilus elevatus.* (a) Digestive Rickettsia I (arrows) in stomach (st); (b) Digestive Rickettsia I surrounded by membrane (arrows); (c) Digestive Rickettsia II (arrow), in digestive diverticula (dd); (d) higher magnification of Digestive Rickettsia II in (c) (arrow); (e) Gill Rickettsia (arrow) associated with gill filament epithelial cells (gfe). Scale bars = 40 µm

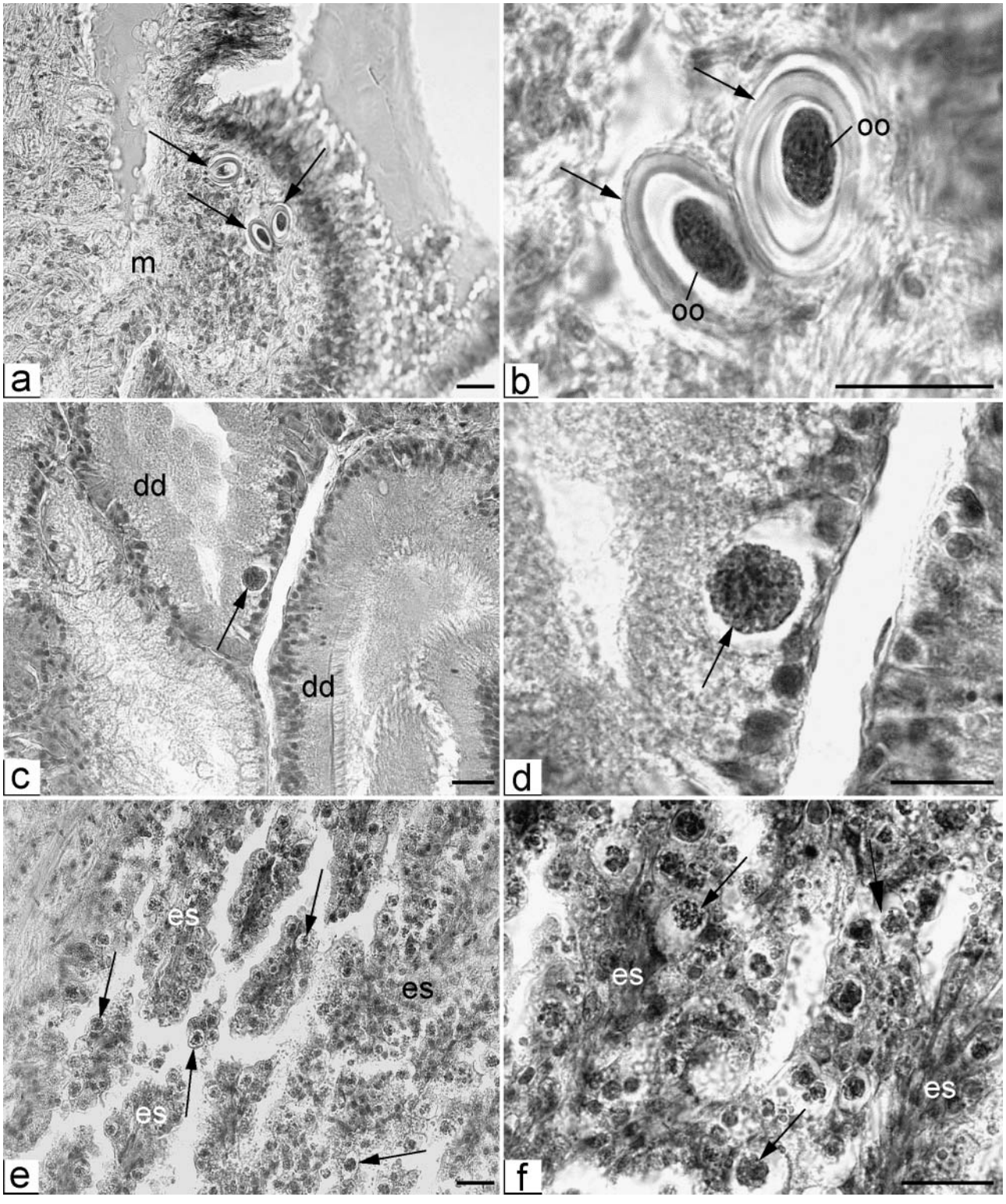

Fig. 3. Types of parasites in *Lepetodrilus elevatus* and *L. fucensis*. (a) Unidentified gregarine protozoan (arrows) parasitizing mantle tissue (m) of *L. elevatus*; (b) gregarine oocyst (oo) within sporocysts (arrows); (c) Bacterial Inclusion I (arrow) in the digestive diverticula (dd) of *L. elevatus*; d) Bacterial Inclusion I (arrow) in *L. elevatus* (note individual bacteria in spherical clusters); (e) Bacterial Inclusion II (arrows) in esophageal tissue (es) of *L. fucensis*; (f) same as (e), but higher magnification of Bacterial Inclusion II (arrows) in esophageal tissue (es). Scale bars = 20 µm

Of 2 bacterial gut inclusions, 1 (Bacterial Inclusion I) was found in epithelial cells of the digestive diverticula of *Lepetodrilus elevatus* from both East Pacific Rise vent sites (Fig. 3c). Bacterial Inclusion I was a basophilic, irregularly shaped bacterial colony, averaging 15 µm (n = 10) in diameter and made up of rod-shaped bacteria ~1 µm in length. Unlike the rickettsia-like inclusions, Bacterial Inclusion I lacked an outer membrane (Fig. 3d).

A second bacterial parasite, Bacterial Inclusion II, was observed in the esophageal tissue of *Lepetodrilus elevatus* from the Oasis vent and *L. fucensis* from the Endeavour vent (Fig 3e). Individual, spherical aggregates were observed under high power and ranged in diameter from 5 to 10 µm (n = 10; Fig. 3f). Inclusions were basophilic with H&E stain.

We observed 2 types of parasites in *Paralepetopsis floridensis* from the Florida Escarpment seep site. Of these, 1 parasite type matched the Bacterial Inclusion I (described above) found in *Lepetodrilus elevatus* from the East Pacific Rise. The second parasite type was a rickettsia-like gut inclusion, Digestive Rickettsia III, found only in *P. floridensis*. Digestive Rickettsia III ranged in diameter from 25 to 30 µm (n = 3) and was thus larger than the previous 2 rickettsia-like gut inclusions described. Digestive Rickettsia III infected the epithelial cells of the digestive tract (Fig. 4a). These inclusions were diffuse, with a filamentous internal

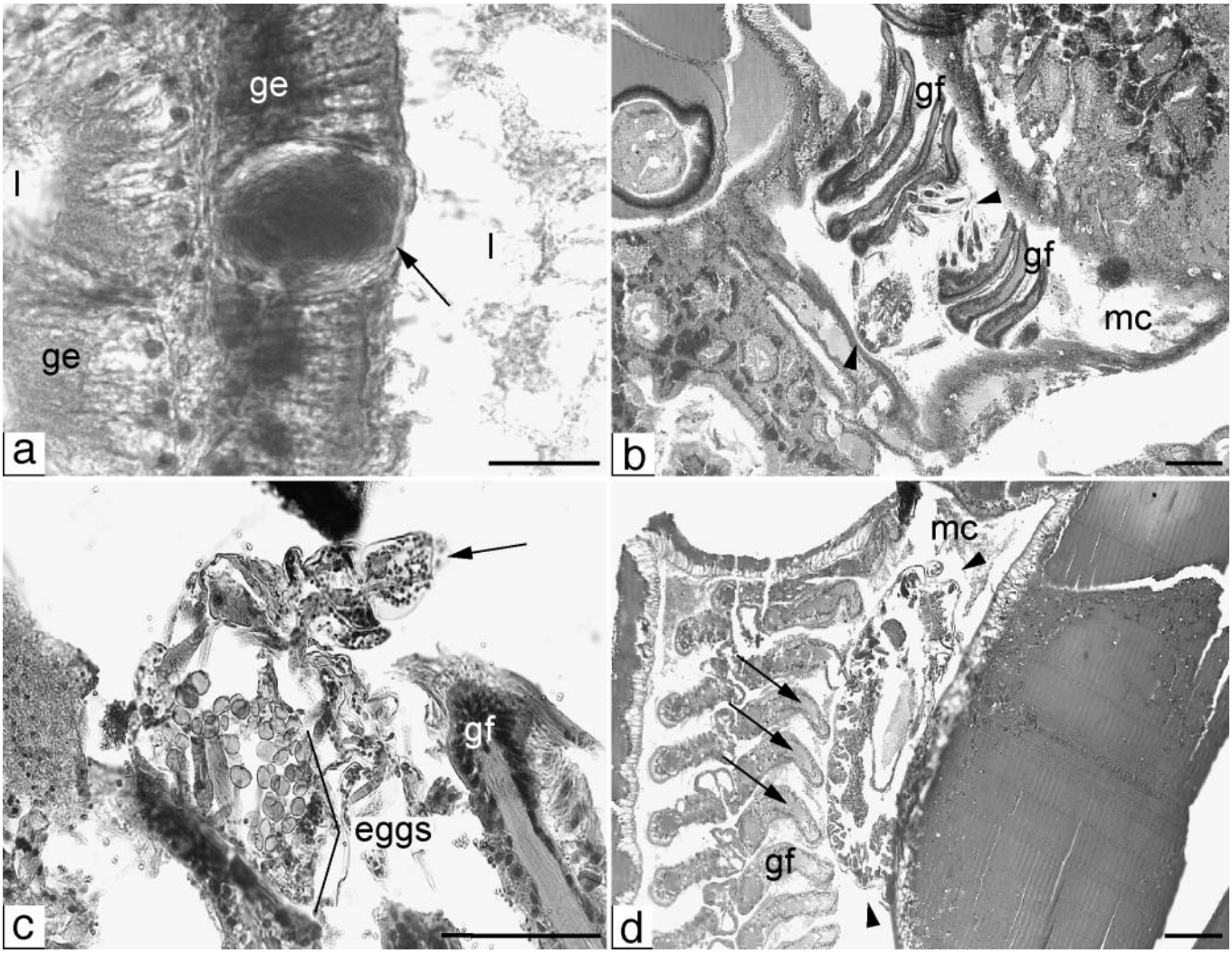

Fig. 4. Types of parasites in *Paralepetopsis floridensis*, and copepods in *Lepetodrilus elevatus*, *Pseudorimula midatlantica*, and *L. fucensis*. (a) Digestive Rickettsia III (arrow) in gut epithelium (ge) of *P. floridensis* (l = lumen); (b) copepod in longitudinal section (between arrowheads), displacing gill filaments (gf) in mantle cavity (mc) of *L. elevatus*; (c) gravid copepod (arrow) between gill filaments (gf) in *P. midatlantica*; (d) copepod (between arrowheads) in mantle cavity (mc) of *L. fucensis*, with gill filament (gf) displacement evident (arrows). Scale bar for (a) = 20 µm, for (b), (c), (d) = 100 µm

structure and with edges lacking a clear definition (Fig. 4a). Inclusions were basophilic with H&E stain. The inclusions appeared to be breaking through the host cell membrane.

Copepods

Unidentified copepods were observed in histological sections of 6 limpets (Table 1). Copepods were found between gill filaments in the mantle cavities of limpets (Fig. 4b), and ranged in size from 165 to 471 µm in length. Female copepods were recognized by the presence of eggs (Fig. 4c). Little tissue damage was observed that could be attributed to the presence of the copepods. Gill filaments were usually pushed aside or apart to make room for the copepod (Fig. 4a,d) and a weak hemocytic response (i.e. increased number of hemocytes) was sometimes observed in the area surrounding the copepod.

Parasite distribution, prevalence and infection intensity in limpets

The highest diversity of parasites was found in *Lepetodrilus elevatus* from vents on the East Pacific Rise. We found 6 types of parasites in *L. elevatus* from Oasis; 3 of these were found in *L. elevatus* from East Wall (Fig. 5). *L. fucensis* limpets from the Endeavour vent site had 2 types of parasites; these were also a subset of the 6 types found in *L. elevatus* from Oasis (Table 1, Fig. 5). No parasite type was common to all vent limpet species; 1 parasite, the gregarine protozoan, was only found in 2 female *L. elevatus* from Oasis (Table 1). No parasites were found in *Pseudorimula midatlantica* from the Snake Pit vent site.

Nearly 50% of limpets sampled from vents had 1 or more parasites (60% if Snake Pit limpets are excluded). Mean infection intensity was variable (16 ± 28 SD parasites per infected limpet). *Lepetodrilus elevatus* from Oasis and East Wall vents each had total parasite prevalences (no. of individuals infected with any parasite) of >60%, but mean infection intensity was nearly 5 times higher at Oasis than at East Wall (Fig. 5), due primarily to the occurrences of Bacterial Inclusion II (Table 1). *L. fucensis* from the Juan de Fuca vent site had a total prevalence of 52%, and a mean infection intensity of about 16 parasite occurrences per limpet (Fig. 5). As in *L. elevatus*, Bacterial Inclusion II contributed most to the mean infection intensity in *L. fucensis* (Table 1)

There was a significant separation in parasite composition and abundance in infected individuals of *Lepetodrilus elevatus* from East Wall and *L. fucensis* from the Endeavour vent (R = 0.662; ANOSIM; Fig. 6), consistent with the observation that these 2 sites do not share any types of parasites. Parasite burdens in *L. elevatus* from Oasis vents could not be distinguished from parasite burdens in *L. elevatus* from East Wall or from parasite burdens in *L. fucensis* from Endeavour vents (R < 0.294; ANOSIM; Fig. 6).

Of the 8 *Paralepetopsis floridensis* limpets sampled from the Florida Escarpment seep, 4 were infected with a parasite, but mean infection intensities were low (1 to 2 parasites individual^{-1}; Table 1).

DISCUSSION

The most dramatic difference in parasite burdens among the 4 species of limpets examined was the apparent absence of any parasite type in *Pseudorimula*

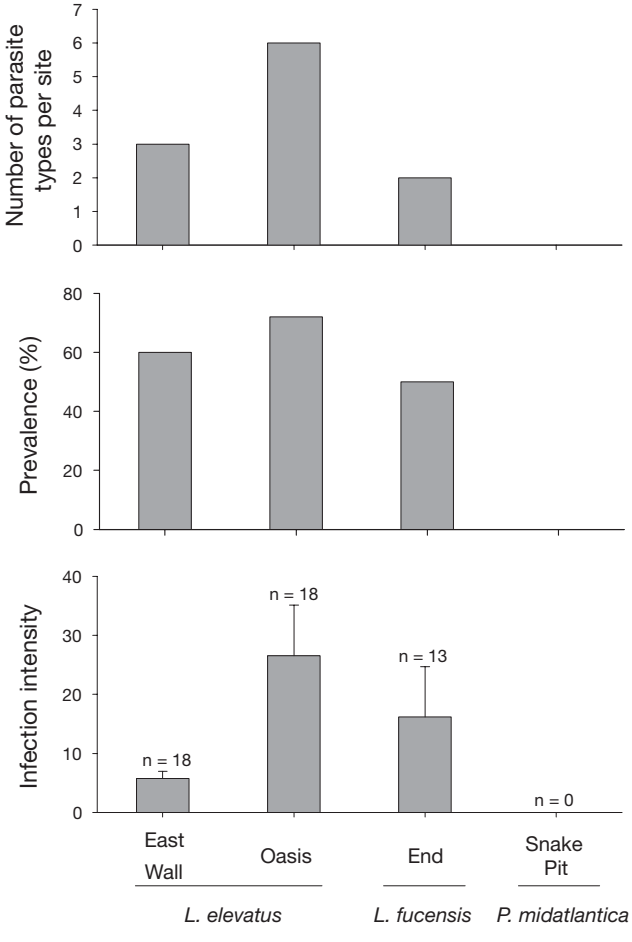

Fig. 5. *Lepetodrilus elevatus*, *L. fucensis*, and *Paralepetopsis floridensis*. Number of parasite types per site, parasite prevalence (percentage of host individuals infected with any parasite), and mean infection intensity (mean number of all parasites per infected individual). n: number of infected individuals; End: Endeavour

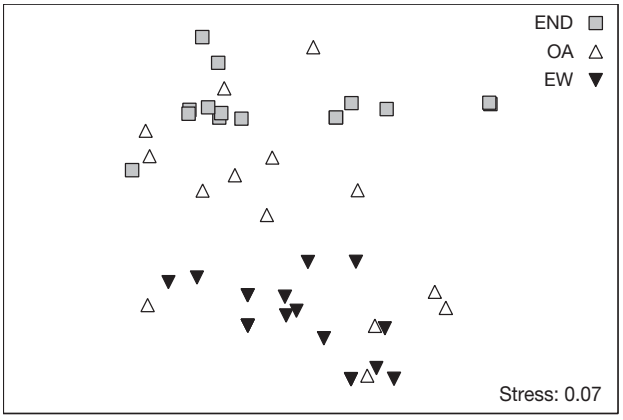

Fig. 6. Unitless MDS plot derived from parasite type—infection intensity matrix. END: Endeavour limpets (*Lepetodrilus elevatus*); OA: Oasis limpets (*L. elevatus*); EW: East Wall limpets (*L. elevatus*). Distances between samples represent dissimilarity in parasite types (and their abundance) infecting individual hosts

midatlantica of the Mid-Atlantic Ridge vent. In contrast, vent limpets from the East Pacific Rise vents and the Juan de Fuca Ridge vent were infected by 3 to 6 types of parasites, with prevalences as high as 72%. Our study was clearly not comprehensive, and a more ambitious survey of parasite burdens is needed to determine if low parasite diversity is typical of Mid-Atlantic Ridge vent invertebrates. Lower invertebrate diversity on the MAR compared to the EPR is known for mussel-bed communities (Van Dover & Trask 2000, Turnipseed et al. 2003, M. Doerries & C. L. Van Dover pers. comm.) and has been attributed to the greater spacing between vents on the MAR (Baker et al. 1995) that in turn may result in a greater probability of extinction due to dispersal limitation (Van Dover 1995). Other non-exclusive explanations for lower diversity at MAR vents, including greater habitat area on the EPR, are possible (Juniper & Tunnicliffe 1997).

The 2 populations of *Lepetodrilus elevatus* that we sampled (East Wall and Oasis populations) were separated by 27° of latitude and shared 3 types of parasites (Bacterial Inclusion I, Digestive Rickettsia I, and Digestive Rickettsia II). The Oasis population had higher parasite intensities and overall greater parasite diversity than the East Wall population. Higher parasite intensities are often correlated with greater host population densities (Price 1990), but in this case, limpet densities at Oasis were 1 order of magnitude lower than limpet densities at East Wall (Van Dover 2003). *L. elevatus* and its congener, *L. fucensis* from the Juan de Fuca Ridge vent site, shared 2 types of parasites (Bacterial Inclusion II and Gill Rickettsia). More definitive, molecular characterization of the parasites is required before we can be sure that these are shared species. To our knowledge, *L. fucensis* is the only vent limpet species known to be colonized by endosymbiotic bacteria (de Burgh & Singla 1984), yet it had the lower parasite prevalence of the 2 congeners. In bathymodiolin mussels from deep-sea seeps and vents, parasitic infection was correlated with endosymbiont density (Ward et al. 2004).

We found 2 types of parasites specific to a single species and/or site: the gregarine protozoan was only found in *Lepetodrilus elevatus* from the Oasis vent on the East Pacific Rise; Digestive Rickettsia III was only found in *Paralepetopsis floridensis* from the Florida Escarpment seep. In general, gregarines and rickettsia-like parasites are not host-specific in shallow-water molluscs (Lauckner 1983); we anticipate that further sampling effort will reveal these types of parasites to be present elsewhere.

All types of parasites found in vent and seep limpets are known to occur in shallow-water molluscs. Gregarines are a common, benign parasite of shallow-water marine molluscs (Lauckner 1983), with prevalences of up to 100% in some cockle populations (Carballal et al. 2001). In vent and seep limpets, however, gregarines have low prevalences, and no gregarines have been identified in mussels from seeps or vents (Powell et al. 1999, Ward et al. 2004).

Rickettsia-like infections represent another parasite type commonly found in shallow-water marine molluscs. Prevalence of rickettsia-like parasites was higher in EPR (East Wall and Oasis) limpets and Juan de Fuca (Endeavour) limpets (up to 52% of the individuals sampled) than commonly found in intertidal mussels and cockles (Kim et al. 1998, Carballal et al. 2001). Rickettsia-like parasites were also identified in *Bathymodiolus* spp. mussels from seeps (Powell et al. 1999, Ward et al. 2004) and vents (Ward et al. 2004). Prevalences of rickettsia-like parasites were lower in EPR and Juan de Fuca Ridge vent limpets than observed in shallow-water hydrocarbon seep mussels by Powell et al. (1999) or in some deep-sea seep and vent mussels by Ward et al. (in press). Rickettsia-like infections have been occasionally linked to fatal diseases in shallow-water molluscs (Lauckner 1983). For example, rickettsia-like infections are implicated in the withering syndrome in *Haliotis cracherodii* (Gardner et al. 1995) and in mortalities of *Placopecten magellanicus* (Gulka et al. 1983). In most cases, high intensities of a rickettsia-like infection are required before the infection becomes fatal (Lauckner 1983). Low intensities of rickettsia-like infections in vent limpets suggest that it is unlikely that these infections were detrimental to their hosts. No evidence for rickettsia-related mortality was found in *Bathymodiolus* spp. mussels from seeps Powell et al. 1999, Ward et al. 2004) or vents (Ward et al. 2004).

We did not find 2 common molluscan parasites, trematodes and viral inclusions, in vent limpets. Trematodes are harmful parasites that occur in molluscs in both coastal environments and shallow-water seeps (Kim et al. 1998, Powell et al. 1999, Montaudouin et al. 2000), but trematode infections have yet to be observed in deep-sea hydrothermal-vent or seep molluscs (Ward et al. 2004, and present study). The absence of trematodes from vents and seeps could be due to environmental factors and the lack of a suitable intermediate host (Ward et al. 2004). Although relatively common in intertidal molluscs, viral infection has not been observed in shallow-water seep mussels or deep-sea limpets (Lauckner 1983, Powell et al. 1999, this study), but a virus has been inferred to have a negative influence on the population structure of a seep mussel (Ward et al. 2004).

Copepods were found between gill filaments and in the mantle cavities of limpets from EPR, MAR and Juan de Fuca Ridge vent fields, but they did not appear to have a detrimental effect on their hosts. Copepod infestation of vent limpets was not correlated with parasite infection of the limpets. The appearance of copepods in marine molluscs, especially in mussels, is not uncommon (Lauckner 1983). Copepods are most frequently associated with the gills and the mantle cavity, where they are rarely observed to cause damage to the organism, and in the digestive tract, where infestation can cause tissue destruction (Lauckner 1983, Cáceres-Martínez & Vásquez-Yeomans 1997, Boxshall 1998). Copepods found near gills and in the mantle cavity are typically thought to have a commensal relationship with their host, and may be adapted to acquire food with the assistance of their host's feeding mechanism (Lauckner 1983). Examination of additional copepod-infested individuals is needed to clarify the relationship between limpets and copepods.

Although we detected no evidence for a strong influence of parasites on host limpet population dynamics in the material we examined from deep-sea chemosynthetic environments, we did discover parasites that have the potential to be ecologically important. It would be useful to track parasite burdens in populations exposed to different environmental conditions within a vent field over the duration of active venting. This kind of time-series and habitat-quality approach to parasitological ecology would complement more traditional ecological approaches that consider population dynamics of invertebrates in relation to habitat quality or biological interactions involving competition, predation, and facilitation.

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