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Diversity and host specificity of shrimp-like crustaceans (Decapoda: Caridea) associated with mesophotic and deep-sea coral communities in the western Atlantic

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Abstract

Background.

Mesophotic and deep-sea coral ecosystems support diverse crustacean assemblages, yet the diversity and host associations of their shrimp fauna remain poorly understood. This study investigates the diversity, species boundaries, and host associations of shrimp-like decapods, primarily caridean shrimps, associated with coral communities in the western Atlantic.

Results.

Through an integrative approach combining morphological analyses, genome skimming, molecular species delimitation, and ecological analyses, we identified 61 species from samples collected between 29 and over 1,800 m depth. Molecular analyses revealed multiple putative cryptic or pseudocryptic lineages. Of the 61 species, 22 were classified as obligate associates, 11 as potential facultative associates, and 28 had no documented symbiotic associations. Octocorals were the most frequently recorded hosts, followed by sponges and black corals. Host use varied among shrimp taxa, ranging from associations with a single host group to broader host ranges. Remotely operated vehicles and autonomous reef monitoring structures sampled complementary assemblages, highlighting the value of combining sampling methods. Rarefaction analyses indicated that species richness remains incompletely documented, particularly below 300 m depth.

Conclusions.

These findings reveal substantial hidden species and ecological diversity among shrimp-like decapods associated with western Atlantic mesophotic and deep-sea coral communities. Integrating morphological, molecular, and ecological evidence improves biodiversity assessments and highlights the need for further sampling and integrative taxonomic studies. This work provides a baseline for future research on host associations and for biodiversity monitoring and conservation of these vulnerable and unknown ecosystems.

Background

Deep-water coral communities remain largely underexplored compared to shallow-water ecosystems due primarily to logistical challenges and limited access [1, 2]. Recent studies indicate that deep-water coral ecosystems, i.e., coral-dominated habitats in mesophotic (in a broad sense, including rariphotic, ~ 50–300 m) and bathyal zones (> 300 m) support a biodiverse fauna that parallels or, in some areas, even exceeds that of shallow coral reefs [3]. Mesophotic and bathyal corals found at depths greater than 50 m, hereafter summarized as deep-water corals, offer habitat heterogeneity that encompasses a vast array of species from various phyla and serve as marine refugia (e.g., [4–7]). The ecological

characteristics of deep-water coral habitats make them similar to their shallow-water counterparts, most notably in terms of their vulnerability and resilience to environmental disturbances. Nevertheless, various stress factors, such as ocean acidification, ocean warming resulting in thermal stress, and increasing anthropogenic activities, including oil spills, pollution, excessive bottom trawling, deep-sea mining etc., are significant concerns for deep-water coral communities (e.g., [8–10]).

One of the largest anthropogenic disturbances to deep-water coral habitats was the *Deepwater Horizon* oil spill that occurred in April 2010 in the northern Gulf of America (formerly called "Gulf of Mexico", referred to hereafter as the Gulf) [11, 12]. Recent expeditions using remotely operated vehicles (ROV) and Autonomous Reef Monitoring Structures (ARMS), surveyed habitats with a focus on mesophotic and bathyal benthic organisms, including invertebrates living in association with various coral species. However, the lack of comprehensive ecological baselines predating the spill limits our ability to assess its impacts on coral-associated communities. Although the detection of large assemblages of invertebrates, including crustaceans, started with the first ecological studies of deep-water corals (e.g., [13]), the nature of most of these relationships remains unknown or at least uncertain.

The structural complexity created by deep-water corals enhances habitat heterogeneity, thereby providing essential resources and shelter for a multitude of sessile and mobile animals, reinforcing the idea that these ecosystems might play a pivotal role in overall marine biodiversity [14]. Moreover, mesophotic ecosystems may serve as important refugia for coral larvae and marine life associated with shallower reefs, as suggested by findings that revealed comparatively better reproductive success and offspring performance in mesophotic environments [15].

The fauna associated with deep-water corals (Anthozoa: Hexacorallia, Octocorallia), defined here as symbiotic fauna in its wider sense [16], has been studied much less compared to shallow-water coral habitats. Most records of deep-water symbiotic animals are limited to sporadic observations and subsequent compilations of previous records (e.g., [17, 18]; and references therein). Yet evidence shows that the presence, abundance and diversity of coral-associated species can act as a reliable bioindicator of coral habitat health [19–22]. However, most biological characteristics of deep-water coral associates remain largely unknown. A better understanding of the diversity and abundance of animals associated with deep-water corals, as well as the type of association (obligate *vs*. facultative) and host specificity, are essential for detecting early signs of ecological disturbance [23]. Studying these relationships will help identify, and possibly predict, effects caused by ecological stressors. For example, such stressors often cause shifts toward less diverse communities (including monospecific assemblages), which are typically less resilient to environmental change [24].

Shrimps in the infraorder Caridea often associate with corals (Hexacorallia: Scleractinia, Antipatharia; Octocorallia) and are among the most abundant and diverse group of symbiotic decapods (e.g., [25–27]). Although Caridea includes large-bodied pelagic and benthopelagic shrimps, the vast majority of carideans are small species, with a total length less than 20 mm; many exhibit background-blending or disruptive color patterns. Several caridean families are notorious for presence of numerous cryptic

(morphologically indistinguishable lineages) and pseudocryptic (morphologically distinguishable but previously overlooked) species (e.g., [28–32]). Currently about 3,850 species of caridean shrimps have been described across 36 families, but the real diversity of the group remains underestimated [33]. The large family Palaemonidae comprises a substantial proportion of symbiotic shrimps [25–27, 33–35]. Palaemonid shrimps exhibit intricate symbiotic relationships with corals and other invertebrates (sponges, sea anemones, bivalves, echinoderms, ascidians, etc.) in both shallow and deeper marine environments (e.g., [26, 27, 35]), but the exact nature of many of these associations remains unstudied [27]. The second most diverse caridean family, Alpheidae, also includes a vast array of symbiotic species, primarily in shallow-water habitats [27, 36, 37], but also in deeper water (e.g., [38]). Alpheid shrimps engage in a multitude of often highly host-specific associations, including with sponges, corals, various burrowing invertebrates and gobiid fishes, creating a highly complex web of ecological relationships [36, 37, 39–42]. While significant progress has been made in taxonomy and ecology of caridean shrimps inhabiting shallow waters, there are still large knowledge gaps in our understanding of biodiversity of symbiotic carideans and their host relationships in deep-water coral-dominated ecosystems. Most deep-sea crustaceans remain poorly studied largely due to the general challenges of sampling and observing deep-sea habitats [43]. Filling these knowledge gaps is critical for assessing the diversity of deep-water symbiotic carideans. This knowledge is crucial to better formulate, implement, and evaluate conservation and restoration strategies aimed at preserving deep-water coral communities as entire complex ecosystems [44, 45].

In the present study, we focus on the diversity and host specificity of caridean shrimps associated with deep-water corals sampled on the continental shelf and slope in the northern Gulf, supplemented by deep-water material collected off Puerto Rico. The main objectives of our study were to: (1) assess the taxonomic and biological distinctiveness of caridean shrimps inhabiting deep-water coral habitats; (2) identify potential cryptic lineages, which in turn would enable further taxonomic studies; (3) detect symbiotic or potentially symbiotic species (symbionts), in contrast to species that opportunistically use these habitats for shelter and/or food source (non-symbionts); and (4) assess whether the obligate symbiotic shrimps are host specialists or generalists or across broad host categories.

Methods

Sampling and data collection

Most samples were collected during multiple expeditions in the Gulf (Fig. 1) using two methods: (1) Remotely Operated Vehicles (ROV) and (2) triplicate sets of Autonomous Reef Monitoring Structures (ARMS). Several expeditions were part of the Mesophotic and Deep Benthic Communities (MDBC) restoration projects selected by the Open Ocean Trustee Implementation Group to restore natural resources injured by the 2010 *Deepwater Horizon* oil spill. ROV operations included: NOAA Ship *Pisces* 2022 (PC2202L1), NOAA Ship *Pisces* 2023 (PC2302L2, PC2302L3), M/V *Island Intervention* 2024 (II2401/II2402), NOAA Ship *Pisces* 2024 (PC2403, PC2404), R/V *Pelican* 2024 (PE2507 MERCI4), and R/V *Western Flyer* 2024 (WF2506). The samples were collected using the ROV *Mohawk* (owned by the

National Marine Sanctuary Foundation and operated by the University of North Carolina Wilmington-Undersea Vehicle Program) aboard the NOAA Ship *Pisces*, the ROV *Beagle* (Marine Applied Research and Exploration [MARE]) aboard the R/V *Pelican* (Louisiana Marine Universities Consortium [LUMCON]), the ROV *Taurus* (Florida Institute of Oceanography [FIO]) aboard the R/V *Western Flyer*, and a Schilling Robotics UHD ROV aboard the M/V *Island Intervention* (C-Innovation, LLC). This material was supplemented by shrimp samples collected during other ROV expeditions, including specimens collected by the NOAA Ship *Okeanos Explorer* in the Gulf (EX1711, 2017) and off Puerto Rico (EX1811, 2018), and specimens collected by the Schmidt Ocean Institute R/V *Falkor (too)* off Puerto Rico in 2023 (Fig. 1).

Autonomous Reef Monitoring Structures (ARMS) were deployed in 2019 and retrieved in 2022 with ROV assistance as triplicate sets at seven sites in the study area: Stetson Bank, Diaphus Bank, Alderdice Bank, McGrail Bank, East Flower Garden Bank, and Bright Bank (Fig. 1). The deployments and retrievals were conducted as part of the NOAA-funded project Connectivity of Coral Ecosystems in the Northwestern Gulf of Mexico (CYCLE). See Table 1 for details of expeditions with ROV and ARMS operations.

Table 1
Table summarizing expeditions involving ROV or/and ARMs operations including dates, depth range and number of shrimps collected.

Cruise	Vessel	ROV	Dates	Depth Range (m)	Samples lots (n)
PC2202L1	*NOAA Ship Pisces*	Mohawk (UNCW)	June – July 2022	53–116	15
PC2302L2/PC2302L3	*NOAA Ship Pisces*	Mohawk (UNCW)	June – July 2023	47–460	41
PC2403/PC2404	*NOAA Ship Pisces*	Mohawk (UNCW)	June – July 2024	45–694	26
II2401/II2402 SATFADS	M/V *Island Intervention*	Schilling Robotics UHD	July – August 2024	29–1624	35
WF2506	R/V *Western Flyer* (FIO)	Taurus (FIO)	September 2024	1486–2261	2
PE2507/PC2508 MERCI4	R/V *Pelican* (LUMCON)	Beagle (MARE)	September – October 2024	65–192	9
CYCLE_2021	*R/V Point Sur*	Mohawk (UNCW)	April –May 2022	54–85	95 (145 specimens)
EX1711	*NOAA Ship Okeanos Explorer*	Deep Discoverer and Seirios	November – December 2017	1863,6	1
EX1811	*NOAA Ship Okeanos Explorer*	Deep Discoverer and Seirios	October – November 2018	412–474	4
FKt230417	R/V *Falkor (too*)	SuBastian	April – May 2023	19–383	3
NF22-02	*NOAA ship Nancy Foster*	Global Explorer	April 2022	578	1

Ecological data on shrimp-host associations were collected using the following criteria: (1) associations detected in ROV video footage, recorded along with field notes in the expedition database; (2) associations observed on deck and in the wet laboratory while retrieving samples from ARMS and ROV bio-boxes and quivers; and (3) associations revealed during sorting and accessioning of the historical material (e.g., shrimps found clinging to previously collected corals or crinoids, or found at the bottom of a jar containing corals or sponges). A selection of deep-water corals, which serve as hosts for shrimps, as well as an example of ARMS (with associated crinoids) deployed in the mesophotic zone, are shown in Fig. 2.

Material deposition and specimen identification

All herein studied material is deposited in the crustacean collection of the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM) (see Supplementary Table 1). All specimens were examined under a dissecting microscope and identified to species or morphospecies. Species identifications were made using available taxonomic literature in conjunction with a major regional checklist [46] for additional biogeographical context. To validate identifications, combined morphological and molecular data from 24 samples collected between 1998 and 2005 and deposited in the USNM were included for comparison. Type specimens from the USNM collection were also revised although not sequenced (see Supplementary Table 1).

WGS: library preparation, amplification and sequencing

Tissue for DNA analyses was typically extracted from one or two posterior pleopods (which have no taxonomic value), in some cases from coxae of already detached walking legs, gills (on one side) or pooling 1–3 eggs. DNA was extracted from recently collected samples (2021–2024) using the AutoGen platform with a phenol-chloroform protocol in 96-well plates. Historical samples were extracted using the Qiagen DNeasy extraction kit. DNA quality and quantity were assessed post-extraction using Qubit and Quant-iT assays (Thermo Fisher Scientific). Two sequencing approaches were employed: genome skimming (i.e., low-coverage whole genome sequencing (WGS) for samples collected between 2021 and 2023, and Sanger sequencing of the mitochondrial cytochrome c oxidase subunit I (COI) gene for samples collected in 2024 and for historical samples collected before 2021.

For the WGS protocol, we prepared libraries from quantities of DNA ranging 1–100 ng with the NEBNext Ultra II FS DNA Library Prep Kit, following the manufacturer's instructions with a few modifications. The reaction volume was reduced by half, and fragmentation/end-prep incubation times were adjusted to 10 minutes for contemporary samples and 2.5 minutes for historical samples. Instead of the NEBNext Adaptor, we used 5 µL of iTru Y-yoke adaptor [47], with an adaptor ligation time of 30 minutes. Bead cleanups were performed using KAPA Pure Beads, and indexing was done with iTru i5 and i7 indices [47]. PCR enrichment was carried out for 10 cycles. To monitor potential contamination, we included a negative control on each plate during library preparation. All DNA libraries were quantified and assessed using a Qubit fluorometer High Sensitivity Assay and TapeStation 2200 (Agilent). Final pools were prepared for sequencing on an Illumina NovaSeq (150 bp paired-end (PE) reads) targeting ~ 10 million reads per sample. The Illumina sequencing was outsourced to Admera Health (South Plainfield, New Jersey US). The DNA extraction, library preparation and DNA amplification were carried out at the Laboratories of Analytical Biology at the Smithsonian Institution National Museum of Natural History.

WGS Data processing

Quality raw reads of sequences generated with WGS samples were assessed using FastQC v0.12.1 (https://www.bioinformatics.babraham.ac.uk/projects/fastqc/). PolyG tails, adaptors and low-quality bases were removed with fastp v0.23.4 [48] and Trimmomatic v0.39 [49]. Contaminants were removed by mapping the trimmed reads against the human and PhiX genomes using Bowtie2 v2.5.3 [50]. Cleaned and quality-trimmed reads were aligned to the BOLD, SILVA SSU, and SILVA LSU databases using bbmap v39.06 (https://sourceforge.net/projects/bbmap/). Matching reads were then assembled with metaSPAdes v3.15.5 [51] under default parameters. To detect rRNA genes, we applied barrnap v0.9 (https://github.com/tseemann/barrnap) to the metagenomic assemblies for each sample. Taxonomic identification of the resulting mtCOI, 18S rRNA, and 28S rRNA barcodes was performed through BlastN searches [52], and the longest sequence per barcode and target organism was extracted using a combination of bedtools v2.31.1 [53], seqtk v1.4 (https://github.com/lh3/seqtk), and seqkit v2.8.1 [54]. To enhance mitochondrial barcode recovery, partial mitochondrial genomes were also assembled with MitoFinder v1.4.1 [55] and MITObim v1.9.1 [56], from which full-length COI barcode sequences were retrieved for downstream analyses.

Sanger sequencing

DNA amplification was carried out to target COI using the following pairs of primers: LCOI 1490 and HCO2198 [57, 58]; BF2 and BR2 [59]. These pairs of primers have shown excellent performance for crustaceans in previous studies (e.g., [60, 61]). Thermal conditions followed Rodríguez-Flores et al. [61] with an annealing temperature ranging from 45°C to 50°C. Amplicons were visualized in an agarose 1% gel, using GelRed as a nucleic acid stain for the gel. DNA was purified using the enzymatic protocol ExoSAP-IT (Thermo Fisher Scientific) before running the cycle sequencing of both forward and reverse strands. Amplicon sequencing was carried out in an ABI 3700 96-well capillary sequencer at the Laboratories of Analytical Biology at the Smithsonian Institution National Museum of Natural History. Quality controls of Sanger sequences (forward and reverse) were conducted using the software Geneious Prime 2024 Build 2024-04-12 19:00 (https://www.geneious.com/), prior to downstream phylogenetic and species delimitation analyses. Potential pseudogenes among mitochondrial COI sequences were screened using the ExPASy Translate tool (https://web.expasy.org/translate/) with the invertebrate mitochondrial genetic code to identify unexpected stop codons and other translation anomalies. COI sequences obtained through Sanger sequencing were aligned with mitochondrial sequences recovered through genome skimming using MAFFT [62] and subsequently trimmed manually in AliView [63] to match the length of the PCR-amplified fragment. Ribosomal gene sequences were aligned separately using MAFFT with the G-INS-i iterative refinement strategy and subsequently inspected and edited in AliView.

Phylogenetic and species delimitation analyses

We compiled two distinct datasets to address separate study objectives. The first dataset consisted of 227 mitochondrial COI sequences generated in this study. Rather than unveiling phylogenetic

relationships, this dataset uses the COI gene as a standard marker for species delimitation to determine the number of species inhabiting deep-water coral communities in the study area; these delimited units were subsequently used for diversity assessments and downstream ecological analyses. The second dataset, designed to investigate evolutionary patterns, is a concatenated matrix of three genes (COI, 18S, and 28S) comprising a subset of 39 specimens of selected obligate symbiotic species in the morphologically similar palaemonid genera *Pseudocoutierea*, *Pseudopontonides*, *Lipkebe* and *Veleroniopsis*. This dataset was analyzed to test whether the species from these four genera form a monophyletic group and to reconstruct the evolution of host-switching patterns. For most specimens in the concatenated dataset, host association data were available directly from field observations or inferred as described above. Hosts included octocorals (Malacalcyonacea: *Placogorgia*, *Thesea*, *Muricea*, *Swiftia*), hexacorals (Antipatharia: *Tanacetipathes*, *Elatopathes*), demosponges, glass sponges, and crinoids (Comatulida), among others. Two species currently placed in the genus *Periclimenes* (*P. tenellus* and *P. iridescens*) were used as outgroups.

Bayesian inference (BI) analyses were run using MrBayes v3.2.7 [64]. A partition scheme by gene (COI + 28S + 18S) was selected, in the case of the concatenated dataset, with the substitution parameters set to 'mixed' to sample across all possible reversible substitution models, and the rates set as 'invgamma'. Four Markov Chain Monte Carlo (MCMC) simulations were run for 50 million generations, sampling trees and parameters every 5,000 generations to estimate posterior probabilities. In all analyses, the final average standard deviation of split frequencies was below 0.01. The first 25% of generations were discarded as burn-in before summarizing the trees from the MCMC analysis. Maximum Likelihood (ML) analyses were performed using W-IQ-TREE online v.1 [65], partitioned by gene. Branch support was assessed with ultrafast bootstrap approximation UFBoot2 [66] using 1,000 pseudoreplicates, and the substitution model for each partition was automatically determined during the analysis using the 'auto' option. Phylogenetic trees were plotted and edited on the online platform Interactive Tree of Life (iTOL), available at: https://itol.embl.de.

A phylogenetic tree was inferred using BEAST v2.6 (https://www.beast2.org; [67]) to enable character mapping analyses using the concatenated data of the obligate symbiotic species to illustrate the variation of the character "host" within obligate symbiotic clades. The package bModelTest [68] was used to select the substitution model best fitting our data. A relaxed log-normal clock model was chosen since it allows rate heterogeneity among branches. Our objective was only to obtain an ultrametric tree, and not to calibrate the molecular clock for divergence time estimation. Therefore, the clock rate was set to 1.0. We set the tree prior to the Birth–Death model with a Birth rate distribution uniform (Lower = 0.0, Upper = 1,000), and a Death rate distribution uniform (Lower = 0.0, Upper = 1.0). Chain length for the MCMC run was set to 10,000,000 generations logging every 1000 generations. A maximum clade credibility tree was obtained, after discarding 25% of the trees, using TreeAnnotator (ver. 2.1.2, see https://www.beast2.org/treeannotator/).

To test species hypotheses, we performed single-locus species delimitation analyses using the COI dataset. This marker has a large utility in taxonomy and species delimitation in crustaceans, as well as

broad data availability for comparison (e.g., [35, 69, 70]). We employed two heuristic methods for these analyses, (1) a distance-based method: Assemble Species by Automatic Partitioning method (ASAP) [71], and (2) a tree-based method, based on the Phylogenetic Species Concept: Bayesian Poisson Tree Process (bPTP) [72]. The results from these methods were compared with our phylogenetic and morphological findings. We ran ASAP through the online server (available at: https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html) using simple distances (p-distances) as the substitution model, with the probability for group split set at 0.01. For bPTP, analyses were performed on the bPTP online server (available at: http://species.h-its.org/ptp/), using an unrooted Maximum Likelihood (ML) tree generated with IQTREE (using the same parameters as previously described). The analysis was run for 5×10^5 MCMC generations, with a thinning interval of 500, burn-in set at 25%, and without any outgroup.

Habitat specificity, host-associations and diversity analyses for symbionts vs. non-symbionts

To investigate patterns of association between shrimp species and other invertebrates, we compiled a dataset integrating species occurrences based on delimitation analyses (consensus of molecular and morphological identifications) and the type of host with which shrimps were associated. Hosts include corals (class Hexacorallia: orders Antipatharia and Scleractinia, class Octocorallia: order Malacalcyonacea), crinoids (class Crinoidea: order Comatulida), and sponges (phylum Porifera). Hosts were assigned to five functional categories; sponges (Porifera), black corals (Antipatharia), octocorals (Octocorallia), stony corals (Scleractinia) and crinoids (Comatulida), based on their ecological and structural characteristics. Although these categories do not correspond to equivalent taxonomic ranks, they represent distinct habitat types for associated crustaceans and were therefore used as the analytical units in host-association analyses. A “non-associated” category was assigned to specimens not found on a particular host or collected incidentally (no host information available). The dataset also incorporates metadata such as sampling method (ROV *vs.* ARMS), depth, locality, and developmental stage (larva or juvenile *vs.* adult).

The dataset was imported into an R environment and cleaned using the dplyr and tidyr packages. To evaluate diversity, compositional differences in shrimp communities across host type, depth, and sampling method, we used the vegan v2.6-10 [73] and ggplot2 [74] packages to generate bar plots and dot plots for visualization. Species-accumulation and rarefaction analyses were conducted in R (v. 4.x) using the packages iNEXT, tidyverse, dplyr, and ggplot2 [74–77]. Individual records were first imported and assigned to depth categories by converting depth values to numeric and classifying samples as Mesophotic (50–300 m) or Deep-sea (> 300 m). For each depth zone, abundances were calculated by summing the number of individuals per species. The resulting abundance table was then converted into list format for use with iNEXT, which was employed to generate individual-based rarefaction and extrapolation curves (q = 0) based on species abundances. Graphical outputs were produced using

ggiNEXT, with additional customization. This approach allowed direct comparison of species richness patterns between depth zones based on standardized sampling units.

Patterns of host specificity were explored using Non-Metric Multidimensional Scaling (nMDS) based on species presence–absence data and bipartite network analyses. In this context, we defined host range as the number of hosts occupied by a given shrimp species at the following taxonomic level: Octocorallia (class), Antipatharia and Scleractinia (orders), Porifera (phylum). nMDS was used to ordinate a subset of 38 species of shrimps with detected associations in a low-dimensional space based on the similarity of their host usage profiles, using Jaccard distance and trymax = 100. Therefore, shrimps with a host range of one (host_range = 1) were considered specialists, while those associated with multiple host types (host_range > 1) were considered generalists. The resulting ordination preserves pairwise dissimilarities among species, allowing us to visualize clustering of species that share similar host associations.

Bipartite network analyses were conducted using the vegan and bipartite v2.07 [73, 78] R packages. Interaction networks were visualized using the plotweb function to depict the structure of shrimp–host associations. Network modularity, a measure of the extent to which interactions are partitioned into subcommunities, was quantified using computeModules and visualized via plotModuleWeb. These analyses enabled the identification of modular patterns and clustering within the host–shrimp interaction network [78, 79]. Network-level specialization (H2'), connectance, and nestedness were calculated with H2fun and networklevel, while modularity (Q) was estimated using computeModules and compared against 100 null networks generated with the r2dtable algorithm. Species-level specialization (d') was computed to assess how strongly each host group deviates from random partner use.

Investigation of host switches

In the second dataset (see above), we investigated the distribution of observed host associations across individuals, including intraspecific variability, i.e., host switching events within the same species, by stochastic mapping of discrete characters on the ultrametric concatenated-genes phylogeny obtained with BEAST. Analyses were conducted in R using the package phytools v.2.4-4 [80]. Outgroups and specimens with missing host-association data were pruned from the tree prior to analysis. Host association was treated as a discrete multi-state character, with each state corresponding to a host taxon.

Stochastic mapping was implemented using the function make.simmap under an equal-rates (ER) model to simulate the distribution of host states along branches. The resulting mappings were summarized across simulations, and character histories were visualized by plotting state-specific colors directly onto tree branches. To emphasize observed ecological variation, tip states were overlaid with colored symbols corresponding to the recorded host association of each specimen. No ancestral state probabilities were displayed at internal nodes and the mapping is therefore intended to illustrate the

distribution of host associations across lineages and among individuals rather than to infer ancestral host use.

Results

Data summary and morphological identification

We examined approximately 300 shrimp specimens (including non-caridean shrimp-like decapods, such as Stenopodidea and Axiidea), included in 253 lots, of which 231 lots were collected by ARMS and ROV as part of MDBC and supplemental expeditions (Table 1): 136 lots included specimens collected by ROV from eight MDBC expeditions, PC2202_L1 (15 lots), PC2302_L2 and PC2302_L3 (41 lots), II2401/II2402 (35 lots), PC2403/PC2404 (26 lots), PE2507 (9 lots), WF2506 (2 lots); and 97 lots including 145 specimens collected by ARMs from the 2021 CYCLE project expedition PS2204. An additional 28 specimens included in 20 lots from other recent expeditions (e.g., NOAA Ship *Okeanos Explorer*, R/V *Falkor (too)* and NOAA Ship *Nancy Foster*) and USNM legacy collections were also examined (Table 1, Supplementary Table 1). Of these specimens, 228 specimens were successfully sequenced for the mt COI gene (see Supplementary Table 1). Of those 228 specimens, 48 were genome skimmed and 180 were Sanger sequenced. Morphological examination resulted in the identification of 48 morphospecies, species based in their morphological characters (46 morphospecies successfully sequenced) contrasting with 60 molecular Evolutionary Significant Units (ESUs) (see below) across 27 genera within the infraorder Caridea (some examples shown in Fig. 3). The family Palaemonidae is by far the most diverse group with a total of 23 species, followed by Alpheidae (12 species), Hippolytidae (4 species), Pasiphaeidae (3 species), Disciadidae (2 species), Bathypalaemonellidae (2 species), Pandalidae (2 species), Alvinocarididae (1 species), Bythocarididae (1 species), Lysmatidae (1 species) and Thoridae (1 species). In addition, we identified several non-caridean shrimp taxa, distributed among the following families: Stenopodidae [infraorder Stenopodidea] (4 species: 2 species of *Stenopus* and 2 species of *Odontozona*), Spongicolidae [infraorder Stenopodidea] (1 species of *Spongiocaris*), Axiidae [infraorder Axiidea] (2 species: *Coralaxius nodulosus* and *Eiconaxius agassizii*), and Penaeidae [suborder Dendrobranchiata] (1 species: *Parapenaeus politus*).

For some taxa, identifications based on distinguishing morphological characters cited in taxonomic literature were challenging. Noteworthy cases include the distinction among species of the *Periclimenes iridescens* and *P. pandionis* complexes [81, 82]; between *Pseudocoutierea stephanieae* and *P. acutidorsata* [83, 84]; between *Leptochela bermudensis* and *L. papulata* [85]; and between *Trachycaris rugosa* and *T. restricta* [86, 87]. The identifications provided herein for these taxa are either incomplete (e.g., *Leptochela* sp., *Trachycaris* sp.) or tentative (e.g., *Periclimenes* aff. *pandionis*, *Pseudocoutierea* cf. *acutidorsata*, *P.* cf. *stephanieae*) and will be revised / confirmed after examination of additional material and/or type material.

Automatic species delimitation and consensus

Automatic species delimitation estimated between 52 and 79 ESUs (species) present in our samples depending on the partition. ASAP analyses suggest the presence of 59 species (asap-score = 13.50, threshold genetic distance = 2.6%). Although not the most statistically significant partition, 59 species was the most reasonable estimate given the results of the morphology-based identifications and bPTP analysis. The bPTP analysis estimated a species richness ranging from 60 to 79 putative species, with a mean of 68.63. The analysis yielded a relatively balanced number of proposed merges (n = 49,848) and splits (n = 50,152), and an acceptance rate of 0.262, suggesting a stable MCMC convergence. To reach a consensus among automatic species delimitation and morphological species, we accepted the most conservative number of splits (ASAP, bPTP = 59 species) that considered species identification based on morphology. For instance, we were unable to obtain molecular data for *Discias serratirostris* and *Spongiocaris hexactinellicola*; therefore, the number of morphologically delimited species in this study stands at 61. The presence of singletons was generally low in our dataset, all of them corresponding to morphologically distinctive species. Overall, our results support the presence of considerable cryptic diversity within our dataset, corroborating patterns observed in morphological and other molecular analyses. See the summary of the morphological species, bPTP, ASAP and consensus species in Supplementary Table 2.

Two or more divergent lineages, currently classified under the same species name and corresponding to putative cryptic / pseudocryptic species, were revealed by species partitions in ASAP and bPTP. These included the palaemonids *Periclimenes iridescens* (species complex: 4 species), *P. pandionis* (species complex: 3 species) and *Palaemonella americana* (2 species); the alpheids *Synalpheus townsendi* (species complex: 4 species), *Alpheopsis labis* (2 species), *Alpheus packardii* (2 species; however, part of a much larger species complex, Anker et al., in prep.), and the hippolytids *Tozeuma serratum* and *Trachycaris rugosa* (each with 2 species) (Fig. 4).

Phylogenetic results of COI matrix

The COI-based tree (Fig. 4) lacks support at the deepest nodes (bootstrap support [Bs] < 90), as was expected for a fast-evolving mitochondrial marker known for its saturation, combined with a significant taxonomic disparity within our dataset (ranging from populations within the same species to species belonging to different infraorders). Therefore, this tree does not represent a phylogeny, although it may reflect close relationships at the branch tips, i.e., between closely allied species within the same genus. However, our primary goal was not to resolve deep phylogenetic relationships but to test species hypotheses and delineate boundaries between identified morphospecies.

Several species were recovered in well-supported monophyletic clades at genus level, including *Trachycaris*, *Synalpheus*, *Palaemonella* and *Tozeuma* (Fig. 4). Conversely, multiple genera were not retrieved as monophyletic entities, including *Periclimenes* (known to be a non-monophyletic species assemblage, see [26, 35] and references therein), *Pseudocoutierea* (represented by only one species in the phylogeny of Chow et al. [88]) and *Alpheopsis* (previously shown to be non-monophyletic by Anker et al. [36] and Chow et al. [89]) Within *Periclimenes*, morphologically similar specimens preliminarily assigned as *P.* aff. *pandionis* and *P.* aff. *iridescens* were recovered in distinct molecular lineages, at some

distance from the other *P. pandionis* and *P. iridescens*. Examples of cryptic / pseudocryptic species pairs or species complexes (with 3 or more species) were observed, for instance, in *Alpheus*, *Alpheopsis*, *Synalpheus*, *Periclimenes* (*s. lat*.), *Pseudocoutierea*, *Palaemonella*, *Tozeuma* and *Trachycaris*. Some taxa, such as *Anchistioides antiguensis* (sponge symbiont) and *Periclimenaeus ascidiarum* (ascidian symbiont) were represented by a single individual, reflecting a clear bias in the sampling methods, which were focused mainly on corals.

Our data revealed at least four phylogenetic clades composed of species that are regarded as obligate associates: (1) *Pseudocoutierea* + *Lipkebe* + *Veleroniopsis* and *Pseudopontonides*, hereafter PPLV clade (analyzed separately, see below); (2) *Bathypalaemonella*; (3) *Periclimenes iridescens* complex; and (4) *P. pandionis* complex.

Phylogenetic results of the concatenated matrix (PPLV clade)

The interspecific relationships within the symbiotic PPLV clade containing four palaemonid genera (*Pseudocoutierea* + *Pseudopontonides* + *Lipkebe* + *Veleroniopsis*) inferred from the multi-gene phylogeny (Fig. 5a) are largely congruent with the COI-based results (Fig. 4). *Pseudocoutierea* was again retrieved as non-monophyletic. According to our results, *Pseudopontonides principis* is sister to *Pseudocoutierea* cf. *stephanieae*, with *Veleroniopsis kimallynae* in a weakly supported (Bs = 74) sister relationship to that clade. *Lipkebe holthuisi* clusters with this group with moderate support (Bs = 93), whereas *Pseudocoutierea* cf. *acutidorsata* forms a clade with *P. antillensis* (Bs = 73), which is nested within the PPLV clade. In addition, a single specimen of an additional, apparently undescribed species (tentatively referred to as *Pseudocoutierea* sp.), was recovered as sister to the rest of the species in the PPLV clade (Fig. 5a).

The PPLV clade includes mainly species associated with mesophotic octocorals and black corals, with one notable exception being the crinoid-associated *Lipkebe holthuisi* (see below). In addition, some species of *Pseudocoutierea* and *Pseudopontonides principis* also occur in shallower water, although typically below 15 m [90–92]. Stochastic discrete character mapping of the multistate character “host” on the tree (Fig. 5b) suggests that none of the shrimp species in the PPLV clade shows host specificity at the genus level of corals. These results support the hypothesis that these species convergently evolved to live in association with octocorals (possible ancestral host group), with multiple host switching events in the course of evolution: (1) from one octocoral genus to another; (2) from octocoral to black coral; (3) from one black coral genus to another; and (4) from octocoral to crinoid, this last one representing the most striking host switch within the PPLV clade.

Nevertheless, all members of the PPLV clade exhibit a certain degree of host specificity at taxonomic levels ranging from order to class (unknown for *Lipkebe holthuis*, see below). In other words, these shrimps can be found living on different host genera or species of corals (Fig. 5b). For example, *Pseudocoutierea* cf. *stephanieae* was collected only from two species of octocorals (tentatively identified

as *Thesea rubra* and *Muricea pendula*) and shows a higher host specificity than *P.* cf. *acutidorsata*, which was found on the same two plus two additional octocoral genera (*Placogorgia* and *Swiftia*). *Pseudocoutierea antillensis* and *Veleroniopsis kimallynae* were also found on octocorals (*Thesea* for *P. antillensis* and *Thesea* and *Muricea* for *V. kimallynae*), but the limited sample sizes for these taxa hinder any firm conclusions on their host specificity. Finally, *Pseudopontonides principis* was found associated with black corals (Antipatharia: *Elatopathes*, *Tanacetipathes*) in our study, whereas all specimens of *Lipkebe holthuisi* were retrieved from unidentified crinoids (Comatulida) (Supplementary Table 1; Fig. 5).

Ecological diversity

Our statistical analyses reveal a greater diversity and uniqueness of shrimp taxa collected by ROV compared to ARMS. However, combining both methods captured a more complete assemblage (Fig. 6a, b). Overall, our sampling covered a depth range from 29 m to more than 1800 m, however, sampling was heavily biased towards mesophotic depths (50–250 m), and there is a notable gap between 700 and 1200 m (Fig. 6c). Mean depth of occurrence per species (Fig. 6c) suggests some lineages within species complexes are restricted to specific bathymetric ranges. Individual-based rarefaction (q = 0) identified 61 species from the pooled dataset. As expected, ROV samples showed higher richness (51 species; n = 129) than ARMS (20 species; n = 92). Depth-stratified rarefaction indicated 49 species across 193 individuals in the mesophotic zone (50–300 m) and 12 species across 28 individuals in the deep-sea zone (> 300 m). Richness increased with sampling effort across all curves, with ARMS and deep-sea subsets exhibiting lower richness consistent with smaller species pools and sample sizes (Fig. 6d). The rarefaction curves suggest that most of the shrimp species diversity has not been observed / sampled, especially for depths > 300 m (Fig. 6e).

ARMS and ROV represent complementary but non-comparable sampling methods. As expected, strictly obligate Anthozoa-associated species (e.g., *Veleroniopsis kimallynae*, *Pseudocoutierea* spp., *Pseudopontonides principis*) were not recovered from ARMS samples (Fig. 6a, b). Instead, ARMS primarily captured fauna associated with Porifera (e.g., *Anchistioides*, *Discias*) and Crinoidea (*Lipkebe*), in addition to numerous free-living species (20 species in our dataset). Overall, of the 61 shrimp species collected by both ARMS and ROV, 28 species have no record or evidence of symbiotic associations; 22 species are obligate associates (specimens retrieved from hosts); and 11 species can be tentatively seen as facultative associates, occurring either in association with some host or found free-living.

The bipartite interaction network (Fig. 7) shows that most shrimp species collected from mesophotic and deep-sea coral habitats are either not associated with other invertebrates or are found in association with multiple types of hosts (e.g., Octocorallia and Porifera). Examples include species of *Synalpheus*, *Alpheopsis*, *Alpheus* (Alpheidae) and *Periclimenes sensu lato* (Palaemonidae). Conversely, some shrimp species, such as those in the genera *Pseudocoutierea*, *Pseudopontonides*, *Veleroniopsis*, *Lipkebe*, *Bathypalaemonella* and *Tozeuma*, seem to be associated with a single type of host at the level of order or family, but do not exhibit a host specificity at a lower taxonomic rank, such as genus or species (Fig. 5). For symbiotic taxa represented by less than 4 specimens (e.g., *Tozeuma serratum*), the level of host

specificity is difficult to ascertain, and more specimens with reliable host data are needed to better describe the nature of these associations.

By far the most common hosts for caridean shrimps in our dataset are octocorals (Octocorallia: 14 shrimp species), followed by sponges (Porifera: 9 shrimp species) and black corals (Antipatharia: 7 shrimp species), with occasional associations with other taxonomic groups (Figs. 4, 6a). However, in some cases, these occasional “associations” represent merely an accidental encounter (e.g., an individual of *Leptochela* found in a hermit crab shell). The bipartite network analysis also reveals a high degree of host sharing among associated shrimp species, indicating a substantial overlap in host use across taxa (Fig. 7).

Connectance is moderate (C = 0.18), showing that only a subset of all possible shrimp–host interactions were realized. Nestedness is low to moderate (N = 21.3) indicating from a weak to a moderate nested structure. Although the observed modularity is relatively high (Q = 0.54), it does not differ from null model expectations (p = 1), indicating that the apparent modules are not stronger than those expected by chance. Species-level specialization vary markedly among host groups, with the highest values observed for Porifera (d'=0.73) and Comatulida (d'=0.72), indicating that shrimps associated with these hosts show strong partner specificity, whereas associations with other host groups (Antipatharia: d’=0.50; Scleractinia d’=0.42; Octocorallia d’=0.30) are by comparison more generalized.

The nMDS analyses show clusters of species using similar hosts. *Lipkebe holthuisi*, which is found exclusively in association with comatulids, was the most distinctive and specialized species (Fig. 8). Several species clustered together by host type. For instance, octocoral specialists (host range = 1), including *Bathypalaemonella serratipalma, Veleroniopsis kimallynae* and *Pseudocoutierea* spp.; antipatharian specialists, *Pseudopontonides principis* (occasionally associated with octocorals, see [93]) and *Bathypalaemonella texana*; and sponge (Porifera) specialists such as *Synalpheus* spp., *Discias serratirostris*, *Bythocaris* cf. *floridensis, Spongiocaris hexactinellicola*, *Anchistioides antiguensis* and *Eiconaxius agassizi* each formed separate clusters. The nMDS analyses also revealed host generalists (host range > 1), for instance, *Periclimenes* spp. (found on several anthozoan hosts), *Tozeuma* cf. *serratum* (found in association with both scleractinians and black corals) and one species in the *Synalpheus townsendi* complex (found in association with both corals and sponges). Our data also suggest that there may be more generalist species at mesophotic depths than at bathyal depths, but the bathyal depth range was not adequately covered by our sampling.

Discussion

Taxonomy of caridean shrimps inhabiting mesophotic and deep-sea corals with notes on their phylogenetic relationships

The present study provides the first analytical assessment of the caridean shrimp diversity of mesophotic and deep-sea coral ecosystems in the Gulf and, more generally, the western Atlantic, including host repartition and specificity, molecular data and species delimitation. Despite the fact that this region is well studied in general for decapods (e.g., [46, 94, 95] and references therein), several of the recovered ESUs represent previously undetected cryptic lineages, including undescribed species. Given the growing evidence that many decapod species with broad reported bathymetric distributions comprise complexes of morphologically similar but genetically distinct taxa (e.g., [96]), some of these lineages may reflect cryptic diversity hidden within nominal species. Overall, the total number of species (61) found in mesophotic and deep-sea coral communities represents a quarter of the total diversity of caridean and stenopodidean shrimps reported in the Gulf [46]. However, this estimate should be interpreted considering the sampling design, as ARMS were deployed at the upper mesophotic (~ 50–100 m), whereas ROV sampling covered a much broader depth range. Consequently, differences in species richness between sampling methods may partly reflect bathymetric variation, which cannot be fully disentangled from methodological effects.

Although our study was not designed to address phylogenetic relationships between the taxa, our preliminary and exploratory analyses suggest patterns consistent with paraphyly and polyphyly in several caridean clades. The non-monophyly of both families Palaemonidae and Alpheidae, which have been shown as monophyletic entities in family-focused analyses [26, 36, 88, 89, 97, 98], is due to limited potential of the mitochondrial COI marker to resolve phylogenetic relationships at deeper (i.e., suprageneric) taxonomic levels. Given the scope of this study, a detailed exploration of this pattern is beyond the present analysis. The problematic “waste-basket genus” *Periclimenes* has been recovered as polyphyletic (Fig. 4), corroborating previous studies (e.g., [26, 33, 35]). However, *Pseudocoutierea* was also recovered as non-monophyletic, nesting *Pseudopontonides*, *Lipkebe* and *Veleroniopsis* (Fig. 4). These taxonomy *vs.* phylogeny conflicts are often driven by morphological convergence (e.g., [32]), particularly among symbiotic species in which similar morphological traits, (i.e., characters on the carapace and pereopods), evolved in response to comparable ecological niches (e.g., coral or sponge hosts). However, to address these phylogenetic incongruences and possible taxonomic implications, a more comprehensive dataset, including more species and genetic markers, will be analyzed in a future study.

Uncovering hidden diversity in Caridea is not surprising, given the remarkable species richness of this group [33] and the increase in exploration of mesophotic and deep-water ecosystems [2] using sophisticated sampling methods, such as submersibles and ROV [35]. High diversity, varying degrees of ecological specialization, wide host range, morphological plasticity and small body size of many caridean shrimps represent traits that often contribute to cryptic speciation and taxonomic underestimation. For instance, the presence of two lineages in *Trachycaris* may be related to the problematic distinction between *T. restricta* and *T. rugosa* and the possible presence of both species in the western Atlantic [86, 87]. Our results also confirm observations of De Grave and Anker [99], who briefly commented on the presence of several undescribed species in the *Periclimenes iridescens* species complex. The two lineages identified as *Alpheus* aff. *packardii* are part of a much larger *A.*

normanni – A. packardii species complex, which is currently under study ([100]; AA, pers. obs.). In contrast, the *Synalpheus townsendi* species complex may represent a case of speciation driven by bathymetric segregation rather than host-driven diversification, as seen in other alpheid species (e.g., [101]). Bathymetric segregation can promote allopatric speciation when adaptation to different depth ranges restricts dispersal and gene flow between populations. Such depth-associated barriers to gene flow have been observed in various crustacean groups and other marine invertebrates (e.g., [96]). Allopatric speciation, which seems to be the most common speciation process in Alpheidae and other carideans (e.g., [29, 102, 103]). However, the relative importance of bathymetric segregation compared with other speciation mechanisms within caridean families remains to be established. Additionally, our data highlight the presence of multiple sister species, as well as lineages representing putatively undescribed taxa, such as *Pseudocoutierea* sp. and *Periclimenes* aff. *pandionis* (Fig. 4). Undescribed species should be confirmed using both molecular data and morphological characters before formal description [104], even in the case of morphologically distinctive new species, such as the alpheids *Salmoneus karenae* and *Alpheopsis gorei*, described over the course of this study [105, 106].

The diversity of shrimp-like decapods documented by our study for relatively limited geographic areas (northern part of the Gulf and southern and western Puerto Rico, Fig. 1) confirms that the true diversity associated with deep-water corals remains largely underestimated [33, 107]. The use of complementary sampling methods in this study allowed us to examine a broader community of associated species, underscoring the importance of methodological diversity for biodiversity assessments. In this context, accurate estimates of species diversity depend on sustained mesophotic and deep-sea exploration programs, such as MDBC [108]. Consistent with this need, our results highlight the importance of additional sampling at greater bathymetric ranges in the Gulf to obtain a more complete picture of the diversity of shrimps and other decapods (Fig. 6). Therefore, environmental biases during sample collection must be considered when analyzing biodiversity data and designing new inventory strategies [109].

Symbionts vs. non-symbionts in mesophotic and bathyal coral communities

In our dataset, more than half of the shrimp diversity in mesophotic and bathyal coral ecosystems in the Gulf consists of obligate (often morphologically specialized) and non-obligate or facultative (morphologically less or non-specialized) symbionts, while the remaining species are free-living but seem to use deep-water coral habitats opportunistically because they provide both shelter and food. Cnidarian hosts have more symbiotic shrimps than sponges and crinoids, with octocorals (especially gorgonians) hosting more symbionts than black corals. Despite an overall generalized network structure, certain host groups, particularly crinoids and sponges, seem to support highly specialized shrimp assemblages, suggesting that host specificity should be investigated at species level (including for the hosts).

The degree of host specificity between shrimps and their hosts is variable. Some associations are obligate, especially those involving sponges, octocorals and black corals, whereas other shrimps seem to be generalists using several different host types (Figs. 6, 7). Host specialization is generally common among palaemonids, with many species engaging in obligate relationships with specific groups of animals, influencing both biodiversity and community dynamics in coral ecosystems [26]. Both chemical and visual cues have been shown to mediate host recognition, indicating a high degree of evolutionary adaptation to specific hosts [110]. Reproductive strategies of symbionts are often closely tied to these associations, with many species depending on structural complexity of coral colonies for mating, brooding and larval development, reinforcing the integral role of habitat-forming corals in their life histories (e.g., [111]). These relationships highlight the ecological importance of deep-water coral ecosystems, reinforcing the need to protect, restore, and monitor these habitats and to recognize the essential ecosystem services and benefits they provide.

Our data also show generalist tendencies in several caridean groups, confirming previous observations. For instance, the two lineages of the *Tozeuma serratum* clade (Hippolytidae) can be found on a variety of hosts, including octocorals, black corals and scleractinian cup corals, while Criales [112] reported *T. serratum* associated with hydrozoans. These observations suggest a certain degree of ecological flexibility in this group, although further taxonomic resolution of *T. serratum* is required to determine possible host preferences for the two members of this clade or narrow down their host range. Similarly, members of the non-monophyletic *Periclimenes iridescens* species complex (Palaemonidae) occur on a variety of hosts, including sponges and black corals [99, 113].

The genera included in the PPLV clade (*Pseudocoutierea*, *Pseudopontonides*, *Lipkebe* and *Veleroniopsis*) exhibit a significantly higher degree of host specificity with octocorals and black corals, and in one case (*Lipkebe*) with crinoids (e.g., [90, 114–116]; [83, 84, 92]; present study). Criales [113] reported that some of these species maintain a very close association with their coral hosts. For instance, *Pseudocoutierea* spp. and *Pseudopontonides principis* inhabit coral polyps and can emerge from them at night [113], based on observations made in the Caribbean at shallow depths (< 50 m). These shrimps also display multiple morphological adaptations of the carapace and pereopods to facilitate attachment to and moving around on the corals [88]. *Veleroniopsis kimallynae* was originally described based on a single specimen found in a “relict *Montastraea* coral” (Scleractinia) [116] at a depth of 18.3 m, which is in contrast to its only octocoral affinities at mesophotic depths (present study). The lack of records of *V. kimallynae* in shallow water suggests that its original record from *Montastraea* may have been incidental. Finally, *Lipkebe holthuisi* was reported to be associate of the crinoid *Comactinia meridionalis* [114] and was confirmed as a crinoid associate in our study, with the crinoid host yet to be identified, representing an interesting case of a group-level host switch from cnidarians (octocorals and black corals) to crinoids.

Beyond any doubts, the PPLV clade represents a very interesting model group for studies of evolution of symbioses, host specificity and host switches. However, at least four other western Atlantic and eastern Pacific palaemonid genera not included in our dataset (*Neopontonides*, *Coutierea* and *Veleronia*,

Pseudoveleronia) and additional specimens from the PPLV clade (especially from the Caribbean, Florida and Brazil, and with reliable host data) will need to be included in a more comprehensive analysis of the PPLV clade, before more conclusive evolutionary hypotheses can be proposed. In the eastern Atlantic, D'Udekem d'Acoz [117] reported a wide range of hosts, including octocorals, black corals and even sponges for *Balssia gasti*, a member of a genus that may be part of or at least related to the PPLV clade. Several Indo-West Pacific palaemonid genera also show morphological resemblances with the PPLV clade that may be nested within or closely related to the PPLV clade. It must be noted that host switches have been reported in several shallow-water palaemonid clades [26, 118]. Host switching is common in the evolution of Palaemonidae [88].

The importance of symbiotic shrimps for conservation and restoration of MDBC habitats

Caridean shrimps represent a diverse and ecologically important animal group in most marine ecosystems [27]. They represent a significant percentage of animals living in obligate and facultative associations with corals, sponges, annelids, mollusks, echinoderms, ascidians, fishes and other benthic animals (e.g., [26, 119–123]; [124]; see also review in [27]). Symbiotic relationships between caridean shrimps and corals are particularly well documented, especially among members of the family Palaemonidae, which exhibit various degrees of host specificity [26, 27, 88]. These associations are crucial not only for shrimp survival, since corals provide shelter and thus protection from predators, and access to food (e.g., coral mucus and therein trapped organic particles and small organisms), but also seem to significantly contribute to coral health through shrimp's cleaning behaviors, including removal of necrotic tissue and parasites, and supplementing nitrogen to the coral in the form of feces and molts (e.g., [25, 27, 113]). In addition, symbiotic snapping shrimps (*Alpheus lottini* species complex) together with trapeziid crabs (*Trapezia* spp) protect their host colonies against corallivorous crown-of-thorns starfish, *Acanthaster* spp. [125], and similar mutualistic behaviors may also exist in the deep sea.

Due to their reliance on specific hosts, shrimps associated with corals, along with other symbionts, may serve as excellent bioindicators of healthy coral communities. Just like in shallow coral reefs, shrimps and other symbionts of mesophotic and bathyal corals may be highly beneficial to their hosts by reducing incidence of diseases and parasites, deterring predators, and/or providing additional food source [23, 27]. Consequently, the relationship between habitat-forming corals and their invertebrate symbionts may be a delicate balance that can be easily disrupted by environmental stressors [22]. A sharp decrease in the diversity of coral taxa would certainly lead to a substantial decline in symbiotic species [23]. Conversely, a decline in symbiotic species would significantly impact biodiversity and likely overall ecosystem health [126–128].

Many of the herein reported shrimp species appear to be free-living or opportunistically associated with corals or sponges; therefore, they are considered to be habitat generalists and may be more resistant to environmental changes. In contrast, other shrimp species, such as some members of the PPLV clade, are intimately associated with deep-water corals and are therefore highly restricted in their ecological

niche breadth. Host specialization comes with evolutionary trade-offs. Studies suggest that once a lineage adopts a symbiotic lifestyle, reversion to a free-living lifestyle is constrained, making specialized shrimps potentially more vulnerable to environmental disturbances [27]. This underscores the importance of understanding host specificity in the context of ecological resilience and conservation planning.

Caridean shrimps and decapods in general are largely excluded from deep-water ecosystem monitoring programs, especially when ROV collections are involved [43]. This exclusion is due to challenges in collecting / sampling active and agile animals, time constraints, limited baseline data, lack of taxonomic expertise, and heavy bias towards corals and other larger sessile or slowly moving animals. However, expanding sampling of a broader community of associated fauna, including caridean shrimps and other invertebrate symbionts, is critical for improving our understanding of coral ecosystem health. Because these invertebrate associates and symbionts play key roles in trophic interactions, habitat maintenance, and overall ecosystem function, their omission can lead to incomplete or misleading assessments of community condition. Accordingly, explicitly sampling associated fauna is an integral component of comprehensive implementation and evaluation strategies and frameworks for the restoration and conservation of deep-water coral communities [45, 129].

Limitations of our study

Our study uncovered a combination of previously known and unsuspected diversity of symbiotic relationships between caridean shrimps and various groups of marine invertebrates, primarily corals, and is a significant contribution to the knowledge of the biodiversity patterns in the deep-water coral ecosystems of the Gulf. However, our findings and analyses are exploratory and should be interpreted with caution until more standardized and spatially balanced sampling is achieved. Future monitoring programs should adopt standardized sampling protocols across sites and depths, while exploring environmental DNA (eDNA) as a complementary, non-invasive approach to detect caridean shrimps and minimize disturbance to coral habitats. One of the limitations of the present study is the species delimitation based on a single molecular marker (COI), which may confound biologically distinct species with population structure of the same, genetically variable species, and should always be tested with additional molecular and morphological data [104]. Uneven depth sampling may have impeded a more complete biodiversity assessment, since some host co-occurrences differed from the known associations of the species and/or ROV *in situ* observations. Nevertheless, our study provides a basis for further studies of the symbiotic deep-water shrimp biodiversity in the Gulf, which can support ongoing and future conservation and restoration efforts.

We are also aware of the general limitations of sampling symbiotic and non-symbiotic deep-water decapods with ROVs and ARMS, especially when compared to dredges. The main advantage of ROVs (or manned submersibles) is the possibility to observe at least some relatively large animals *in situ* and to “cherry-pick” them together with their hosts. Thus, ROV sampling can record a great number of associations with video, although ROV sampling typically results in a low number of specimens in comparison to dredging/trawling, for example. In contrast, ARMS are standardized artificial structures

that might not be suitable for settlement of large sessile animals, such as corals, even when they remain on the bottom for several years and are completely overgrown. The strength of ARMS is thus not to sample symbiotic taxa but small benthic cryptofauna, though they nevertheless occasionally collect associates of encrusting sponges, young coral colonies, hydroids, ascidians, etc., (e.g., [130]).

Conclusions

Our study reveals substantial diversity and previously underrecognized taxonomic complexity among shrimp-like decapods associated with mesophotic and deep-sea coral ecosystems in the western Atlantic. The identification of 61 species, including multiple putative cryptic and pseudocryptic lineages, underscores the need to integrate detailed morphological assessments with molecular evidence to achieve reliable biodiversity inventories. Beyond taxonomic diversity, our results reveal varied ecological relationships, from obligate host associations to broader host use, with octocorals representing the most frequently recorded hosts. Together, these findings highlight the complexity of coral-associated crustacean communities and the extent to which their diversity and ecological relationships remain incompletely understood. The complementary assemblages recovered by remotely operated vehicles (ROVs) and autonomous reef monitoring structures (ARMS) demonstrate the value of combining sampling approaches, while rarefaction analyses indicate that substantial diversity remains undocumented, particularly below 300 m. Future work should combine standardized sampling across depths and locations with detailed documentation of host associations and multilocus molecular analyses to resolve species boundaries and better characterize ecological relationships.

More broadly, our findings reinforce that taxonomy is essential for understanding and protecting biodiversity. Accurate species identification, especially in groups with high levels of cryptic diversity, such as caridean shrimps, relies on taxonomic expertise integrating detailed morphological studies and molecular analyses (e.g., [26, 31, 35]). Reliable knowledge of the species inhabiting an ecosystem and their ecological relationships is a fundamental prerequisite for effective conservation, restoration, and monitoring [93]. We cannot adequately protect ecosystems and the communities they support without understanding their diversity, species composition, and ecological functions. Integrating taxonomic expertise into restoration and monitoring programs, as demonstrated by the MDBC portfolio [108] is therefore crucial for establishing biodiversity baselines, evaluating restoration outcomes, and informing effective conservation measures. These efforts are also essential for training and inspiring the next generation of taxonomists. Ultimately, a better understanding of biodiversity and ecological interactions is fundamental to protecting deep-water coral ecosystems and assessing the consequences of species loss or gain.

Abbreviations

ARMS: Autonomous Reef Monitoring Structures

COI: Cytochrome c Oxidase Subunit I

F: Free living shrimps

MDBC: Mesophotic and Deep Benthic Communities

PPLV: *Pseudocoutierea* + *Pseudopontonides* + *Lipkebe* + *Veleroniopsis* clade

ROV: Remotely Operated Vehicles

S: Symbiotic shimps

Declarations

Supplementary Information

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Ethics approval and consent to participate

No ethics approval was required for the work presented in this manuscript.

Competing interests

The authors declare no competing interests.

Author Contribution

PCRF, AA and ST conceived and discussed the idea. AA provided most identifications of Decapoda. AQ, MSN and SH provided the resources. PCRF, HS, AQ, SH, and ST generated and curated data; PCRF analyzed data; PCRF produced the figures, HS produced the maps. PCRF produced the first draft with AA's help. All authors contributed to writing and gave their final approval for the publication.

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Data Availability

The dataset and alignments supporting the conclusions of this article, are available in the Harvard Dataverse repository: https://doi.org/10.7910/DVN/MP584RRaw data of genome skimming is available in NCBI, Bioproject PRJNA1135238 Mesophotic and Deep Benthic Communities

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Figures

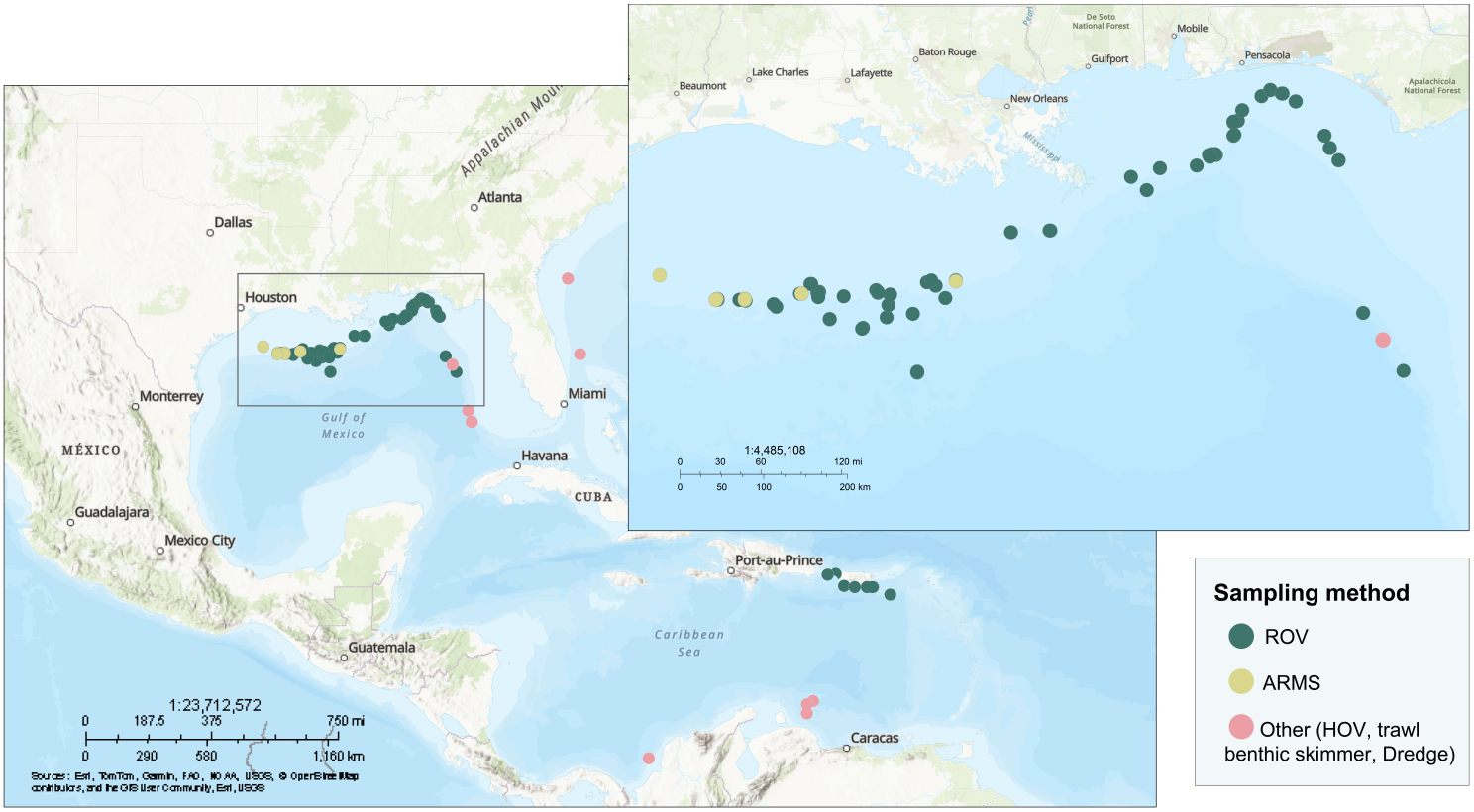


Figure 1

Map showing the sampling localities analyzed in this study. Different color symbols represent the type of collection method employed at each site. ROV=23 sites, ARMS=7 sites, Other = 9 sites.

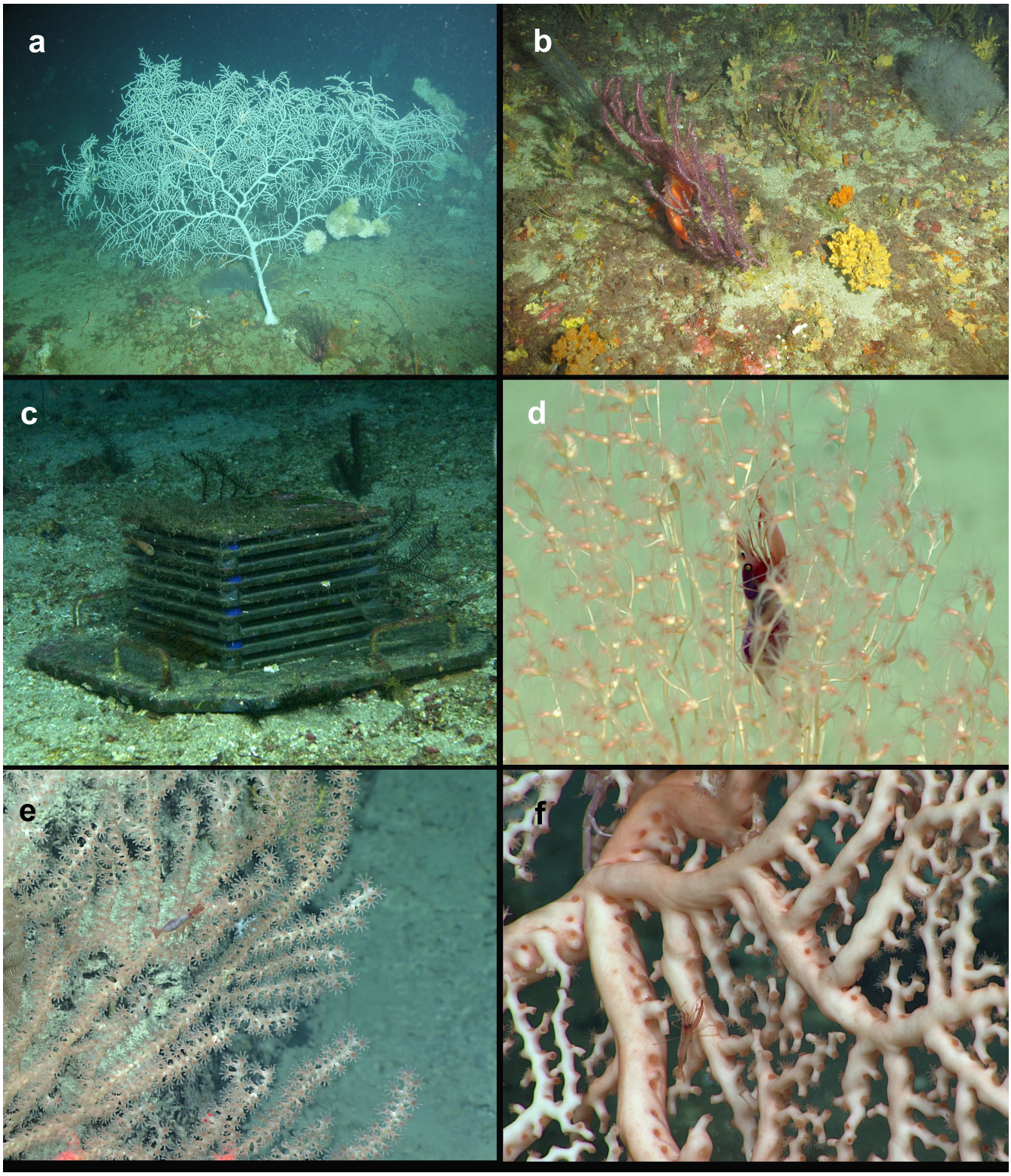


Figure 2

Examples of deep-water hosts for some of the caridean shrimps examined in the present study, including octocorals (a, b, d–f) and crinoid (c): (a) *Muricea pendula*, Mississippi-Alabama shelf, 67 m; (b) *Thesea nivea* (next to a yellow sponge), Mississippi-Alabama shelf, 57 m; (c) unidentified black feather stars on ARMS deployed on Bright Bank, 83 m; (d) *Acanella* sp. with the shrimp *Bathypalaemonella serratipalma*, Bathypalaemonellidae, West Florida Escarpment, 1862 m; (e) bamboo coral, Keratoisididae,

with an associated shrimp, *Periclimenes* sp.(?), Palaemonidae, West Florida Escarpment, 778 m; (f) *Madrepora* sp, with symbiotic shrimp, *Periclimenes* sp.(?), Palaemonidae, or (less likely) young *Bathypalaemonella* sp. (Bathypalaemonellidae), Texas-Louisiana slope, 1147 m. Photographs taken by ROV *Mohawk* (a–c) on NOAA Ship *Pisces*, P022_L2, and ROV *Deep Discoverer* on the E/V *Okeanos Explorer*, EX1711, ROV Shakedown (d–f).

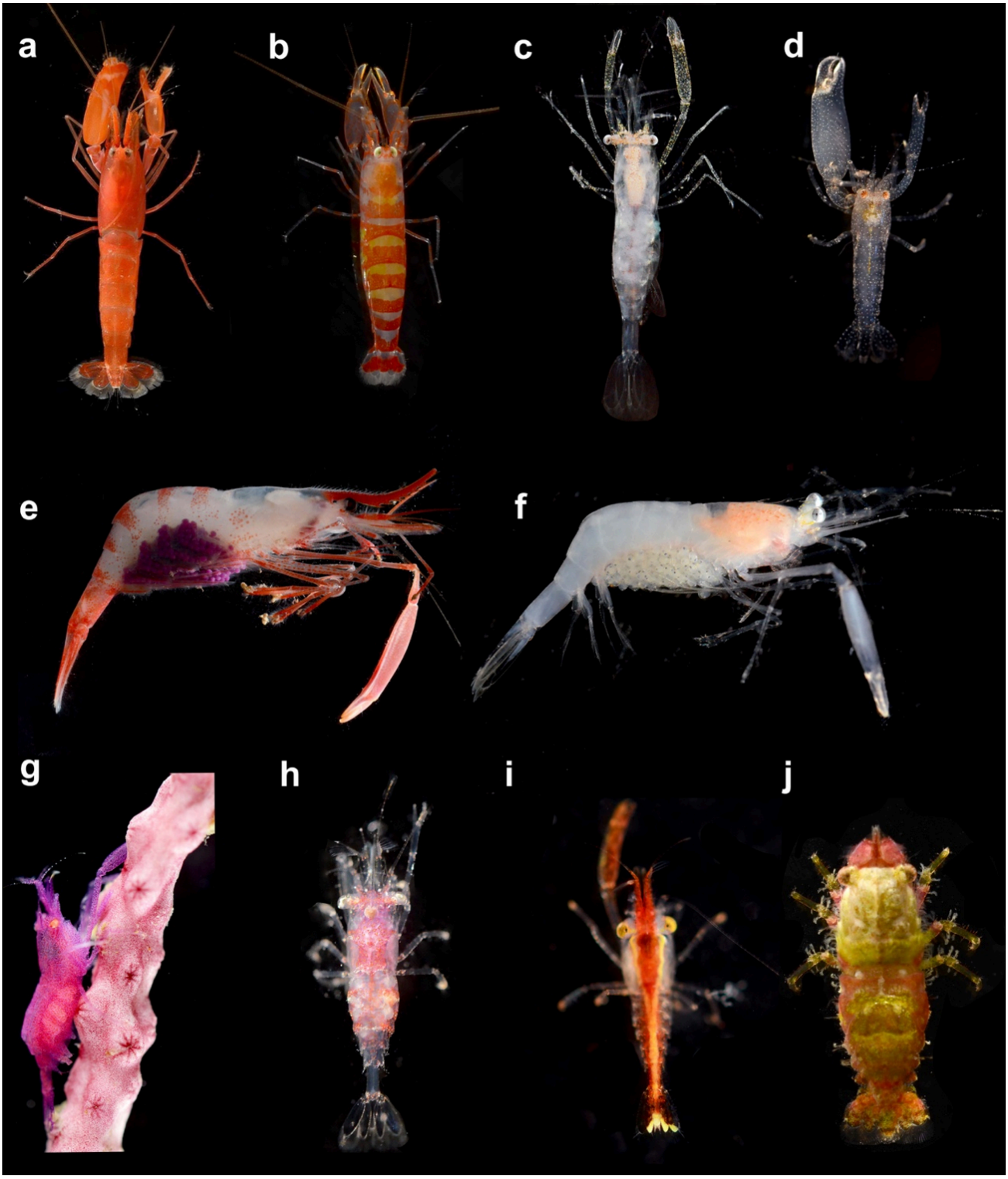


Figure 3

Some symbiotic [marked with (S)] and presumably free-living (marked with (F)] caridean shrimps collected during the MDBC cruises: (a) *Alpheus lentiginosus* (F), Diaphus Bank, 82 m (USNM 1745040); (b) *Alpheopsis gorei* (F), Diaphus Bank, 81 m (USNM 1745065); (c) *Periclimenes tenellus* (S), Tunica Mound, 343 m (USNM 1721156); (d) *Periclimenaeus ascidiarium* (S), East Flower Garden Bank, 81 m (USNM 1745000); (e) *Bathypalaemonella texana* (S), Shephard Mound, 617 m (USNM 1721010); (f) *Periclimenes* cf. *pandionis* (S?), Tunica Mound, 343 m (USNM 1721182); (g) *Pseudocoutierea* cf. *stephanieae*(S), Sackett Bank, 63 m (USNM 1721222); (h) *Pseudocoutierea* cf.*acutidorsata* (S), Sackett Bank 86 m (USNM 1721202); (i) *Lipkebe holthuisi* (S), Bright Bank 83 m USNM 1744997; (j) *Trachycaris* sp. (F), McGrail Bank, 85 m (USNM 1745081). Photographs by Sarah Tweedt SI-NMNH (a, b, d, i, j) and P. C. Rodríguez-Flores/SI-NMNH (c, e–h).



Figure 4

Maximum Likelihood phylogenetic tree inferred using IQ-TREE. Species hypotheses, based on consensus between ASAP and bPTP molecular delimitation methods and supported by morphological examination, are indicated by colored bars on the right side. Color-highlighted lineages show clades or species associated with corals (Scleractinia, Antipatharia, Octocorallia) or sponges (Porifera). PPLV clade is highlighted on the tree.

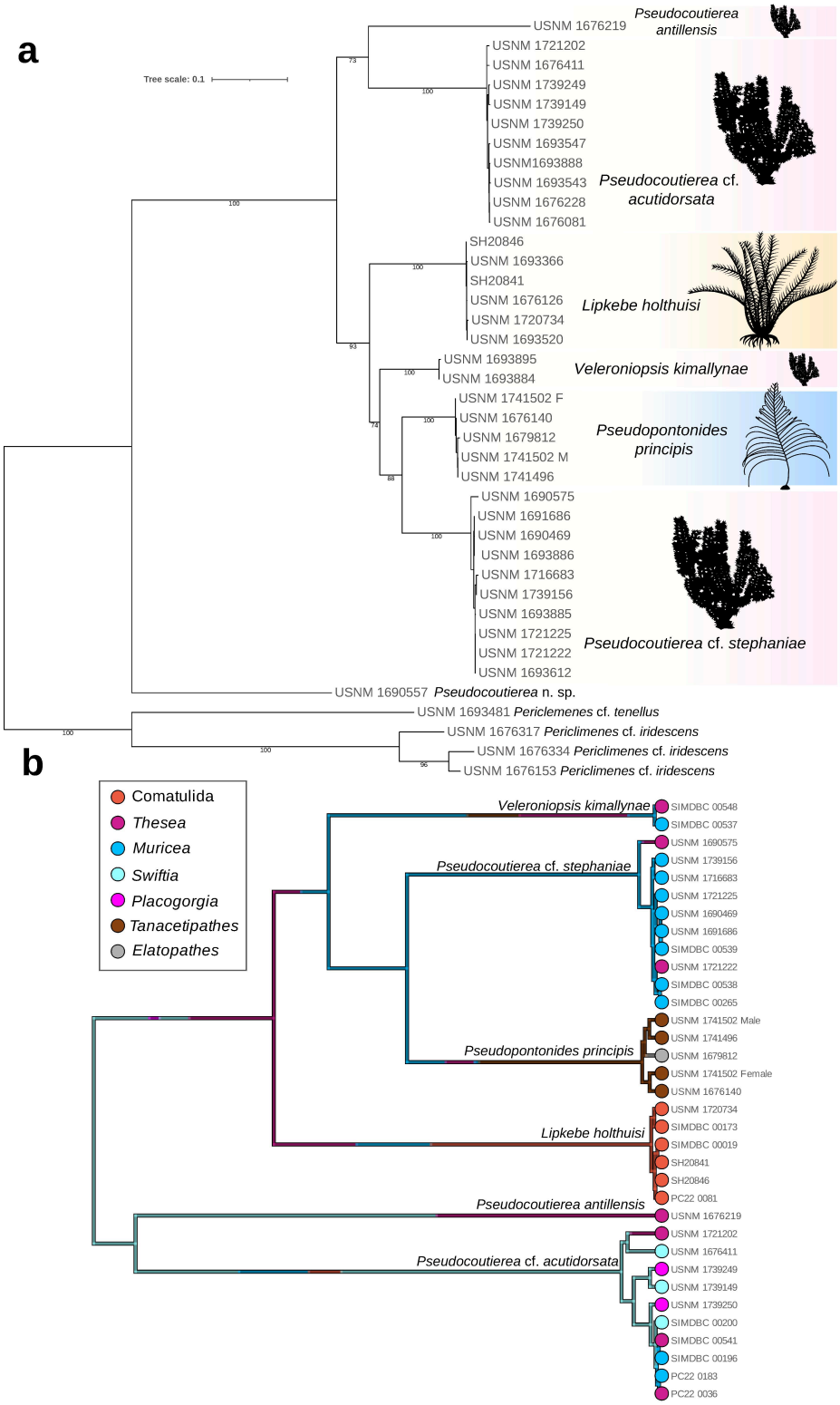


Figure 5

Symbiotic PPLV clade of the Palaemonidae: (a) phylogenetic hypothesis based on three concatenated genes: COI, 28S and 18S using IQ-TREE; numbers above branches represent Bootstrap support (Bs); (b) stochastic character mapping for the multistate character “host” (black coral and octocoral genera or comatulid crinoids) on the ultrametric tree, including discrete states at the tips.

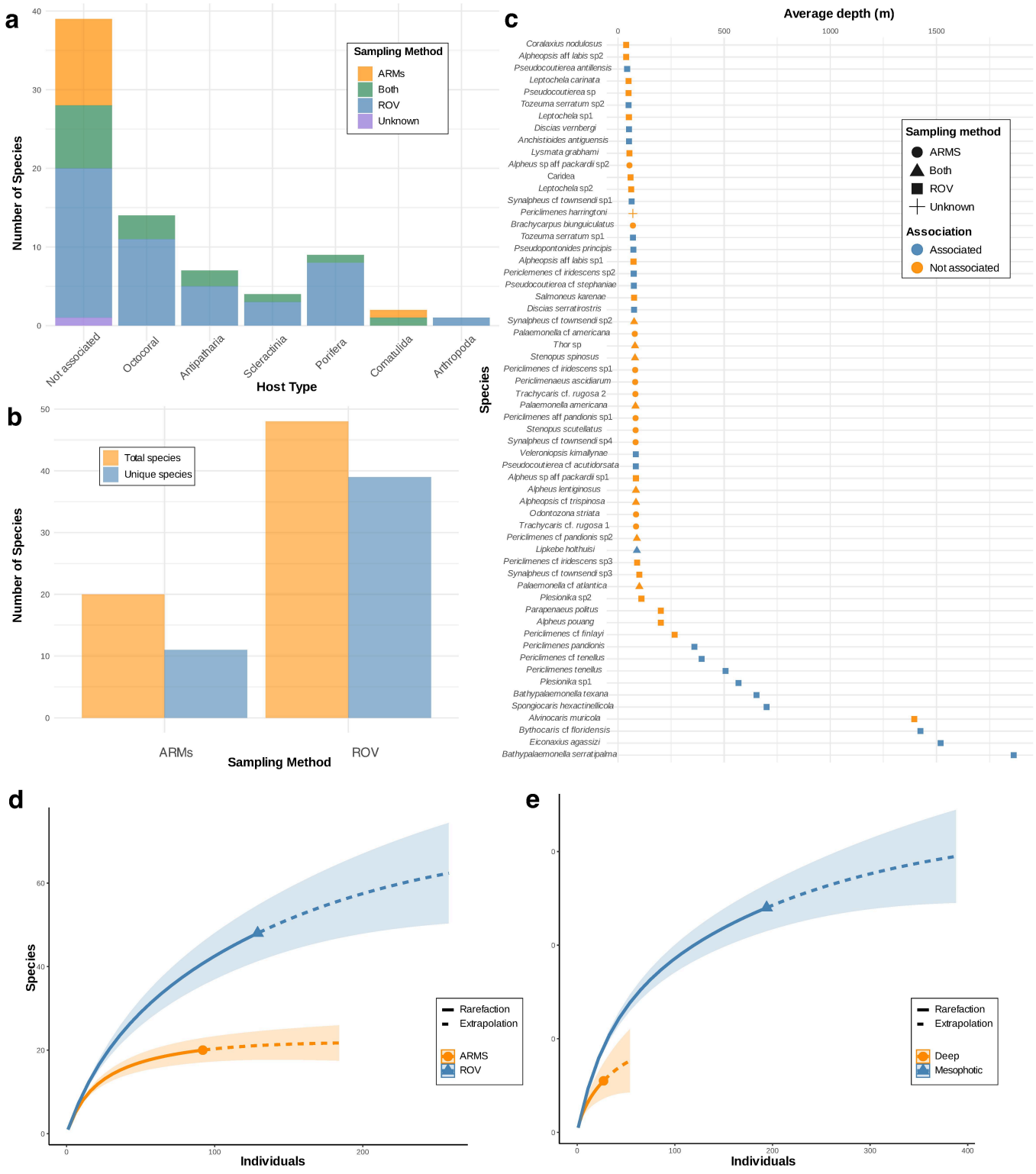


Figure 6

Comparison of collection methods and host for mesophotic and deep-sea shrimps: (a) bar plot showing the number of symbiotic (associated with one or multiple hosts) and non-symbiotic (not associated with any host) shrimps collected by different methods: ARMS, ROV, both ARMS + ROV, and trawls / dredges (other); (b) bar plot showing the number of total vs. unique (only retrieved with one of the sampling methods) species collected by ARMS and ROV; (c) graph representing the mean depth for each species

and collection method; rarefaction curves shows sampling method (d) and depth-related (e) patterns of shrimp diversity.

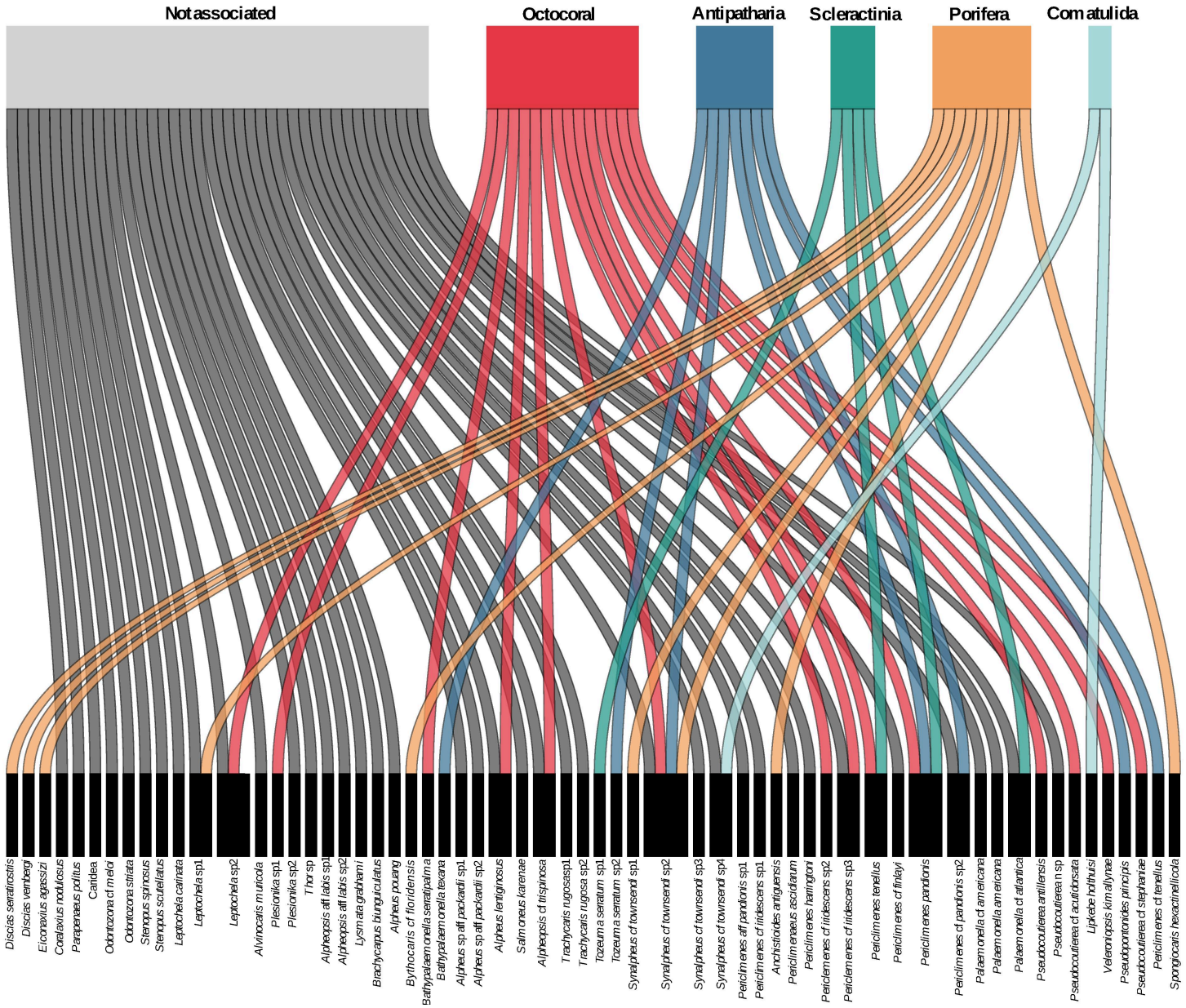


Figure 7

Bipartite network graph of interactions between shrimp species (bottom) and their invertebrate hosts (top), the bar size indicates the host specificity for the guests and for the host, preference by the guest.

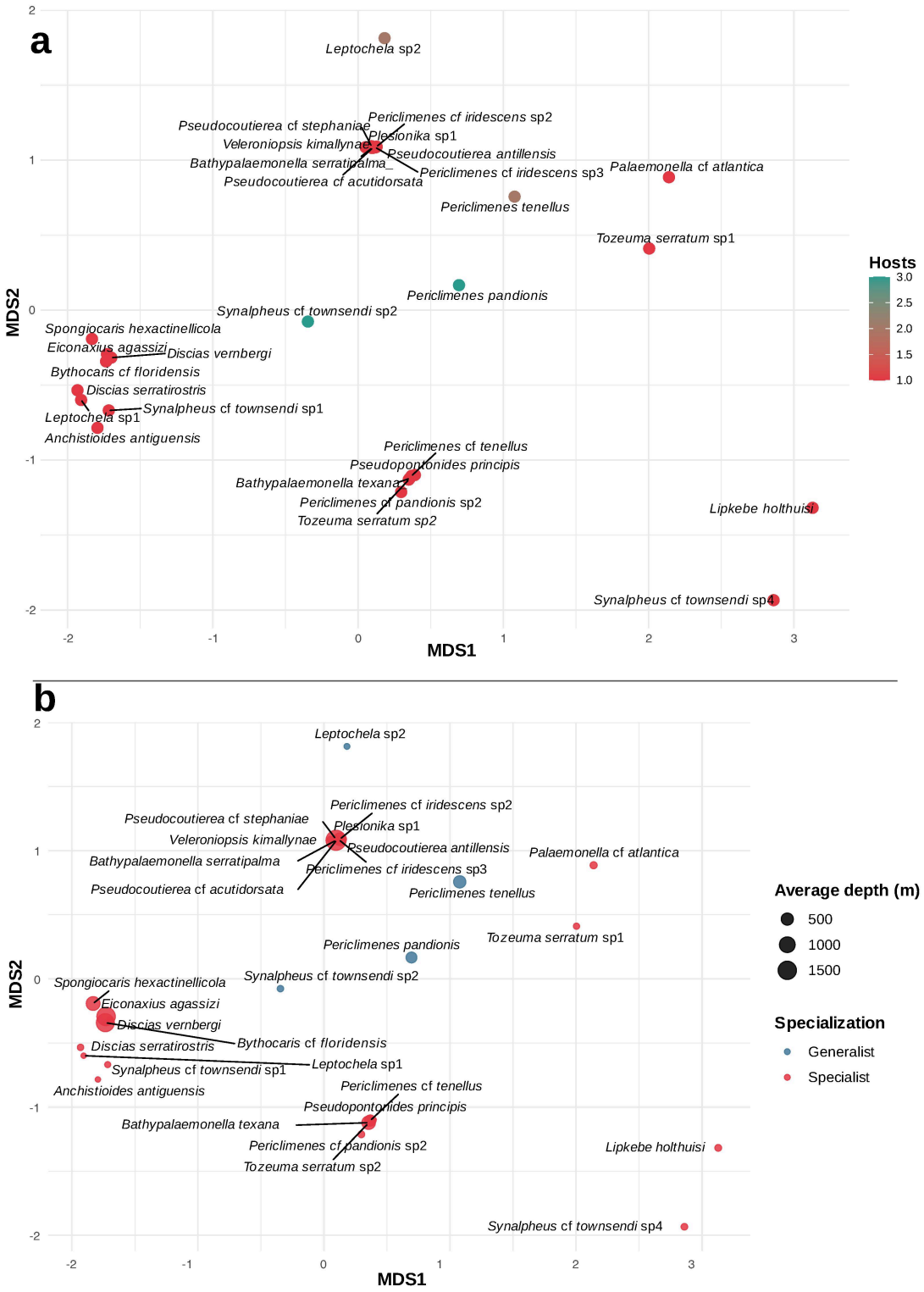


Figure 8

Non-metric multidimensional scaling (nMDS) ordination of shrimp species based on presence–absence host association data using Jaccard distance. (a) Species positioned according to similarity in host use. (b) The same ordination highlighting host specialization, where specialists (one host type) and generalists (>1 host types) are shown in relation to their average depth of occurrence.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementaryTable1.xlsx
- SupplementaryTable2.xlsx