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Amphipods associate with epibiotic filamentous bacteria at a shallow-water hydrothermal vent

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In the deep ocean, hydrothermal vents sustain remarkable animal–microbial symbioses, in which bacteria colonizing animal external or internal tissues use reduced chemicals from venting fluids to perform chemosynthesis and nourish their host. Hydrothermal vents also occasionally occur within the photic zone, but the prevalence of photosynthesis within these settings is considered to override the development of chemosymbiotic interactions; animal–microbial associations such as those observed at deep-sea vents have rarely been recorded at shallow vents. During 2019 sampling of the Strýtan hydrothermal vent site, Eyjafjörður, Iceland (16–70 m depth), amphipods in the genus *Ischyrocerus* were opportunistically collected from near the top of the tallest vent chimney. A subset of these were found to have microbial mats specifically colonizing their antennae, with prevalent bacteria in these mats demonstrating genetic similarity to deep-sea hydrothermal vent bacteria, including ectosymbionts of vent-endemic crustaceans. These findings demonstrate the importance of vent productivity to the development of unique associations between animals and putatively chemosynthetic bacteria even in environments where photosynthesis dominates, highlighting a pathway through which more intimate vent symbioses may arise, as well as the influence of vent environments in animal evolution throughout ocean depths.

1. Introduction

Symbioses with microbes are essential to the nutrition of animals within deep-ocean hydrothermal vents, where specialized invertebrates from tubeworms to crabs feed on bacteria capable of chemosynthesis that colonize their external surfaces or tissues [1]. In the absence of light, chemosynthetic productivity at vents represents a crucial food source in an otherwise food-limited deep ocean.

Although rarer, hydrothermal vents also occur within shallow, photic zone waters, and represent dynamic energy-rich environments in which both photosynthesis and chemosynthesis co-occur owing to the simultaneous presence of light and reduced compounds [2–4]. An obvious difference between shallow-vent habitats and their deep-sea counterparts is a general lack of specialized invertebrates exhibiting symbioses with chemosynthetic bacteria. The absence of such interactions is considered to be a consequence of a lack of energetic advantage, and thus evolutionary pressure, to develop such associations [3]. However, examples of metazoans with chemosynthetic symbioses are reported from a number of shallow vent sites (<200 m water depth), including a vestimentiferan in Kagoshima Bay, Japan [5], a crab from Kuishan Island, Taiwan [6], a nematode from the Bay of Plenty, New Zealand [7], and a platyhelminthes from Deception Island, Antarctica [8]. Where vent-specialist taxa have been discovered at shallow-water vents, their diet appears to include considerable input from photosynthetic productivity [9,10]. Nevertheless, the occurrence of chemosynthetic symbioses at shallow vents is likely to confer additional benefits to the host and could thus be potentially widespread, given the ubiquity of chemosynthetic symbioses in the oceans [11].

The Strýtan hydrothermal vent site (also known as Big Strýtan; Strýtan herein) occurs at 16 to 70 m depth within the Eyjafjörður fjord of northern Iceland, and represents a cluster of active, basalt-hosted vent cones or chimneys located within the photic zone [12] that probably started forming at the end of the last Ice Age (11 000 years ago) [13]. Comprised mainly of the clay mineral saponite, these chimneys emit warm (<70°C) alkaline fluids (pH < 10.2) with elevated concentrations of hydrogen and methane [13–16]. Strýtan macrofauna consist of algae and benthic invertebrates representing usual hard substrate fauna in the region [13], which cover much of the chimneys aside from vent fluid outlets that are more abundant in their upper sections. Microbial communities exhibit high similarity to terrestrial hot springs, whereas elevated concentrations of hydrogen sulfide in Strýtan vent fluids as well as abundant dissimilatory sulfate-reducing microorganisms indicate the presence of active sulfur cycling [12]. The biological communities of these chimneys are, however, little studied, and it is not known how fauna interact with vent fluids emitted at this unique site.

Unexpectedly, we found amphipods with abundant filamentous bacteria attached to their exoskeletons following faunal sampling at Strýtan. We characterized these bacteria and their association with the amphipods using fluorescence *in situ* hybridization (FISH), 16S rRNA amplicon sequencing, phylogenetics, and bacterial sequence comparison tools. Our findings show that anterior appendages of these *Ischyrocerus* sp. amphipods are covered mainly by *Cocleimonas* (Gammaproteobacteria) and *Sulfurovum* (Campylobacteria) bacteria that are also present on other marine fauna on the chimneys, such as hydroids, and exhibit genetic similarity to chemosynthetic ectosymbionts of deep-sea hydrothermal vent crustaceans.

2. Material and methods

(a) Sample collection

Amphipod sampling of the main Strýtan hydrothermal vent chimney, Eyjafjörður, Iceland (65.82883 N, 18.1115 W; supplementary material, figure S1), took place through SCUBA diving on 16–17 June 2019 (research permit reference UST201812-041/P.V.B. of the Environment Agency of Iceland; export permit reference 2-019-010-015/43-0 of the Icelandic Institute of Natural History). A VideoRay Pro 4 remotely operated vehicle was used to perform video surveys and take still images of Strýtan and its fauna. Amphipods were captured opportunistically during the collection of hydroid clumps and a vent chimney fragment, placed by divers into sealed plastic pots. Samples were kept cold until processing, preserved using RNAlater or 80% ethanol (supplementary material, table S1), and were photographed before and after preservation using a Canon 500D DSLR camera attached to a Leica MZ9.5 stereomicroscope. During post-preservation microscopy, it was noticed that a subset of collected amphipods (4 out of 33 amphipods collected in total), in particular males recognized by enlarged second gnathopods, had microbial mat coatings associated primarily with their second antenna. These four male specimens were selected for further analysis, and their morphology was examined. Bryozoans, hydroids, sponges, a bivalve and a microbial mat from Strýtan and nearby sites (supplementary material, table S1 and figure S1) were also selected for comparative microbiome analysis (see §2c).

(b) DNA extraction, PCR amplification, and sequencing

A single second antenna was removed from amphipod specimens, and DNA was extracted from the above as well as from bryozoan and hydroid branches, bivalve gill, a microbial mat clump, and sponge body tissue (supplementary material, table S1) using a Qiagen DNEasy Blood and Tissue Kit, following manufacturer instructions but using 100 µl elution volumes. To aid taxonomic identification of amphipod specimens, an approximately 650 bp fragment of the cytochrome c oxidase I (COI) gene was amplified and sequenced using the primers LCO1490 and HCO2198 [17] as in [18]. Our amphipod sequences were aligned with NCBI GenBank sequences from across the Ischyroceridae family, with Photidae species as an outgroup [19], using MUSCLE [20] in Geneious v.10.2.5 [21]. The best-fitting substitution model for the DNA alignment (GTR+I+G) was detected using jModelTest v.2.1.10 [22,23], and the phylogenetic analysis was performed using MrBayes v.3.2.6 [24].

(c) Microbiome sequencing and data processing

Processing of sample DNA for microbiome analysis was performed by targeting the V4 variable region of the 16S SSU rRNA gene. Libraries were sequenced on an Illumina MiSeq platform to obtain amplicon sequence lengths of approximately 298 bp,

and resulting reads were handled using the qiime2 microbiome amplicon analysis tool v. 2026.1 [25] and packages within to demultiplex samples, remove primers, perform quality filtering, remove chimeras, denoise reads to infer prokaryote amplicon sequence variants (ASV), assign taxonomic classification to the ASVs, and calculate Bray–Curtis and UniFrac distances following rarefaction of the reads to 100 000 (see supplementary material, code.txt). Five samples that had filtered reads below 100 000 were not included in distance calculations (Bryozoa_125, Bryozoa_139, Bryozoa_140, Hydrozoa_100, and Mytilus_146). In R [26], the packages *tidyverse* [27], *phyloseq* [28], *vegan* [29], and *ANCOMBC* [30] were used to analyse and visualize the amplicon dataset. Permutational multivariate analyses of variance (PERMANOVA) were conducted on Bray–Curtis and UniFrac distances using 999 permutations and the R package *vegan* to test whether microbial community composition varied between four groups of host taxa (amphipods, bryozoans, hydroids and sponges). An Analysis of Composition of Microbiomes (ancombc2) was performed using *ANCOMBC* to determine which prokaryote ASVs and genera drove differences in community composition between the above four groups, with amphipods used as the reference.

Amplicon sequences of the 10 most abundant ASVs were queried using the SILVA Alignment, Classification and Tree Service [31], using the option to add them to a tree computed on neighbours' full-length sequences, as recommended for short reads. This analysis outputs an unrooted tree in which query sequences are placed alongside closest matches from the SILVA reference database (and is not intended to represent deeper evolutionary relationships). These sequences were also used to query metagenome projects deposited in the NCBI Sequence Read Archive (SRA) using Logan-Search [32].

(d) Fluorescence *in situ* hybridization

The remaining second antenna of the four selected amphipods was used for FISH. Amphipod tissues were post-fixed in 3% formalin solution prepared with 1× phosphate-buffered saline (PBS) for 2 h at room temperature. They were subsequently rinsed in 1× PBS, dehydrated using a graded ethanol series from 70% to 100%, and placed within cavity slides. Samples were hybridized for 3 h at 46°C with the following probe and fluorophore combinations: Eub338-Alexa488 [33], Gam42a-Cy3 [34], Epsy914-Cy5 [35], mixed within hybridization buffer prepared as in [36]. Following this, samples were washed in tubes using washing buffer (also as in [36]) for 15 min at 48°C, rinsed with autoclaved distilled water, then dried, placed on slides, covered with Slow Fade Gold antifade reagent containing 4',6-diamidino-2-phenylindole (DAPI, Invitrogen), and sealed with a cover slip. Visualization was performed using a Zeiss AxioImager.Z2 equipped with an Apotome.2 sliding module and Colibri.7 LED system light technology, and a Zeiss LSM 780 confocal microscope using the photon counting method to reveal and quantify fluorescence as a spectrum. All micrographs were acquired with Zeiss Zen software.

3. Results

(a) Amphipod identification

Morphological investigation and COI phylogenetic analysis (supplementary material, figure S2) indicate that individuals with microbial-coated second antennae collected from near the summit of the main Strýtan vent chimney belong to the genus *Ischyrocerus* Krøyer, 1838. Additional *Ischyrocerus* sp. amphipods collected during Strýtan sampling, both male and female, did not have obvious microbial coatings. This genus is widely reported from the North Atlantic, Arctic and subarctic, although the taxonomy of the clade is unresolved and in need of revision [37]. Our specimens are a morphological match to the species *Ischyrocerus* sp. T-2, collected from Greenland and described and illustrated in [38]. This morphospecies is characterized (in male specimens) by the propodus of gnathopod 2 being more slender than those seen in *Ischyrocerus minutus* Liljeborg, 1851 and *Ischyrocerus anguipes* Krøyer, 1838, with a straight posterior margin and a rounded protuberance distally. The basis of pereopods 5–7 is slender with nearly parallel anterior and posterior margins; spines on the telson are slender with the outer spine of each pair longer than the inner spine. COI genetic distances of 0.9–2.2% (supplementary material, table S2) suggest our specimens are closely related to *Ischyrocerus* sp. from Hudson Bay and the Northwestern Passages, Canada. Notably, species of the genera *Jassa* and *Microjassa* are nested among *Ischyrocerus* species; a more comprehensive phylogenetic analysis using more markers would be needed to assess the monophyly of *Ischyrocerus*.

(b) Prokaryotic community characterization

Our amplicon dataset consisted of 6 208 259 filtered reads, representing 87% of the total raw reads (supplementary material, table S3). The 10 ASVs with the most reads comprised 26% of the dataset. When classified taxonomically, the majority of ASVs belonged to the classes Gammaproteobacteria, Bacteroidia, Alphaproteobacteria, Verrucomicrobiae, and Campylobacteria (supplementary material, figure S3). At the family level, Thiotrichaceae Gammaproteobacteria were notably abundant in some amphipods and also some hydroids. Flavobacteriaceae, Rhodobacteraceae, Saprospiraceae, and Sulfurovaceae were present in high proportions in one or more amphipods, as well as in varying proportions in the other sampled taxa (supplementary material, figure S3). Francisellaceae was abundant in some hydroids only. *Cocleimonas* and *Sulfurovum* ASVs contributed the greatest proportions of reads to amphipod samples (figure 1). Additionally, *Aliivibrio*, unclassified Saprospiraceae, *Pseudoalteromonas*, and *Neorickettsia* ASVs contributed highly to one or more *Ischyrocerus* sp. T-2 individuals. *Sulfurovum* ASVs were also prominent in several hydroids, while on the whole different *Cocleimonas* ASVs dominated amphipod and hydroid samples (figure 1). A *Francisella* ASV was

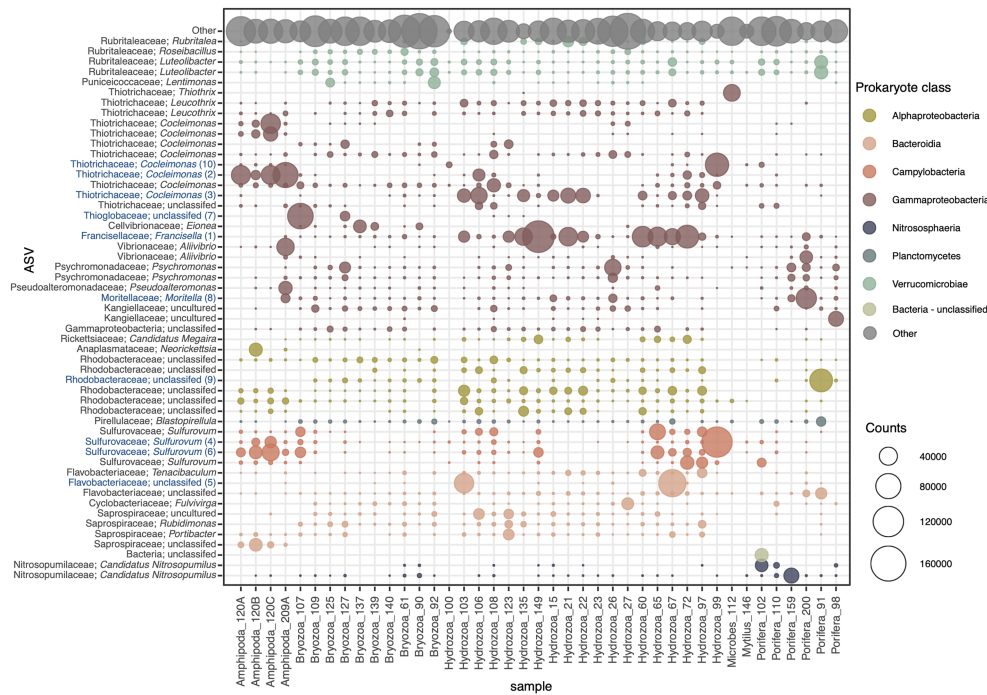


Figure 1. Relative abundances of the most common ASVs for a 16S amplicon dataset, including *Ischyrocerus* sp. T-2 amphipods as well as bryozoans, hydroids, sponges, a microbial mat and a mussel from Strýtan and two additional Eyjafjörður sites. Bubbles are coloured by bacterial class, whereas family and genus (or lowest possible taxonomic identification) are provided as labels. ASVs with counts lower than 20 000 across the dataset were pooled into the category 'Other'. Blue labels indicate the 10 most abundant ASVs in the dataset, with their rank given in parentheses.

notably abundant in hydroids but not in other phyla, as well as an unclassified Flavobacteriaceae ASV in two of the hydroid samples. A *Moritella*, an unclassified Rhodobacteraceae, and two *Nitrosopumilus* (Nitrosopumilaceae) ASVs were also prominent in sponges.

The PERMANOVA analysis based on Bray–Curtis distances indicated a significant difference in microbial community between the sample groups ($F = 2.81$, $R^2 = 0.27$, $p = 0.001$, $n = 36$). PERMANOVA analyses based on weighted and unweighted UniFrac distances were also significant ($F = 2.75$, $R^2 = 0.26$, $p = 0.001$, and $F = 2.50$, $R^2 = 0.24$, $p = 0.001$, respectively), with sample grouping being more apparent according to unweighted UniFrac distance (supplementary material, figure S4). Unweighted UniFrac distance grouped all four *Ischyrocerus* sp. T-2 specimens together, with these showing greatest similarity to a vent fluid-influenced hydroid specimen from a separate sample. ANCOMBC2 analysis identified only a single ASV that differed significantly between amphipods and any of the other groups, a *Roseibacillus* ASV (supplementary material, table S4). With ASVs grouped by genus, ANCOMBC2 results identified 23 genera to vary significantly between amphipods and other groups, with the genera *Roseibacillus*, *DEV007*, *Ulvibacter* and *Yoonia-Loktanella* differing significantly between amphipods and all other groups (supplementary material, table S5). The genera *OM190*, *Blastopirellula*, *Nitrosopumilus* and *Cocleimonas* varied significantly between amphipods and bryozoans and amphipods and sponges, whereas *Sphingorhabdus*, *Rubritalea* and unclassified Cyclobacteriaceae varied significantly between amphipods and bryozoans and amphipods and hydroids.

Silva ACT placed *Cocleimonas*, *Sulfurovum* and Thioglobaceae ASVs alongside 16S reference sequences from bacteria sampled at hydrothermal vent, submarine volcano, and cold seep environments, including many symbionts of deep-sea hydrothermal vent crustaceans and molluscs (supplementary material, figure S5). *Francisella* and unclassified Rhodobacteraceae ASVs were mainly placed alongside environmental (seawater, sediment) sequences; *Moritella* ASV exhibited similarities to fish gut microbiome sequences; and the unclassified Flavobacteriaceae ASV showed similarity to both a fish intestine and environmental sequences. Logan-search results that exactly matched kmers from the 10 most abundant ASVs in the dataset (kmer coverage equal to 1; supplementary material, table S6) notably showed a high proportion of matches to 16S rRNA sequences contained in hydrothermal vent metagenomes for four of the ASVs (supplementary material, figure S6b,e–g), with the majority of matches overall reflecting marine metagenomes, including seawater and sediment. Six of the ASVs (1_ *Francisella*, 3_ *Cocleimonas*, 5_ Flavobacteriaceae, 6_ *Sulfurovum*, 9_ Rhodobacteraceae, 10_ *Cocleimonas*) matched to SRA sequences from a previous study of microbial communities from Strýtan vent fluid and chimney samples [12].

(c) Fluorescence *in situ* hybridization

Microbial mats on *Ischyrocerus* sp. T-2 second antennae (figure 2a, b) were more apparent and distinguishable from setae following FISH with general Gammaproteobacteria and Campylobacteria probes (Gam42a and EPSY-914, respectively). Filamentous bacterial mats were densest on the middle joint of the second antennae, but varied in coverage between individuals

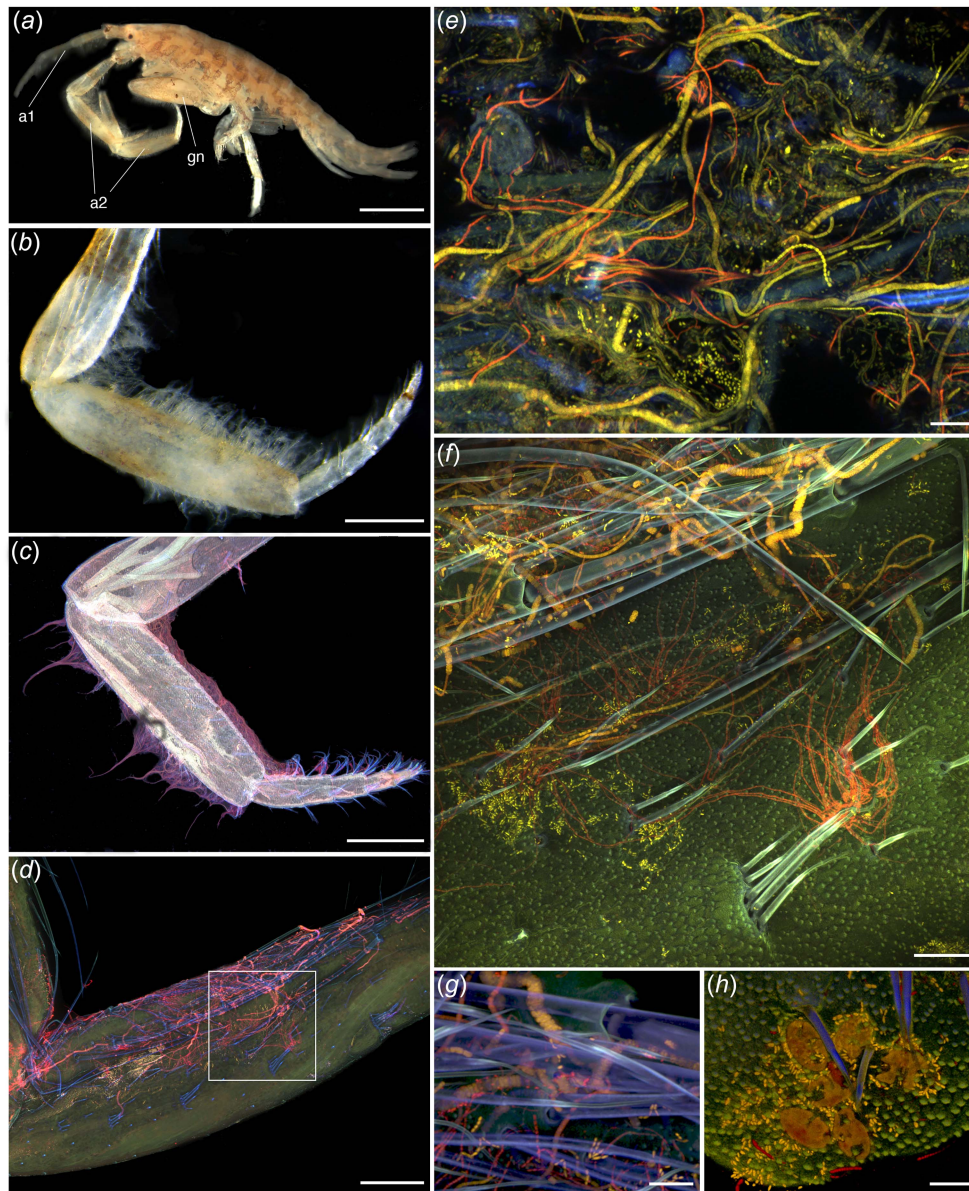


Figure 2. Bacteria colonizing the second antennae of *Ischyrocerus* sp. T-2 amphipods from the Strytan hydrothermal vent chimney, Iceland. (a,b) Light microscopy images. (a) Complete view of an amphipod specimen 120A; scale bar is 1 mm. Abbreviations: a1, antenna-1; a2, antenna-2; gn, gnathopod. (b) Light microscopy detail of amphipod antenna-2 (specimen 120A) with a filamentous microbial coating. Scale bar, 400 μ m. (c–h) FISH microscopy images, whereby samples are hybridized with the probes Gam42a-Cy3 to visualize Gammaproteobacteria (in yellow) and Epsi914-Cy5 to visualize Campylobacteria (in red); sample tissues are stained with DAPI (blue). (c) Antenna-2 of amphipod specimen 120A. Scale bar, 400 μ m. (d) Antenna-2 of amphipod specimen 120C. Scale bar, 100 μ m. Box shows location of (f). (e) Detail of antenna-2 surface of amphipod specimen 120A. Scale bar, 10 μ m. (f) Detail of microbes in (d) (probes as above). Scale bar, 20 μ m. (g) Detail of three main filamentous microbial morphotypes (specimen 120C). Scale bar, 10 μ m. (h) Detail of rod-shaped Gammaproteobacteria (specimen 120C). Scale bar, 10 μ m.

(figure 2c,d). The thickest filaments (up to 2.5 μ m in diameter) had a stacked appearance, were hybridized with the Gammaproteobacteria probe (figure 2e, in yellow) and occurred tangled among amphipod setae. This morphotype was occasionally not hybridized with either probe, possibly owing to low vigour, giving it a pale orange appearance (figure 2f,g). Two additional bacterial morphotypes hybridized with the Gammaproteobacteria probe: chains of rods approximately 0.6 μ m in diameter (figure 2e,g), and individual rods, with an approximately 1 μ m long axis (figure 2f,h). The Campylobacteria probe primarily hybridized a single filamentous morphotype up to 0.8 μ m in diameter, which under greater magnification appeared segmented (figure 2e–h, in red) and occurred as clusters attached to, or tangled among, setae with other bacterial morphotypes.

4. Discussion

Despite a limited amphipod sample size given the opportunistic nature of the discovery presented here, our analyses nevertheless demonstrate colonization of *Ischyrocerus* sp. T-2 antennae primarily by *Cocleimonas* and *Sulfurovum* bacteria that demonstrate genetic similarity to types found at deep-sea hydrothermal vents.

The prevalence of gammaproteobacterial and campylobacterial taxa in these mats was apparent in both 16S amplicon and FISH results (figures 1 and 2). The largest filaments that were hybridized by the general gammaproteobacterial probe (figure 2e) correspond to reported morphotypes of Thiotrichaceae, such as for the genera *Leucothrix* and *Thiothrix* [39–41]. Rods and rod-chains hybridized with the Gammaproteobacteria probe (figure 2e,f,h) may, on the other hand, represent the *Cocleimonas* ASVs present in high proportions in 16S amplicon results [42]. As *Sulfurovum* was the main type of Campylobacteria present in our 16S amplicon results, it is possible that this genus corresponds to the thin filaments hybridized with the EPSY-914 probe observed using FISH (figure 2e–h).

Although further sequencing would be required to refine their identity, the closest matches to *Cocleimonas*, *Sulfurovum*, and Thioglobaceae from the surfaces of Strýtan amphipods, bryozoans, hydroids and sponges are bacteria commonly found within marine environments, particularly hydrothermal vents, as well as types that occur as ectosymbionts on deep-sea hydrothermal vent crustaceans (supplementary material, figures S5–S6 and table S6). The ectosymbionts of deep-sea vent crustaceans such as *Kiwa* sp. and *Rimicaris exoculata* are considered to be chemolithoautotrophs [43] and chemolithoheterotrophs [44] reliant on reduced compounds, and at Strýtan similar bacteria could be exploiting the hydrogen, methane or sulfide available in Strýtan vent fluids [12,14]. Other prominent bacteria associated with fauna sampled at Strýtan (*Francisella*, *Moritella*, unclassified Flavobacteriaceae and Rhodobacteraceae) probably represent heterotrophic members of the microbial community.

The most parsimonious interpretation for the nature of the association between Strýtan *Ischyrocerus* sp. T-2 and the bacteria colonizing them would suggest bacterial fouling of the amphipod antennae. Although the microbial community colonizing Strýtan *Ischyrocerus* sp. T-2 antennae was significantly distinct from that of bryozoans, hydroids, and sponges from Strýtan and two additional Eyjafjörður sites, the microbial taxa that drove these differences were largely not the bacteria dominating the dataset (supplementary material, tables S4 and S5). The genera *Cocleimonas* and *Sulfurovum* found in high proportions in Strýtan *Ischyrocerus* sp. T-2 samples were also present in the hydroids that they were found amongst (figure 1; supplementary material, figure S4), and not all *Ischyrocerus* sp. T-2 individuals demonstrated obvious microbial coatings. It is, however, surprising that bacteria associated with the four Strýtan *Ischyrocerus* sp. T-2 sequenced herein were found on the same body part of the amphipods, the second antenna. In the cave amphipod species *Niphargus ictus*, chemoautotrophic *Thiothrix* bacterial symbionts were observed mainly on the joints of antennae and gnathopods [45], similar to our observations. These bacteria were interpreted to be ‘hitch-hiking’ on mobile amphipods, to benefit from host traversal between oxic and anoxic microenvironments to access both sulfide and oxygen. Bacterial mats of densely packed putative sulfur-oxidizing Gammaproteobacteria and Campylobacteria have also been observed on the antennae of four deep-sea hydrothermal vent shrimp species [46], with their presence noted as unusual given the sensory function of antennae. In the above study, it was hypothesized that these bacteria are not fouling the antennae but may have a detoxification, nutritional, or sensory function. *Cocleimonas* and *Sulfurovum* bacteria adapted to exploiting vent conditions and growing on hydroid clumps could also be opportunistically transferred to a subset of *Ischyrocerus* sp. T-2 amphipods occupying this habitat. It is possible that some individuals permit the growth of these bacteria on their appendages, with a distinct *Cocleimonas* ASV subsequently proliferating in this microhabitat (figure 1). A distinct microbial community in terms of composition also appears to establish on the amphipods; however, with variability of dominant bacteria between host individuals (supplementary material, figure S4).

Although further sampling and analysis would be required to establish whether the bacteria observed on Strýtan *Ischyrocerus* sp. T-2 are symbionts, the existence of this interaction at the little-studied Strýtan hydrothermal vent site, along with a much wider body of literature on invertebrate–chemosynthetic–bacterial associations from a range of aquatic settings [40,41,45], including shallow-water vents [5–8], indicates a potential pathway through which symbiotic interactions may arise at hydrothermal vents, even in environments where photosynthetic production dominates. Reducing fluids provide an additional niche that can be exploited, and depending on their concentration and stability, offer favourable conditions for bacterial growth on invertebrate tissues that could pave the way for the establishment of mutualistic nutritional symbioses.

The results presented here also shed light on faunal microbiomes at the Strýtan vent site, highlighting novel aspects of the prokaryotic community, as well as overlaps with microbiomes of Strýtan vent fluids and chimney surfaces [12]. These ‘cobionts’ emphasize a wealth of prokaryote–animal interactions that can be further explored to understand the ecology of unique marine sites such as Strýtan, as well as the diversity of ocean microbiomes more generally [47].

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The 16S amplicon dataset generated during this study is available through the NCBI SRA under BioProject accession number PRJNA957948 and sample accession numbers SAMN34274287 to SAMN34274327. *Ischyrocerus* sp. T-2 COI sequences used in the phylogenetic analysis are available on NCBI GenBank under accession numbers OQ850035 and OQ850036. Code used to analyse amplicon data and generate figures and a description of the data are available as part of the supplementary material [48].

Declaration of AI use. ChatGPT 5.5 (OpenAI; accessed April–May 2026) was used to assist with setting up and running qiime2 using singularity on a compute cluster. No AI tools were used to interpret data or in the writing of the article.

Authors' contributions. M.N.G.: conceptualization, data curation, formal analysis, funding acquisition, investigation, visualization, writing—original draft, writing—review and editing; L.D.: formal analysis, methodology, visualization, writing—review and editing; M.-A.C.: funding acquisition, project administration, supervision, writing—review and editing; C.T.S.L.: conceptualization, data curation, funding acquisition, investigation, writing—review and editing; G.B.-C.: data curation, investigation, writing—review and editing; J.T.C.: conceptualization, data curation, funding acquisition, investigation, writing—review and editing; E.C.D.S.: formal analysis, writing—original draft, writing—review and editing; P.E.: visualization, writing—review and editing; J.S.: investigation, writing—review and editing; E.B.: investigation, writing—review and editing; A.G.G.: conceptualization, data curation, funding acquisition, investigation, project administration, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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