RESEARCH ARTICLE

Filter feeders living on suspension feeders: New insights into the lifestyle and distribution of Arcturidae Dana, 1849 (Crustacea: Isopoda) around Iceland

Vivien Lukas Hartmann[1] | Emanuel Pereira[2,3] | Nancy F. Mercado-Salas[4] | Anne-Nina Lörz[5] | Jörundur Svavarsson[6] | Saskia Brix[1]

[1]Senckenberg am Meer, Department German Center for Marine Biodiversity Research (DZMB), University of Hamburg, Hamburg, Germany

[2]Instituto de Biodiversidad y Biología Experimental y Aplicada (IBBEA, UBA-CONICET), Buenos Aires, Argentina

[3]Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Departamento de Biodiversidad y Biología Experimental (DBBE), Buenos Aires, Argentina

[4]Leibniz Institute for the Analysis of Biodiversity Change, Centre for Taxonomy and Morphology, Hamburg, Germany

[5]Institute of Marine Ecosystem and Fishery Science (IMF), Center for Earth System Research and Sustainability (CEN), University of Hamburg, Hamburg, Germany

[6]Faculty of Life and Environmental Sciences, University of Iceland, Reykjavík, Iceland

Correspondence
Vivien Lukas Hartmann, Senckenberg am Meer, Department German Center for Marine Biodiversity Research (DZMB), University of Hamburg, Biocenter Grindel, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany.
Email: v.hartmann@tutanota.com

Abstract

The focus of the present study was on arcturid isopods occurring in the subarctic region around Iceland. Data from two decades of sampling with an epibenthic sledge (EBS) during numerous expeditions of the BIOICE (Benthic Invertebrates of Icelandic Waters; 1992–2004) and IceAGE (Icelandic marine Animals: Genetics and Ecology; 2011—ongoing) projects were incorporated into an integrative taxonomy approach. This approach linked distribution records, morphological and molecular examinations, with video and image data observed during recent expeditions in 2018 (MSM75) and 2020 (SO276) using the Remotely Operated Vehicles (ROVs) PHOCA and Kiel 6000 from GEOMAR. The resulting dataset from 120 sampling locations included 6852 specimens, a large percentage of which were fixed in formalin during BIOICE. Ethanol-fixed specimens collected during IceAGE were used to link morphotypes with haplotypes and occurrence locations, focusing on the coral association of the genus *Astacilla* Cordiner, 1793. The IceAGE sampling was complemented by ROV image and video data and noninvasive sampling, making it possible to obtain pictures of living specimens of *A. longicornis*. The species *A. longicornis* Sowerby, 1806 showed a distribution linked to cold-water occurrence and was sampled from *Paramuricea placomus*. *Astacilla boreaphilis* Stranky & Svavarsson, 2006, occurring only south of Iceland, showed high morphological variation in the spine pattern of adult females, while the molecular results indicated no clear pattern of potentially ongoing species radiation or cryptic species. *Astacilla granulata* was exclusively found north of Iceland. Thus, the species' distribution is potentially influenced by the Greenland-Faroe Ridge, which separates the North Atlantic from the Arctic Ocean.

KEYWORDS
associated fauna, *Astacilla*, cold-water corals, crustacea, Iceland, North Atlantic

1 | INTRODUCTION

The ocean around Iceland has diverse hydrographic and topographic features, making it unique. The region is characterized by the extensive Greenland-Iceland-Faroe Ridge (GIF Ridge), which extends from Greenland to Scotland and separates the Nordic Seas and the Arctic Ocean from the Atlantic Ocean. With its maximum saddle depths of 820 m (Hansen & Østerhus, 2000), the ridge separates the cold (<−0.9°C) deep waters of the Nordic Seas from the warmer (2°C–3°C) deep Atlantic. Furthermore, the Reykjanes Ridge (RR) separates the northernmost North Atlantic into the western Irminger Basin and the eastern Iceland Basin (Brix & Svavarsson, 2010; Hansen & Østerhus, 2000; Malmberg & Valdimarsson, 2003). The region is additionally shaped by a complex set of weak and strong currents, potentially influencing the local and regional fauna (e.g., Dolan et al., 2008; Davies et al., 2009; Buhl-Mortensen et al., 2001; Mohn et al., 2014). The GIF Ridge and its associated hydrographic conditions form a natural barrier for the dispersal of species in the North Atlantic Ocean and the Arctic Ocean (see Pampouli et al. (this issue)). The ridges and the Icelandic shelf may represent favorable conditions for epifauna that depend on highly hydrodynamic environments, which provide them with a steady stream of water for suspension feeding (Burgos et al., 2020; Davies et al., 2009; Mohn et al., 2014; Sundahl et al., 2020).

The crustacean family Arcturidae (Isopoda: Valvifera) occurs globally and consists of species, that are all supposed to be filter feeders due to the presence of long filter setae on their anterior pereopods 2–4 (King, 2003; Poore, 2001; Riisgård, 2015; Stransky & Svavarsson, 2006; Wägele, 1987). Arcturids are benthic crustaceans without free larval stages (King, 2003; Poore, 2001; Riisgård, 2015; Stransky & Svavarsson, 2006; Wägele, 1987). They are commonly found on various elevated hard substrata for better exposure to currents and thus to food supply (Moreira, 1973a, 1973b; Schultz, 1978; Wägele, 1987). Some valviferan species, such as *Astacilla gorgonophila* Monod, 1925, *A. sawayae* Moreira, 1973b, *A. andresmeixidei* Taboada et al., 2019, and *Antarcturus spinacoronatus* Schultz, 1978 have been observed on cold water corals (Monod, 1925; Moreira, 1973b; Taboada et al., 2019; Wägele, 1987); in particular, *Astacilla andresmeixidei* and *A. gorgonophila* were described as commensals on their respective gorgonian hosts (Monod, 1925; Taboada et al., 2019).

Within the family, the genus *Astacilla* Cordiner, 1793 comprises 49 species (WoRMS—World Register of Marine Species, 2024), while six species are reported to occur in the North-East Atlantic north of 55° N (*Astacilla arietina* Sars, 1883, *A. boreaphilis* Stransky & Svavarsson, 2006, *A. caeca* Benedict, 1898, *A. granulata* Sars, 1877, *A. intermedia* Goodsir, 1841, *A. longicornis* Sowerby, 1806, and *A. pusilla* Sars, 1873).

The distribution of isopod families around Iceland has been discussed in Brix et al. (2018). A closer look, adding new data to the family Arcturidae, reveals new insights. Here, we evaluate the distribution of this filter-feeding isopod group in Icelandic waters. The evaluation is based mainly on samples taken from many localities in the region using epibenthic sleds. Additionally, we specifically analyze the presence of these isopods clinging to cold-water corals, which potentially may provide an elevated habitat suitable for this feeding type. This association with corals has previously been shown for another North Atlantic species (Taboada et al., 2019), but not for arcturids that occur around Iceland.

The aim of the present study was to gather all available distribution data of arcturid isopods in the subarctic region and to implement different data types, focusing on the observed coral association of *Astacilla* species from the most recent samples. Additionally, an integrative taxonomy approach was used to clarify the presence of highly diverse morphotypes within Astacilla boreaphilis Stransky & Svavarsson, 2006.

2 | MATERIALS AND METHODS

2.1 | Sampling design

All samples were taken in Icelandic and international waters during the BIOICE (Benthic Invertebrates of Iceland) and the IceAGE (Icelandic Marine Animals: Genetics and Ecology) projects with various research vessels. All arcturid isopods were available from epibenthic sledge (EBS; Brenke, 2005 and Rothlisberg & Pearcy, 1977) samples and remote operated vehicles (ROV) samples were included in this study. In total, 5838 arcturids from BIOICE samples were available, and 1014 from IceAGE samples (937 from EBS, 62 from ROV). In addition, during two IceAGE expeditions, the ROVs PHOCA (2018 during MSM75) and KIEL 6000 (2020 during SO276) of GEOMAR were used to collect corals and their associated fauna. EBS samples of the IceAGE project were taken during the IceAGE 1, 2, 3, and RR expeditions, on board RV Meteor (M85/3; Brix et al., 2011), RV Poseidon (POS456; Brix, 2013), RV Maria S. Merian (MSM75; Devey et al., 2018), and RV Sonne (SO276; Brix et al., 2020). For EBS samples, the treatment of isopods is described in Brix et al. (2018). The ROV samples were collected using the arm of the ROV to take a branch of the coral, but never the whole coral. This branch was moved into the drawer of the ROV holding a so-called "biobox," which closes completely with a lid, keeping the water inside and thus everything clinging to the coral (see Video S1).

The taxon information about the corals hosting the analyzed specimens is taken from Korfhage et al. (2022), who provided molecular fingerprinting of the collected taxa. To evaluate the presence of arcturids on cold-water corals, associated fauna samples were collected during the IceAGE 3 and RR expeditions using either ROV Kiel 6000 (IceAGE3) or ROV PHOCA (IceAGE RR). The corals were individually placed in separate bioboxes during diving and preserved separately along with their epibionts. In total, samples of corals from 32 distinct locations were analyzed (Figure 1; Data S2).

All samples were treated in a cooling chain according to Riehl et al. (2014) and examined at the laboratories of the DZMB (German Center for Marine Biodiversity Research) in Hamburg. Samples were preserved in 96% undenatured ethanol and stored at 4°C until further processing. Examined specimens were identified to the lowest possible taxonomic level (Data S3). Specimens of the isopod family Arcturidae (Data S4) were identified to species level according to
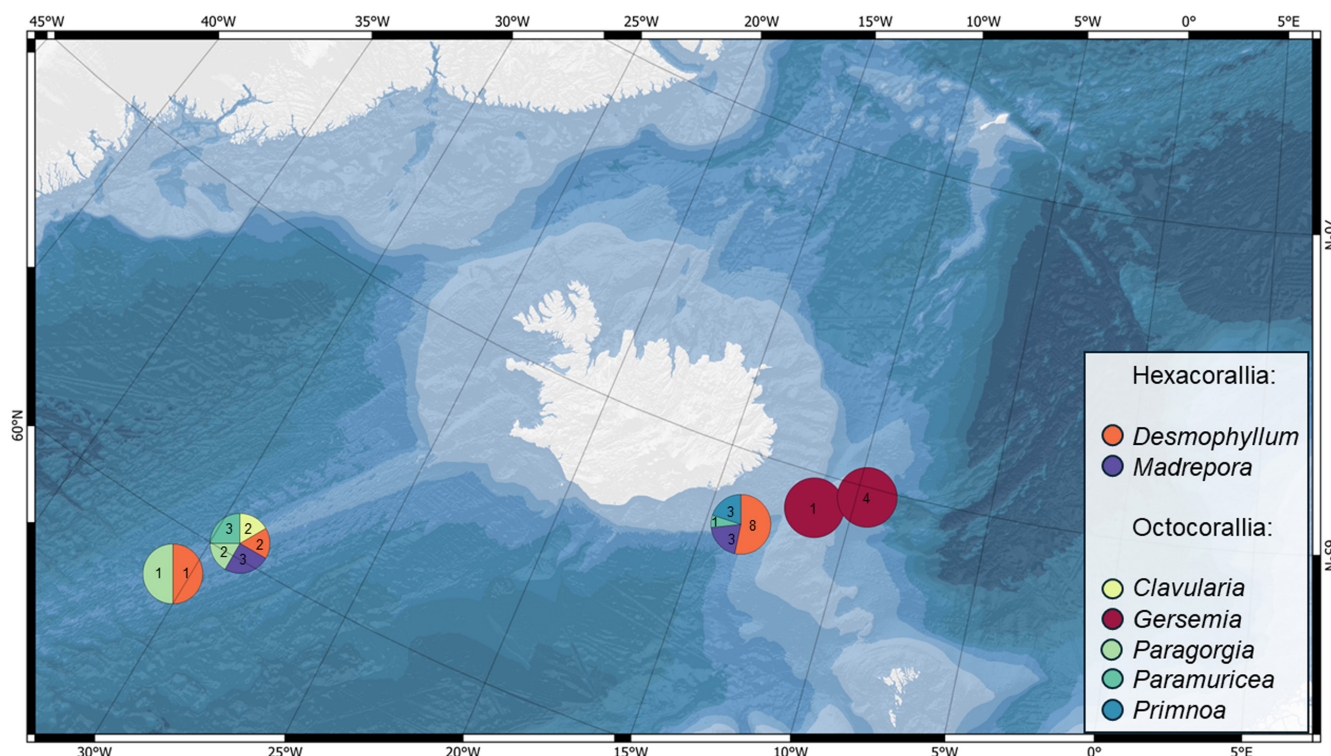
FIGURE 1 Sample sites of cold-water corals sampled during the IceAGE project. Pie chart location indicate area of sampling, colors represent coral genera, numbers indicate sample size.

the available literature using a Leica MZ12.5 dissecting microscope. Photos of arcturid specimens were taken with a Keyence VHX-7000 digital microscope (Leibniz Institute for the Analysis of Biodiversity Change, Morphology Lab Hamburg) and edited with the software GIMP (The GIMP Development Team, 2023).

BIOICE arcturids are stored in the Náttúrufræðistofnun Íslands | Icelandic Institute of Natural History (curator: Gudmundur Gudmundsson, Reykjavik). The cold-water coral-associated taxa remain in the DZMB "working collection," available upon request.

2.2 | Molecular methods

In total, 67 specimens sampled during the IceAGE expeditions were used for molecular analysis. The workflow and sample treatment are described in Riehl et al. (2014). DNA extractions from whole individuals of Astacilla boreaphilis and A. longicornis were carried out using the Mollusc DNA Kit (Omega Biotek) following the manufacturer's extraction protocol. Specimens were transferred into 96% denatured ethanol afterward and stored at the facilities of the DZMB Hamburg. DNA extracts were deposited at the DZMB biobank (−20°C) after the molecular work was completed. For species delimitation, the mitochondrial large ribosomal subunit (16S fragment) was used, as PCRs using Cytochrome c oxidase subunit I (COI) primers did not yield usable results. Amplification of the 16S fragment was performed using AccuStart II Taq DNA Polymerase (Quantabio) in a 20μL volume tube containing 7μL H2O, 10μL PCR Master Mix, 0.5μL of each primer (10pmol μL^{-1}), and 2μL of DNA

template. The primer pair 16SAR-L/16SBR-H (Palumbi et al., 1991) was used. PCR products were assessed for their length and purity by gel electrophoresis using 1.5% agarose gels. Successful PCR products were purified using ExoSAP-IT PCR Product Cleanup Reagent (ExoSAPIT) and sent to Macrogen Europe, Inc. (Amsterdam-Zuidoost, Netherlands) for bidirectional DNA Sanger sequencing. The Quality of the sequences was assessed with the program GENEIOUS Prime ver. 2019.2.3 (Geneious Bioinformatics Software for Sequence Data Analysis, 2022). Forward and reverse strands were assembled and checked for the correct amino acid translation frame using GENEIOUS. All sequences were searched in GenBank using BLASTN (Altschul et al., 1990) to discard contamination. The 16S Sequences produced during this study are publicly available on the Platform BoLD (Barcode of Life Database, Ratnasingham & Hebert, 2007). All voucher specimens are stored in the DZMB working collection. The BoLD dataset XXXNAMEXXX is available under the following DOI including all information about storage and GenBank numbers.

The dataset consists of 43 sequences of *A. boreaphilis* and 24 sequences of *A. longicornis*. In addition, two sequences of *Antarcturus hodgsoni* Richardson, 1913 were used as an outgroup (Baltzer et al., 2000). A total of 69 sequences were aligned using MUSCLE ver. 3.8.425 (Edgar, 2004). Trees were constructed with Bayesian Inference (BI) in MrBayes ver. 3.2 (Ronquist et al., 2012), using GTR as an evolutionary model for two independent runs, each consisting of four chains for 5×10^6 generations, sampling every 1000 generations. The first 25% of the trees were discarded as burn-in, and run convergence was assessed using Tracer ver. 1.6 (Rambaut et al., 2018). Uncorrected p-distances were calculated using MEGA

ver. 7.0 software (Kumar et al., 2016). Additionally, two species de-limitation models were used to identify the number of putative spe-cies of *Astacilla*: one distance-based (ABGD—Automated Barcode Gap Discovery; Puillandre et al., 2021) and one tree-based (GMYC—Generalized Mixed Yule Coalescent; Pons et al., 2006). For ABGD, we ran the online version (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) using an alignment excluding the outgroup. Settings were as follows: $P_{min}=0.01$, $P_{max}=0.1$, Steps=100, X (relative gap width)=1.5, Nb bins (for distance distribution)=20. Simple distance was used as the distance method.

For the GMYC method, an ultrametric tree was created in BEAST (Bayesian Evolutionary Analysis Sampling Trees ver. 1.8.3) with param-eters set to the GTR nucleotide substitution model, "Strict" clock (SC), and Yule speciation tree prior (Stadler, 2008; Yule, 1925). Posterior probabilities were estimated using 10,000,000 Markov Chain Monte Carlo (MCMC) generations with a sampling frequency of 1000 trees (Drummond et al., 2012). Convergence of the runs was assessed with Tracer ver. 1.6 (Rambaut et al., 2018). A tree with median branch lengths was selected, discarding 25% of the trees using TreeAnnotator ver.1.8.3 (Drummond et al., 2012). The GMYC method was imple-mented in the SPLITS package for R and applied to the ultrametric tree. Additionally, we used the fixed local clock (FLC) in conjunction with the Yule speciation prior and the strict clock with the Coalescent: Constant size tree prior (Kingman, 1982), named "CC" in the following.

In order to assess the geographic distribution of *Astacilla boreaphilis* genetic diversity, a haplotype network was created with popART (Leigh & Bryant, 2015) using the minimum spanning net-work algorithm (Bandelt et al., 1999). Distribution maps were cre-ated in QGIS 3.28.12 "Firenze" (QGIS Development Team, 2023) and R Studio Version 4.0.3 (RStudio, 2019) was used for the creation of plots, using the package ggplot2 (Wickham, 2016).

3 | RESULTS

3.1 | Faunal assemblages of coral-associated crustaceans with a focus on isopods

Cold-water corals were sampled at 32 locations in the North Atlantic below 207 m depth (Figure 1; Data S2). Crustaceans represented the most numerous taxon in the samples, with 9177 specimens and ac-counting for over 50% of specimens at most stations. Among the crustaceans, 644 specimens were identified as isopods, the second most abundant peracarid crustacean group behind the amphipods, which occurred in much higher numbers (Data S3). Amphipoda from IceAGE samples associated with corals are presented by Schwentner and Lörz (2021) and are not the focus of the present study.

Within the order Isopoda, nine isopod taxa were identified: Arcturidae, Bopyridae, Desmosomatidae, Flabellifera, Gnathiidae, Janirellidae, Janiridae, Munnidae, and Munnopsidae. Among these, the most numerous were the families Janiridae Sars, 1897, with 455 specimens, and Munnidae Sars, 1897 (*n*=140), followed by Arcturidae (*n*=31). Janiridae and Munnidae were the most frequently

collected families on all corals, except for the coral genera *Primnoa* Lamouroux, 1812 (only Janiridae), *Gersemia* von Marenzeller, 1878 (only Munnidae), and *Paramuricea* on which Arcturidae were most abundant (Figure 2). The lifestyles of the different isopod families occurring around Iceland have been summarized in Brix et al. (2018).

3.2 | Arcturid samples

Arcturidae collected in association with cold-water corals belonged to the genus *Astacilla*: 26 individuals were identified as *Astacilla longicornis*, whereas the remaining five specimens were identified as *Astacilla* sp. due to being in an early manca stage with species-specific characters not yet visible. The paramurican coral on which these specimens were collected was identified as *Paramuricea placo-mus*, according to Korfhage et al. (2022) (Figure 3; Data S5). The five remaining *Astacilla* specimens could not be identified to species level because they were in an early manca stage.

From all BIOICE and IceAGE samples, a total of 6852 specimens were sorted, belonging to the species: *Astacilla boreaphilis* (6287), *A. granulata* Sars, 1877 (402), and *A. longicornis* (163) (Data S4). Most specimens could be assigned to species level, but in some cases, an assignment was not possible due to poor specimen condition or an early life stage. These specimens received the abbreviation 'cf.'. Together these samples extend the known distribution of the spe-cies in the North Atlantic (Figure 4; Data S6).

A. boreaphilis was sampled between 218 m and 1809 m strictly south of the GIF Ridge, while *A. granulata* was sampled between 391 m and 996 m strictly north of the ridge. *A. longicornis* was sam-pled mostly south of the ridge on the Icelandic shelf between 119 m and 1289 m (Figure 5).

3.3 | *Astacilla boreaphilis* Stransky & Svavarsson, 2006

Among all arcturids examined, 6287 specimens were identified as *Astacilla boreaphilis* based on BIOICE (Stransky & Svavarsson, 2006) and IceAGE collections (Data S4). We observed considerable varia-tions in the spine pattern of female specimens, as most females had varying degrees of development of the dorsal and lateral spines in comparison with the spine pattern of the holotype.

Thus, we defined two morphotypes of *A. boreaphilis* in this study: Of 221 female specimens, only eight show a similar dorsal spine pat-tern to the holotype (herein morphotype I; Figure 6).

Yet, the pattern and size of the spines were inconsistent. Most specimens of morphotype I did not have the fifth dorsal spine pair of pereonite 4, which is present in the holotype. However, a photo taken immediately after sampling on board RV Merian during the IceAGE RR expedition shows a specimen with the complete spine pattern as in the holotype (Figure 7).

In contrast, the morphology of most females (213) varies from morphotype I and is thus named morphotype II (Figure 8). This

FIGURE 2 Isopod families sampled at locations where cold-water coral were present. Values indicate number of individuals per taxon. Parasitic isopod families include Bopyridae and Gnathiidae. These were merged because of taxonomic inconsistencies.

FIGURE 3 *Astacilla longicornis* female (DZMB-HH 61731) sitting on *Paramuricea placomus*, collected at 866 m. Photo taken on board of RV M.S. Merian during MSM75 (2018) by Anne-Helene Tandberg.

morphotype had no dorsal spines on pereonite 3 and only one pair of dorsal spines in the anterior part of pereonite 4 (contrary to the five dorsal spines in the holotype). In addition, these females also lacked most of the dorsolateral spines along the body, except for the distal part of the head, pereonites 5 and 6, and the pleotelson. Lateral spines were also completely missing. Additionally, all spines present were considerably smaller than those from the holotype. Furthermore, tubercle-like structures were visible at the same dorsal spots where spines are present in the holotype. However, considering that only (brooding) females showed inconsistencies in the spine pattern, and the variations in the spine pattern were

also reported in the original description, all these specimens are identified as *A. boreaphilis*.

3.4 | Molecular analysis

The analyzed 16S alignment consisted of 69 sequences of *A. boreaphilis* (43 sequences), *A. longicornis* (24 sequences), and *Antarcturus hodgsoni* (2 sequences) as outgroup. The resulting Bayesian tree reflected the morphological identification of all specimens, resulting in three distinct lineages: one for *A. boreaphilis*, a second for *A. longicornis*, and a third for the antarcturid *Antarcturus hodgsoni*, each supported with a posterior probability of 1.0 (Figure 9). The species delimitation models differed in the number of lineages calculated within our *Astacilla* dataset (Figure 9). All approaches used (ABGD, GMYC, and morphology) recovered *A. longicornis* as a single lineage. ABGD and morphological identifications recovered *A. boreaphilis* as a single lineage, whereas the GMYC calculated between two and three lineages, depending on the evolutionary rate clock used for the analysis (see Figure 9). Uncorrected p-distance within species was below 0.5% for both species and between both species was 27.7% (Data S7).

3.5 | Haplotype networks

Our dataset revealed 10 haplotypes within *Astacilla boreaphilis*, where three haplotypes are the most common (I, II, and III) with more than nine individuals each. Additionally, seven haplotypes
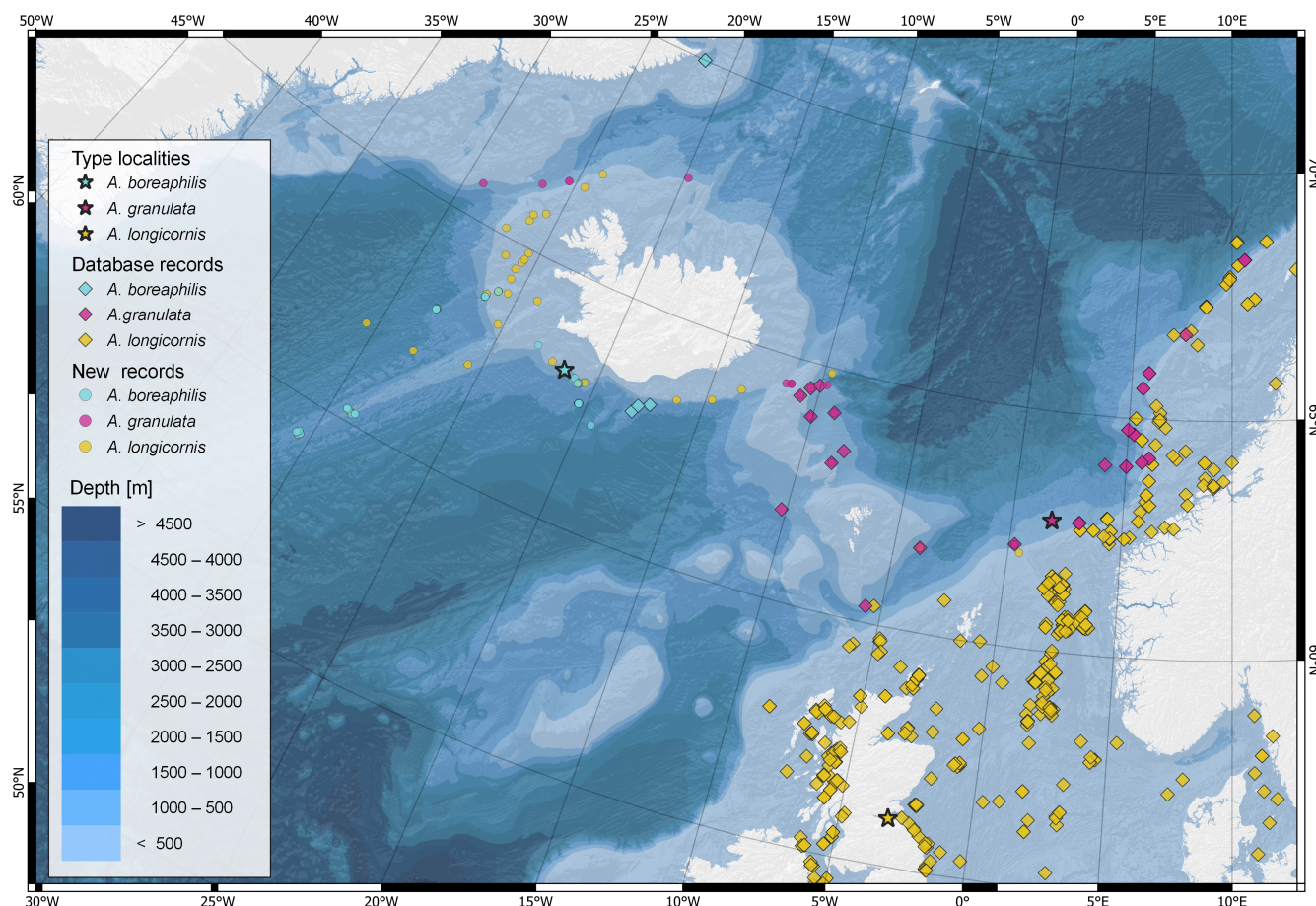
FIGURE 4 Occurrence map with database records of *A. boreaphilis* Stransky & Svavarsson, 2006, *A. granulata* Sars, 1877, *A. longicornis* Sowerby, 1806, including holotype locations (Data S6) and new records from this study.

were found, each of them represented by a single individual (Data S8). The less common haplotypes differed by only one or two mutations from the most common ones (Figure 10). There are three sites (B, C, and D) where more than two haplotypes occur. On sites A and E, only one haplotype occurs (A: Haplotype V; E: Haplotype III), these are also the shallowest sites (A: 218 m; E: 289 m). At least one of the three common haplotypes (I, II, and III) was found at almost all sites except site "A." Haplotype III has the widest depth range, occurring at depths between 289 m and 1594 m, and the widest geographical range.

4 | DISCUSSION

4.1 | Cold-water coral occurrences

Cold-water corals (CWCs) are found globally in the world's oceans at depths as great as 6000 m, being most common in the upper 1000 m (Broch, 1922; Heifetz, 2002; Rogers, 1999; Stone, 2006; Tendal, 2011; Watling et al., 2011). Because of their role as hotspots of biodiversity and being habitat-forming species, deep-sea corals represent an important ecological habitat and can be considered ecosystem engineers (Cathalot et al., 2015; Danovaro et al., 2010; Erwin, 2008;

Jones et al., 1994; Kennedy et al., 2013). Taxa commonly found in the North Atlantic belong to the orders Scleractinia and Octocorallia, viz.: *Desmophyllum pertusum* Linnaeus, 1758, *Madrepora oculata* Linnaeus, 1758, *Paragorgia arborea* Linnaeus, 1758, *Paramuricea placomus* Linnaeus, 1758, *Primnoa resedaeformis* Gunnerus, 1763, *Acanella arbuscula* Johnson, 1862, *Isidella lofotensis* Sars, 1868, *Radicipes gracilis* Verrill, 1884, and *Acanthogorgia armata* Verrill, 1884 (Buhl-Mortensen et al., 2014). Apart from *I. lofotensis*, which has only been found off the coast of Norway, all mentioned species are present south on the Icelandic shelf, the Reykjanes Ridge, and the Greenland-Iceland-Scotland Ridge (Buhl-Mortensen et al., 2014; Buhl-Mortensen & Buhl-Mortensen, 2004b; Roberts et al., 2006).

The associated fauna of cold-water corals is highly diverse (Buhl-Mortensen & Buhl-Mortensen, 2004a, 2004b; Roberts et al., 2006). Buhl-Mortensen and Buhl-Mortensen (2004b) found a total of 983 invertebrate species on 74 CWC species in the North Atlantic. However, for the most part, the relationship between the taxa remains unclear. This makes it difficult to determine the nature of the association, whether it is commensalistic, mutualistic, or parasitic, or if there is an association at all (Buhl-Mortensen & Buhl-Mortensen, 2004b; Roberts et al., 2009). Additionally, many species sampled together with CWCs occur in other habitats without a coral host. For example, Eichsteller et al. (2022) observed ophiuroids in
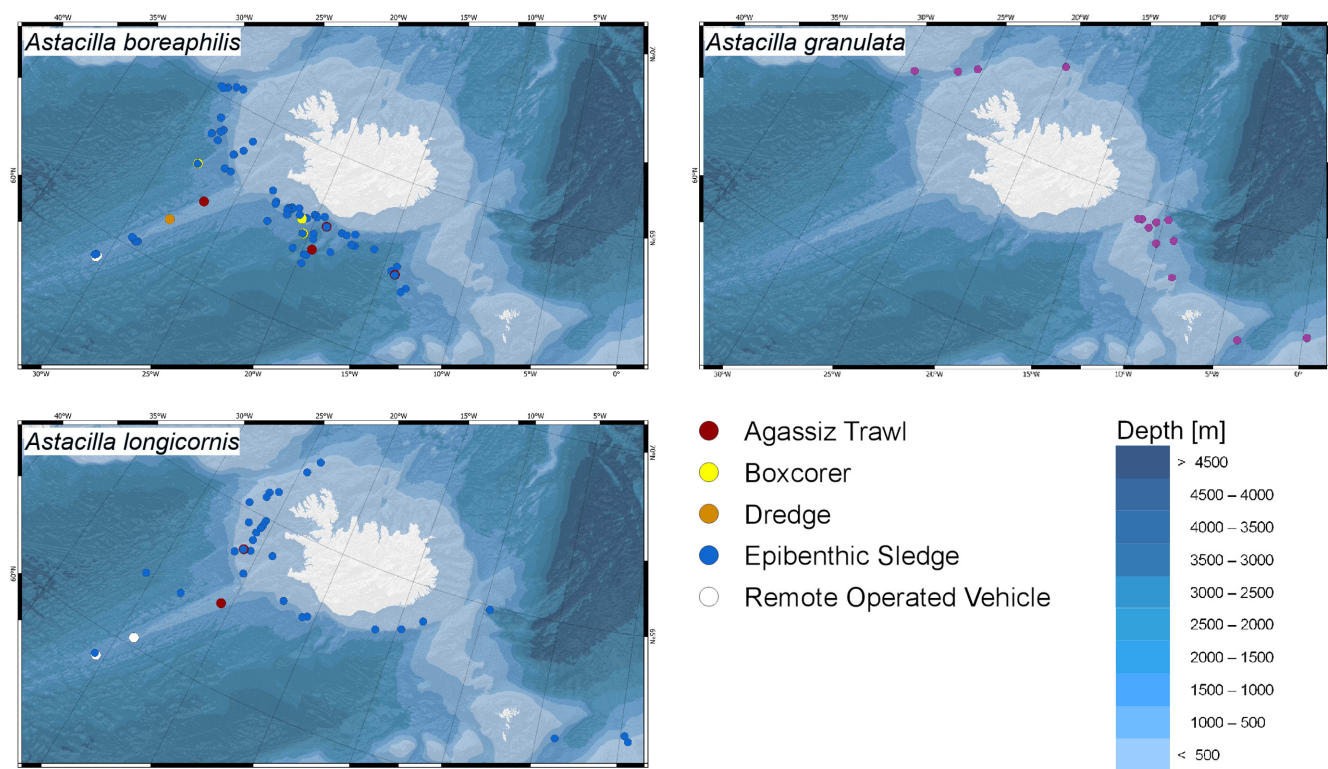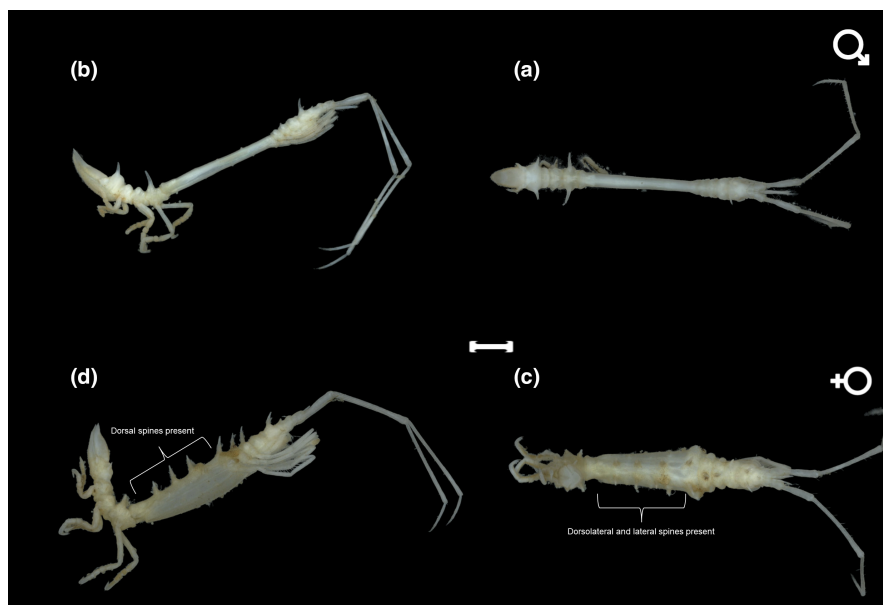
FIGURE 5 Sample locations of Astacilla specimens, colors indicate the sampling gear used.

FIGURE 6 *Astacilla boreaphilis*. Morphotype I, both sexes with the usual spine pattern of this species: Male (DZMB-HH 70272) (a) dorsal, (b) lateral; Female (DZMB-HH 70273) (c) dorsal, (d) lateral. Scale bar: 1 mm.

high numbers on CWCs, but most of the identified species were also highly abundant on the seafloor. Crustacea are reported as the most numerous invertebrate taxa living as symbionts with CWCs (Cairns, 2008; Coleman & Barnard, 1991; Reed & Mikkelsen, 1987; Watling et al., 2011).

Although peracarid crustaceans were the focus of recent studies (Schwentner & Lörz, 2021), little is known about isopods associated with CWCs. Our data present a closer look into CWC-associated isopods, with all specimens identified to family level. A direct association of *Astacilla* specimens with corals had not been observed in

previous EBS sampling in our study area (BIOICE project). The first direct observation was during the IceAGE RR expedition in 2018 with ROV PHOCA on the Reykjanes Ridge and consecutive live observations in the ship's laboratory (Data S5, doi.org/10.5281/ze-nodo.11916170). With these observations, we are able to show how video-based sampling increases our knowledge about this habitat and species interactions.

Even though studies reported single isopod species on CWCs, among them *Munna boecki* Krøyer, 1839, and *Janira maculosa* Leach, 1814 (Frutos et al., 2016; Henry & Roberts, 2007), these species

FIGURE 7 *Astacilla boreaphilis.* Morphotype I, female with complete spination pattern (DZMB-HH 61626). Photo by Katrin Linse and Anne-Helene Tandberg.
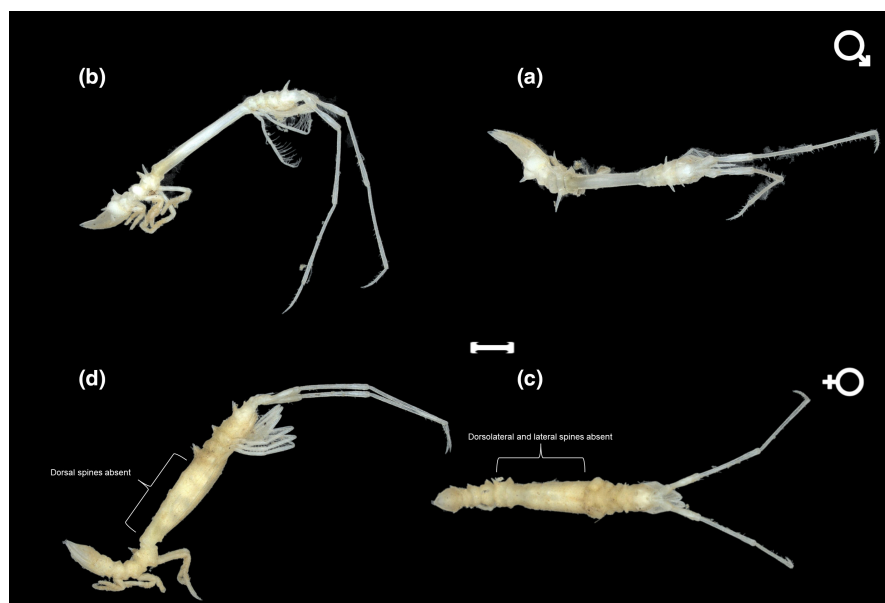
FIGURE 8 *Astacilla boreaphilis.* Morphotype II, both sexes: Male (DZMB-HH 70230) (a) dorsal, (b) lateral; Female (DZMB-HH 70231) (c) dorsal, (d) lateral. Scale bar: 1 mm.

are widely distributed in the area, independently of the presence of CWCs (Brix et al., 2018). In general, Janiridae are found in different depths north and south of the GIF Ridge, with most stations at depths around 400–500 m (Brix et al., 2018). Munnopsidae are very good swimmers and do not depend as much on water masses as other isopod families (Schnurr et al., 2018). A species of the genus *Ilyarachna* has been reported from tropical corals (Cartes et al., 2022), but no record is known for CWCs.

Arcturidae is one of the dominant isopod families in northern polar regions, showing a wide depth distribution from the shelf down to the deep sea (Brix et al., 2018; Poore & Bruce, 2012). They are passive filter-feeding, benthic isopods (Poore, 2001; Wägele, 1987) with a dorsally flexed body, enabling the filtering legs (pereopods) 2–4 to be held above the substrate for feeding while the posterior legs are used for clinging to the substrate (Poore, 2001). Their region of occurrence is known to have very productive surface waters, and high total organic carbon content in the sediments has been observed (Brix et al., 2018). During the expeditions from which we report here, the family was collected at several sites on the GIF Ridge. The ridge sites, influenced by

currents and thus rich in food supply, likely provide their preferential habitat—these may be the same preferences for cold-water corals. Arcturid isopods have been found frequently in BIOICE EBS samples, but the coral association first became visible during the ROV dives during MSM75 in 2018. Due to their lifestyle as filter feeders, this study only concentrates on the Arcturidae.

4.2 | Filter feeders on suspension feeders

On the plexaurid coral *Paramuricea placomus*, Arcturidae was the most prominent isopod family with *Astacilla longicornis* as the only species identified. Examined specimens of this species were often collected either still clinging to the coral or in the same sample. Otherwise, *Astacilla longicornis* was not sampled from any other coral, hinting at an association between this arcturid isopod species and the coral. Interestingly, an adult female of *A. longicornis* was sampled still clinging to its coral host with a manca individual on its second antenna (Figure 11). This observation could hint at extended parental care, which has already been commonly observed in the sister taxon *Arcturus baffini*
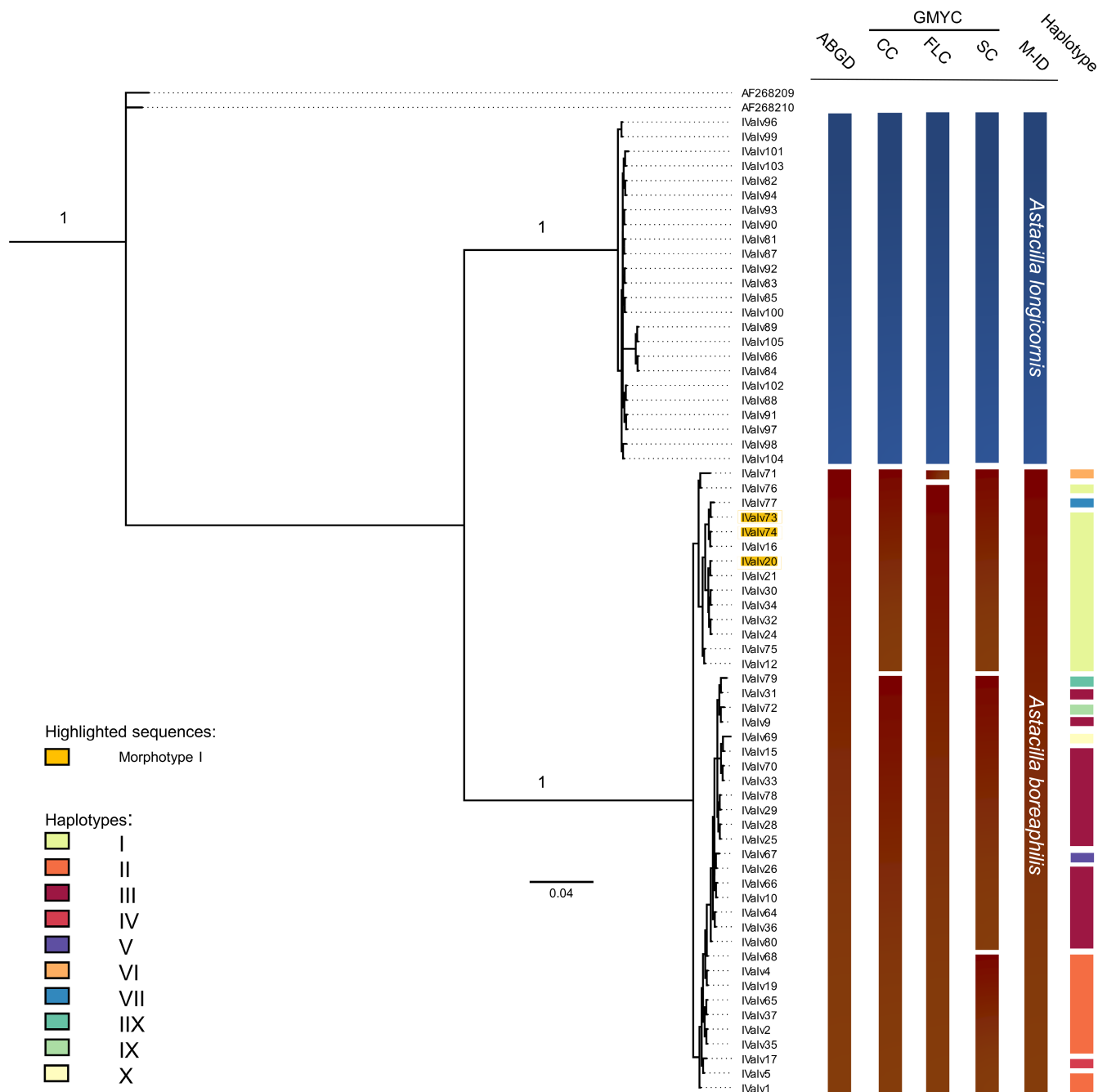
FIGURE 9 Bayesian tree of 16S sequences. Values on top of branches represent posterior probabilities. ABGD, GMYC (CC: Coalescent: Constant size with Strict Clock; FLC, Fixed Local Clock with Yule prior; ST, Strict Clock with Yule prior) and morphological identifications (M-ID) results are shown on the right. Sequence names highlighted in yellow are female specimens showing the typical spination patterns (Morphotype I) of the holotype *A. boreaphilis*.

(Svavarsson & Davídsdóttir, 1995) as well as several other arcturids (Kussakin, 1982; Sars 1895). Apart from the initial description of *A. longicornis* by Goodsir (1841), who observed live individuals climbing up on artificially placed unidentified coral rubble, no other observations about the species' association with corals have been reported. The same applies to the other two arcturid species in this study.

Many species of other valviferan families, such as the Antarcturidae Poore, 2001, Austrarcturellidae Poore & Bardsley, 1992, and Pseudidotheidae Ohlin, 1901 have been

observed to cling to corals, sea pens, hydroids, algae, and sea urchins (Doti et al., 2008; Goodsir, 1841; Sars, 1895; Taboada et al., 2019; Wägele, 1987). Yet, no species, except the arcturid *Astacilla andresmeixidei*, is known to show a specific relationship to its hosts so far, as most observed species would climb on any elevated substrate present in their proximity (Moreira, 1973b; Wägele, 1987). It is assumed that they use elevated substrate for better exposure to currents and, thus, to their food supply (see Figure 5; Data S4; Moreira, 1973a, Moreira, 1973b; Schultz, 1978; Wägele, 1987).
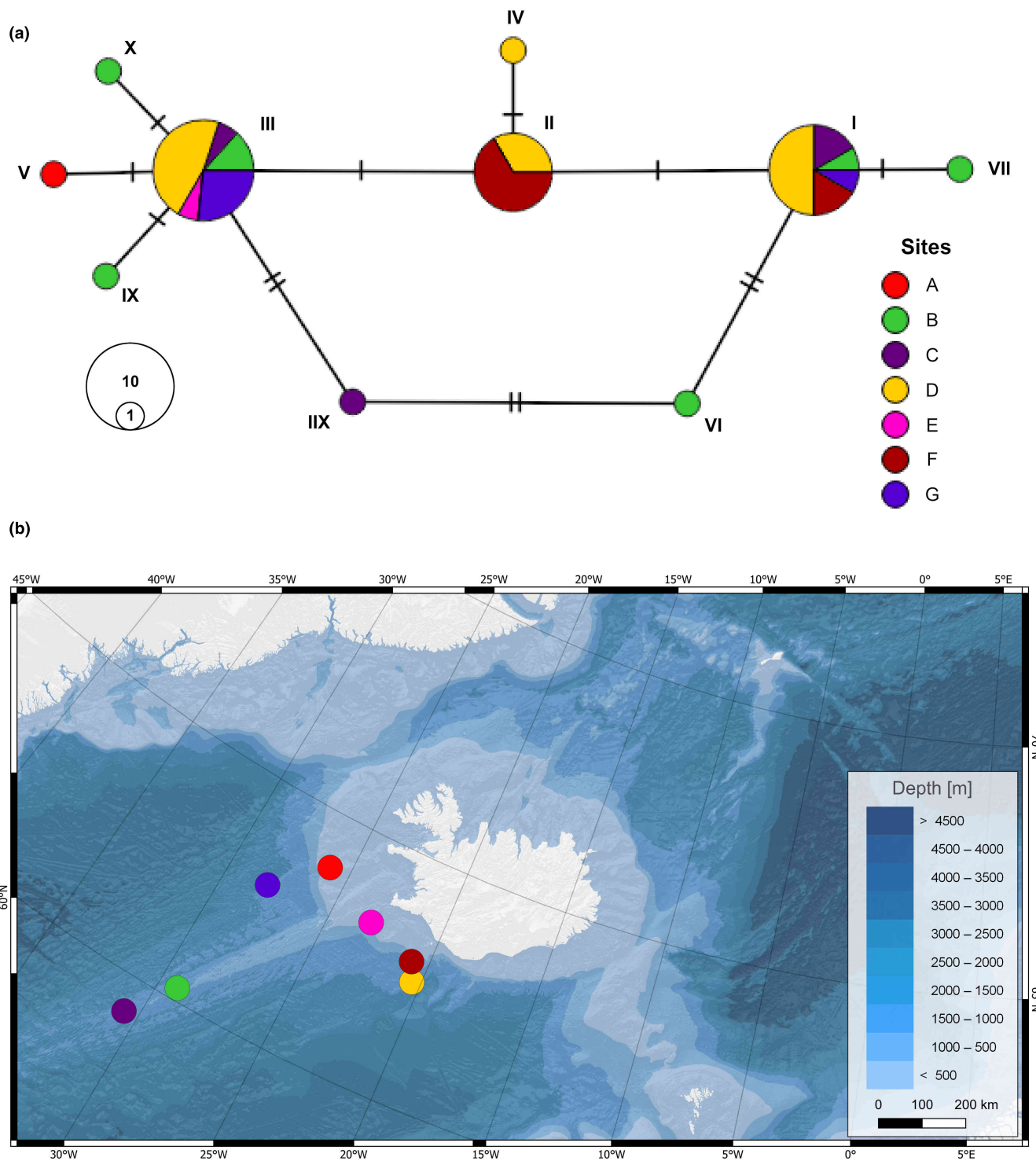
FIGURE 10 (a) Haplotype network for 16S sequences of *A. boreaphilis* circle size represents number of individuals of the specific haplotype, color denotes site origin. Roman letters indicate haplotype number. Hatch marks between haplotypes indicate the number of mutations. (b) Map of the collecting sites of *A. boreaphilis*, colors correspond to the site legend shown in the haplotype network.

As filter-feeders, arcturid isopods (Moreira, 1973b; Poore, 2001; Wägele, 1987) have location preferences that resemble those of their hosts, as both prefer regions with strong and steady currents and a rich food supply provided by highly productive upper water masses (Brix et al., 2018; Hebbeln et al., 2019; Poore, 2001; Roberts et al., 2006; Wägele, 1987).

As evidence increases that suspension or filter-feeding is the primary feeding mode of Antarcturidae, Austrarcturellidae, and Arcturidae, and several species of these three families have been observed to climb on elevated substrate, this raises the question of whether this behavior is common to all species of these sister taxa. Furthermore, it is uncertain whether the relationship between these

FIGURE 11 Brooding female of *Astacilla longicornis* Sowerby, 1806, clinging to *Paramuricea placomus* Linnaeus, 1758, with manca on the second antenna (DZMB-HH 1596). Photographed by Solvin Zankl on board of RV Sonne during the expedition SO276.

taxa and their coral hosts is only facultative as some species have already been reported on various elevated substrata, or if the association of some species with their coral hosts is obligate as of now seems to be the case for *Astacilla andresmeixidei* (Taboada et al., 2019).

4.3 | *Astacilla* Cordiner, 1793 specimens in the samples

4.3.1 | Morphology

Specimens of the genus *Astacilla* identified in this study, belong to three species: *A. boreaphilis*, *A. granulata*, and *A. longicornis*. Unlike *A. granulata and A. longicornis*, *A. boreaphilis* is the only species of the genus found in the North-East Atlantic that has no eyes (Stransky & Svavarsson, 2006), a character shared only with *A. caeca* Benedict, 1898, which occurs in the North-West Atlantic (see Data S6 for distribution data). Moreover, *A. boreaphilis* has a unique spine pattern not found in any other species of the genus. Stransky and Svavarsson (2006) remarked that the spine pattern can vary in adult females as well. In the female preparatory stage, pereonite 4 shows dorsally only two small anterior spines and posterior tubercles, whereas the spines of brooding females are developed, although their size might vary and maybe even more pronounced (Stransky & Svavarsson, 2006). In this study, most examined brooding females had less developed spines, and only a few had similarly pronounced spines as the holotype. This raises the question of whether this can be explained by morphological intraspecific variation, different populations, or a potential species complex.

4.3.2 | Genetics

The genetic results supported the morphological identification of the arcturid specimens in this study. In the Bayesian tree obtained

(Figure 9), *Astacilla longicornis* was represented as one well-supported clade. Both *A. boreaphilis* and *A. longicornis* showed low intraspecific diversity (uncorrected *p*-distance <0.5%) (Data S7).

ABGD and GMYC species delimitation models were congruent with the morphological identifications, recognizing only one lineage of *A. longicornis*. However, in the case of *A. boreaphilis*, only the ABGD species delimitation model and the morphological identifications agreed in recovering the species as a single lineage. In contrast, the GMYC species delimitation model recovered two to three independent lineages. The constant coalescent model recognized two lineages, each corresponding to the subclades of *A. boreaphilis* observed in the topology of the Bayesian tree. The FLC recovered two lineages, the first composed of *A. boreaphilis* specimens except for one single sequence (IValv71), which has been recovered as one independent lineage. The SC model recognized three independent lineages within *A. boreaphilis*. These different lineages recovered by the GMYC model are not supported by our morphological observations. In summary, the observed phenotypic variation within the analyzed *A. boreaphilis* samples was neither supported by the tree topology nor recovered by the species delimitation approaches, indicating no significant genetic divergence between the observed morphotypes. The most common haplotype (Haplotype III) was composed only of individuals with less developed spines (Morphotype II). The second most common haplotype (Haplotype I) was composed of 12 individuals, three of them corresponding to morphotype I (well-developed spination) and nine specimens with less developed spines (Morphotype II). Haplotype I was present at five out of seven sampled sites on both sides of the Reykjanes Ridge (Figure 10), indicating well-connected populations between the sites and contradicting the expected diverging populations due to geographic isolation through the Reykjanes Ridge. The haplotype network suggests gene flow between the sampling sites, as the most common haplotypes occur at most stations. Interestingly, the most common haplotype (Haplotype III) has the widest geographical and bathymetric range.

The observed differences in spination could be related to the varying ages of specimens analyzed and the developmental differences among them. The spine pattern of the holotype was observed only in later developmental stages. A less developed spine pattern has been observed in different developmental stages, including fully developed females with brood pouches. Thus, no correlation between the spine pattern and the maturity of the specimens was observed. Furthermore, the occurrence of the same haplotypes at different locations indicates connectivity along the Icelandic shelf and the Reykjanes ridge. Like all peracarid crustaceans, these isopods are brooders, and their swimming abilities are limited compared to other isopod families like Munnopsidae Lilljeborg, 1864. As filter feeders, they lead a sedentary life (Wägele, 1987). In summary, their dispersal range depends on the locomotion of the adult stage (Brix et al., 2020), and we can only hypothesize that they use the complex hydrographic system and currents around Iceland for their dispersal. If they use the same drift as, for example, coral larvae, this could explain the wide distribution of the *Astacilla* species

found during this study. If all arcturid isopods prefer cold-water corals as elevated habitats, these could potentially serve as "stepping stones."

5 | CONCLUSIONS

Our study revealed differences in cold-water coral-associated isopod assemblages across various cold-water coral genera around Iceland. Certain associated isopod families were more abundant on most corals, while the family Arcturidae almost exclusively occurred on the coral *Paramuricea placomus*. Based on the large number of formalin-fixed specimens sampled during BIOICE, the distribution maps show strong south and north distribution boundaries in Iceland. The samples from IceAGE confirmed the distribution and were supplemented with molecular data. Furthermore, we added new observations of coral association of arcturid species through ROV footage, which were unknown from the previous EBS samples in BIOICE and IceAGE. In reverse, this specific association of *A. longicornis* with P*aramuricea placomus* means that we may match the occurrence of this species with potential coral occurrence. This biogeographic aspect of species association should not be neglected because it allows for a new interpretation of the BIOICE data, highlighting the importance of noninvasive sampling and image data from the deep sea for understanding species distribution patterns. Among all investigated arcturid samples, the species *A. boreaphilis* was the most common. The morphology of most *A. boreaphilis* specimens differed from the original species description in their dorsal spination. Contrary to our hypothesis, genetic analysis of the 16S marker gene did not confirm that the taxon represents a species complex.

CONFLICT OF INTEREST STATEMENT
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available in the supplementary material of this article.

ORCID
Vivien Lukas Hartmann https://orcid.org/0009-0001-2488-0036

REFERENCES
Altschul, S. F., Gish, W., Miller, W., Myers, E. W., & Lipman, D. J. (1990). Basic local alignment search tool. *Journal of Molecular Biology*, *215*, 403–410. https://doi.org/10.1016/S0022-2836(05)80360-2

Baltzer, C., Held, C., & Wägele, J. W. (2000). *Furcarcturus polarsterni* gen. Nov., sp. nov., a large deep-sea arcturid isopod from the Drake Passage, with a preliminary molecular characterization. *Polar Biology*, *23*, 833–839. https://doi.org/10.1007/s003000000160

Bandelt, H. J., Forster, P., & Röhl, A. (1999). Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*, *16*, 37–48. https://doi.org/10.1093/oxfordjournals.molbev.a026036

Brenke, N. (2005). An epibenthic sledge for operations on marine soft bottom and bedrock. *Marine Technology Society Journal*, *39*, 10–21. https://doi.org/10.4031/002533205787444015

Brix, S. (2013). *Cruise Report POS456 IceAGE2 2013*. https://doi.org/10.3289/CR_POS456

Brix, S., Bauernfeind, W., Brenke, N., Błażewicz, M., Borges, V., Buldt, K., Cannon, J., Díaz-Agras, G., Fiege, D., Fiorentino, D., Haraldsdóttir, S., Hoffmann, S., Holst, S., Huettmann, F., Jeskulke, K., Jennings, R., Kocot, K., Khodami, S., Rodriguez, Y., & Yasuhara, M. (2011). *Cruise Report M85/3 IceAGE1 2011 with RV Meteor*. https://doi.org/10.13140/RG.2.2.17251.76322

Brix, S., Stransky, B., Malyutina, M., Pabis, K., Svavarsson, J., & Riehl, T. (2018). Distributional patterns of isopods (crustacea) in Icelandic and adjacent waters. *Marine Biodiversity*, 48, 783–811. https://doi.org/10.1007/s12526-018-0871-z

Brix, S., & Svavarsson, J. (2010). Distribution and diversity of desmosomatid and nannoniscid isopods (crustacea) on the Greenland–Iceland–Faeroe ridge. *Polar Biology*, 33, 515–530. https://doi.org/10.1007/s00300-009-0729-8

Brix, S., Taylor, J., Le Saout, M., Mercado-Salas, N., Kaiser, S., Lörz, A.-N., Gatzemeier, N., Jeskulke, K., Kürzel, K., Neuhaus, J., Paulus, E., Uhlir, C., & Korfhage, S. (2020). Depth transects and connectivity along gradients in the North Atlantic and Nordic Seas in the frame of the IceAGE project (Icelandic marine Animals: Genetics and Ecology).

Broch, H. (1922). Riffkorallen im Nordmeer einst und jetzt. *Naturwissenschaften*, 10, 804–806. https://doi.org/10.1007/BF01565643

Buhl-Mortensen, L., & Buhl-Mortensen, P. (2004a). Crustaceans associated with the deep-water gorgonian corals. *Journal of Natural History*, 38, 1233–1247. https://doi.org/10.1080/0022293031000155205

Buhl-Mortensen, L., & Buhl-Mortensen, P. (2004b). Symbiosis in deep-water corals. *Symbiosis*, 37, 155–168.

Buhl-Mortensen, L., Olafsdottir, S., Buhl-Mortensen, P., Burgos, J., & Ragnarsson, S. (2014). Distribution of nine cold-water coral species (Scleractinia and Gorgonacea) in the cold temperate North Atlantic: Effects of bathymetry and hydrography. *Hydrobiologia*, 759, 39–61. https://doi.org/10.1007/s10750-014-2116-x

Buhl-Mortensen, P., Hovland, T., Fosså, J., & Furevik, D. (2001). Distribution, abundance and size of Lophelia pertusa coral reefs in mid-Norway in relation to seabed characteristics. *Journal of the Marine Biological Association of the UK*, 81, 581–597. https://doi.org/10.1017/S002531540100426X

Burgos, J. M., Buhl-Mortensen, L., Buhl-Mortensen, P., Ólafsdóttir, S. H., Steingrund, P., Ragnarsson, S. Á., & Skagseth, Ø. (2020). Predicting the distribution of indicator taxa of vulnerable marine ecosystems in the Arctic and sub-arctic waters of the Nordic seas. *Frontiers in Marine Science*, 7, 131. https://doi.org/10.3389/fmars.2020.00131

Cairns, S. (2008). A review of the Octocorallia (cnidaria: Anthozoa) from Hawai'i and adjacent seamounts: The genus Narella gray, 18,701. *Pacific Science*, 62, 83–115. https://doi.org/10.2984/1534-6188(2008)62[83:AROTOC]2.0.CO;2

Cartes, J. E., Díaz-Viñolas, D., González-Irusta, J. M., Serrano, A., Mohamed, S., & Lombarte, A. (2022). The macrofauna associated to the bamboo coral Isidella elongata: To what extent the impact on isideidae affects diversification of deep-sea fauna. *Coral Reefs*, 41, 1273–1284. https://doi.org/10.1007/s00338-022-02243-w

Cathalot, C., Oevelen, D., Cox, T., Kutti, T., Lavaleye, M., Duineveld, G., & Meysman, F. (2015). Cold-water coral reefs and adjacent sponge grounds: Hotspots of benthic respiration and organic carbon cycling in the deep sea. *Frontiers in Marine Science*, 2, 37. https://doi.org/10.3389/fmars.2015.00037

Coleman, C., & Barnard, J. (1991). Amatiguakius forsberghi, a new genus and species from Alaska (marine Amphipoda: Epimeriidae). *Proceedings of the Biological Society of Washington*, 104, 279–287.

Danovaro, R., Company, J. B., Corinaldesi, C., D'Onghia, G., Galil, B., Gambi, C., Gooday, A. J., Lampadariou, N., Luna, G. M., Morigi, C., Olu, K., Polymenakou, P., Ramirez-Llodra, E., Sabbatini, A., Sardà, F., Sibuet, M., & Tselepides, A. (2010). Deep-sea biodiversity in the Mediterranean Sea: The known, the unknown, and the unknowable. *PLoS One*, 5, e11832. https://doi.org/10.1371/journal.pone.0011832

Davies, A., Duineveld, G., Lavaleye, M., Bergman, M., Haren, H., & Roberts, J. (2009). Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral Lophelia pertusa (Scleractinia) at the Mingulay reef complex. *Limnology and Oceanography*, 54, 620–629. https://doi.org/10.4319/lo.2009.54.2.0620

Devey, C. W., Brix, S., Barua, A., Bodendorfer, M., Cuno, P., Frutos, I., Huusmann, H., Kurbjuhn, T., Le Saout, M., Linse, K., Matthiessen, T., Palgan, D., Petersen, S., Pieper, M., Rothenbeck, M., Steinführer, A., Tandberg, A. H., Taylor, J., Thorhallsson, D., ... Wenzlaff, E. (2018). Detailed mapping and sampling of the Reykjanes ridge, cruise No. MSM75, 29 June 2018–8 August 2018, Reykjavik—Reykjavik. *Open Polar*, 1–89. https://doi.org/10.48433/cr_msm75

Dolan, M., Grehan, A., Guinan, J., & Brown, C. (2008). Modelling the local distribution of cold-water corals in relation to bathymetric variables: Adding spatial context to deep-sea video data. *Deep Sea Research Part I: Oceanographic Research Papers*, 55, 1564–1579. https://doi.org/10.1016/j.dsr.2008.06.010

Doti, B., Roccatagliata, D., & Scarabino, F. (2008). Range extension of *Pseudidothea Miersii* (Studer, 1884) (isopoda, Valvifera) and new evidence of its likely commensal relationship with a sea urchin. *Crustaceana*, 81, 883–888. https://doi.org/10.1163/156854008784771694

Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, 29(8), 1969–1973. https://doi.org/10.1093/molbev/mss075

Edgar, R. C. (2004). MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32, 1792–1797. https://doi.org/10.1093/nar/gkh340

Eichsteller, A., Taylor, J., Stöhr, S., Brix, S., & Martinez Arbizu, P. (2022). DNA barcoding of cold-water coral-associated ophiuroid Fauna from the North Atlantic. *Diversity*, 14(5), 358. https://doi.org/10.3390/d14050358

Erwin, D. H. (2008). Macroevolution of ecosystem engineering, niche construction and diversity. *Trends in Ecology & Evolution*, 23, 304–310. https://doi.org/10.1016/j.tree.2008.01.013

Frutos, I., Brandt, A., & Sorbe, J. (2016). Deep-Sea Suprabenthic communities: The forgotten biodiversity. In Rossi, S., Bramanti, L., Gori, A., Orejas, C. (Eds.) *Marine Animal Forests* (pp. 475–503). Springer. https://doi.org/10.1007/978-3-319-21012-4_21

Goodsir, H. D., & Royal College of Physicians of Edinburgh. (1841). *On two new species of Leachia*. [Edinburgh].

Hansen, B., & Østerhus, S. (2000). North Atlantic–Nordic seas exchanges. *Progress in Oceanography*, 45, 109–208. https://doi.org/10.1016/S0079-6611(99)00052-X

Hebbeln, D., Costa, R., Wienberg, C., Titschack, J., & Portilho-Ramos, R. (2019). The fate of cold-water corals in a changing world: A geological perspective. *Frontiers in Marine Science*, 6, 119. https://doi.org/10.3389/fmars.2019.00119

Heifetz, J. (2002). Coral in Alaska: Distribution, abundance, and species associations. *Hydrobiologia*, 471, 19–28. https://doi.org/10.1023/A:1016528631593

Henry, L.-A., & Roberts, J. M. (2007). Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal porcupine Seabight, NE Atlantic. *Deep Sea Research Part I: Oceanographic Research Papers*, 54, 654–672. https://doi.org/10.1016/j.dsr.2007.01.005

Jones, C., Lawton, J., & Schachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373–386. https://doi.org/10.2307/3545850

Kennedy, E., Perry, C., Halloran, P., Iglesias-Prieto, R., Schoenberg, C., Wisshak, M., Form, A., Carricart-Ganivet, J. P., Fine, M., Eakin, C. M., & Mumby, P. (2013). Avoiding avoiding coral reef functional collapse requires local and global action. *Current Biology*, 23, 912–918. https://doi.org/10.1016/j.cub.2013.04.020

King, R. (2003). First valid record of Astacilla Cordiner, 1793 in Australia, with description of a new species (crustacea: Isopoda: Arcturidae). *Records of the Australian Museum*, 21, 359–366.

Kingman, J. F. (1982). The coalescent. *Stochastic Processes and their Applications*, 13, 235–248. https://doi.org/10.1016/0304-4149(82)90011-4

Korfhage, S. A., Rossel, S., Brix, S., McFadden, C. S., Ólafsdóttir, S. H., & Martínez Arbizu, P. (2022). Species delimitation of Hexacorallia and Octocorallia around Iceland using nuclear and mitochondrial DNA and proteome fingerprinting. *Frontiers in Marine Science*, 9, 838201. https://doi.org/10.3389/fmars.2022.838201

Kumar, S., Stecher, G., & Tamura, K. (2016). MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33, 1870–1874. https://doi.org/10.1093/molbev/msw054

Kussakin, O. G. (1982). *Marine and brackish-water isopoda of coldand temperate waters of the northern hemisphere. 2. Anthuridea, Microcerberidae, Valvifera, Tyloidea* (p. 461). *Nauka Press*.

Leigh, J., & Bryant, D. (2015). PopART: Full-feature software for haplotype network construction. *Methods in Ecology and Evolution*, 6, 1110–1116. https://doi.org/10.1111/2041-210X.12410

Malmberg, S.-A., & Valdimarsson, H. (2003). Hydrographic conditions in Icelandic waters, 1990–1999. *ICES Journal of Marine Science*, 219, 50–60. https://doi.org/10.17895/ices.pub.19271738

Mohn, C., Rengstorf, A., White, M., Duineveld, G., Mienis, F., Soetaert, K., & Grehan, A. (2014). Linking benthic hydrodynamics and cold-water coral occurrences: A high-resolution model study at three cold-water coral provinces in the NE Atlantic. *Progress in Oceanography*, 122, 92–104. https://doi.org/10.1016/j.pocean.2013.12.003

Monod, T. (1925). Isopodes et Amphipodes de l'Expédition antarctique belge (S. Y. Belgica) [2e note préliminaire]. Retrieved from June 17, 2024. http://archive.org/details/biostor-272468

Moreira, P. S. (1973a). Behavioral aspects of Moreira, 1973 (crustacea, isopoda, Valvifera). *Boletim Do Zoologia e Biologia Marina*, 30, 195–216.

Moreira, P. S. (1973b). Food and feeding behavior of Moreira, 1973 (crustacea, isopoda, Valvifera). *Boletim Do Zoologia e Biologia Marina*, 30, 217–232.

Palumbi, S., Martin, A., Romano, S., McMillan, W. O., Stice, L., & Grabowski, G. (1991). The Simple Fool's Guide to PCR. Department of Zoology and Kewalo Marine Laboratory.

Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., Kamoun, S., Sumlin, W., & Vogler, A. P. (2006). Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology*, 55, 595–609. https://doi.org/10.1080/10635150600852011

Poore, G. (2001). Isopoda Valvifera: Diagnoses and relationships of the families. *Journal of Crustacean Biology*, 21, 205–230. https://doi.org/10.1651/0278-0372(2001)021[0205:IVDARO]2.0.CO;2

Poore, G., & Bardsley, T. M. (1992). Austrarturellidae (crustacea: Isopoda: Valvifera), a new family from Australasia. *Invertebrate Systematics*, 6, 843. https://doi.org/10.1071/IT9920843

Poore, G., & Bruce, N. (2012). Global diversity of marine isopods (except Asellota and crustacean symbionts). *PLoS One*, 7, e43529. https://doi.org/10.1371/journal.pone.0043529

Prime, G. (2022). Geneious Bioinformatics Software for Sequence Data Analysis. https://www.geneious.com

Puillandre, N., Brouillet, S., & Achaz, G. (2021). ASAP: Assemble species by automatic partitioning. *Molecular Ecology Resources*, 21, 609–620. https://doi.org/10.1111/1755-0998.13281

QGIS Development Team. (2023). *QGIS geographic information system*. http://qgis.osgeo.org

Rambaut, A., Drummond, A. J., Xie, D., Baele, G., & Suchard, M. A. (2018). Posterior summarization in Bayesian phylogenetics using tracer 1.7. *Systematic Biology*, 67, 901–904. https://doi.org/10.1093/sysbio/syy032

Ratnasingham, S., & Hebert, P. D. (2007). Bold: The barcode of life data system (http://www.Barcodinglife.Org). *Molecular Ecology Notes*, 7, 355–364. https://doi.org/10.1111/j.1471-8286.2007.01678.x

Reed, J., & Mikkelsen, P. (1987). The molluscan community associated with the Scleractinian coral Oculina Varicosa. *Bulletin of Marine Science*, 40, 99–131.

Riehl, T., Brenke, N., Brix, S., Driskell, A., Kaiser, S., & Brandt, A. (2014). Field and laboratory methods for DNA studies on deep-sea isopod crustaceans. *Polish Polar Research*, 35, 203–224. https://doi.org/10.2478/popore-2014-0018

Riisgård, H. U. (2015). Filter-feeding mechanisms in crustaceans.

Roberts, J., Wheeler, A., Freiwald, A., & Cairns, S. (2009). *Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats*. Cambridge University Press. https://doi.org/10.1017/CBO9780511581588

Roberts, J. M., Wheeler, A. J., & Freiwald, A. (2006). Reefs of the deep: The biology and geology of cold-water coral ecosystems. *Science*, 312, 543–547. https://doi.org/10.1126/science.1119861

Rogers, A. (1999). The biology of Lophelia pertusa (Linnaeus 1758) and other deep-water reef-forming corals and impacts from human activities. *International Review of Hydrobiology*, 84, 315–406. https://doi.org/10.1002/iroh.199900032

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542. https://doi.org/10.1093/sysbio/sys029

Rothlisberg, P., & Pearcy, W. (1977). An epibenthic sampler used to study the ontogeny of vertical migration of Pandalus jordani (Decapoda, Caridea). *Fishery Bulletin*, 74, 994–997.

RStudio Team. (2019). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. http://www.rstudio.com/

Sars, G. O. (1895). *An account of the crustacea of Norway, with short descriptions and figures of all the species* (*Vol. v.1* (*1895*) [*Amphipoda*] [*Text*]). Christiania A. Cammermeyer 1895–1928. https://www.biodiversitylibrary.org/item/16628

Schnurr, S., Osborn, K. J., Malyutina, M., Jennings, R., Brix, S., Driskell, A., Svavarsson, J., & Martinez Arbizu, P. (2018). Hidden diversity in two species complexes of munnopsid isopods (crustacea) at the transition between the northernmost North Atlantic and the Nordic seas. *Marine Biodiversity*, 48, 813–843. https://doi.org/10.1007/s12526-018-0877-6

Schultz, G. A. (1978). More planktonic isopod crustaceans from Subantarctic and Antarctic seas. In *Biology of the Antarctic seas VII* (pp. 69–89). American Geophysical Union (AGU). https://doi.org/10.1029/AR027p0069

Schwentner, M., & Lörz, A.-N. (2021). Population genetics of cold-water coral associated Pleustidae (crustacea, Amphipoda) reveals cryptic diversity and recent expansion off Iceland. *Marine Ecology*, 42, e12625. https://doi.org/10.1111/maec.12625

Stadler, T. (2008). Lineages-through-time plots of neutral models for speciation. *Mathematical Biosciences*, 216(2), 163–171. https://doi.org/10.1016/j.mbs.2008.09.006

Stone, R. (2006). Coral habitat in the Aleutian Islands of Alaska: Depth distribution, fine-scale species associations, and fisheries interactions. *Coral Reefs*, 25, 229–238. https://doi.org/10.1007/s00338-006-0091-z

Stransky, B., & Svavarsson, J. (2006). *Astacilla boreaphilis* Sp. Nov. (crustacea: Isopoda: Valvifera) from shallow and deep North Atlantic waters. *Zootaxa*, 1259, 1–23. https://doi.org/10.5281/zenodo.173137

Sundahl, H., Buhl-Mortensen, P., & Buhl-Mortensen, L. (2020). Distribution and suitable habitat of the cold-water corals *Lophelia pertusa*, *Paragorgia arborea*, and *Primnoa resedaeformis* on the Norwegian continental shelf. *Frontiers in Marine Science*, 7, 213. https://doi.org/10.3389/fmars.2020.00213

Svavarsson, J., & Davídsdóttir, B. (1995). Cibicides spp. (protozoa, foraminifera) as epizoites on the Arctic antenna-brooding *Arcturus baffini* (crustacea, isopoda, Valvifera). *Polar Biology*, 15, 569–574. https://doi.org/10.1007/BF00239648

Taboada, S., Altuna, Á., Sánchez, F., & Junoy, J. (2019). A new species of Astacilla (crustacea: Isopoda: Valvifera) from the Le Danois Bank (N Spain, NE Atlantic), living on Placogorgia sp. (cnidaria: Octocorallia) with notes on the cnidarian host. *Deep Sea Research Part I: Oceanographic Research Papers*, *148*, 108–122. https://doi.org/10.1016/j.dsr.2019.04.016

Tendal, O. (2011). The North Atlantic distribution of the octocoral *Paragorgia arborea* (L., 1758) (cnidaria, Anthozoa). *Sarsia*, *77*, 213–217. https://doi.org/10.1080/00364827.1992.10413506

The GIMP Development Team. (2023). *GIMP*. GIMP. https://www.gimp.org

Wägele, J. W. (1987). The feeding mechanism of *Antarcturus* and a Redescription of *A. spinacoronatus* Schultz, 1978 (crustacea: Isopoda: Valvifera). *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *316*, 429–458.

Watling, L., France, S. C., Pante, E., & Simpson, A. (2011). In M. Lesser (Ed.), *Chapter two—biology of deep-water octocorals*. Academic Press. https://doi.org/10.1016/B978-0-12-385,529-9.00002-0

Wickham, H. (2016). ggplot2. In *Use R!* Springer International Publishing. https://doi.org/10.1007/978-3-319-24277-4

WoRMS—World Register of Marine Species—Astacilla Cordiner, 1793. (2024). *WoRMS—World Register of Marine Species—Astacilla Cordiner, 1793*. https://www.marinespecies.org/aphia.php?p=taxdetails&id=118445

Yule, G. U. (1925). A mathematical theory of evolution, based on the conclusions of Dr. J. C. Willis, F.R.S. *Philosophical transactions of the Royal Society of London Series B, Containing Papers of a Biological Character*, *213*, 21–87.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Hartmann, V. L., Pereira, E., Mercado-Salas, N. F., Lörz, A.-N., Svavarsson, J., & Brix, S. (2024). Filter feeders living on suspension feeders: New insights into the lifestyle and distribution of Arcturidae Dana, 1849 (Crustacea: Isopoda) around Iceland. *Marine Ecology*, *00*, e12826. https://doi.org/10.1111/maec.12826