



The deep-water bamboo coral *Acanella arbuscula* (Johnson, 1862) as a key habitat in soft bottom areas

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Abstract

Acanella arbuscula (Johnson, 1862) is a cosmopolitan deep-water octocoral that can form dense fields in soft bottom areas. Here we investigated its role as habitat for other species through examination of 623 colonies collected from bottom trawling in the Northwest Atlantic between 2003 and 2018, from mean depths of 79–1439 m. In addition, in 2021 we used a remotely operated vehicle at 1317 m to collect three paired sediment push-cores (with and without *A. arbuscula*) to investigate the potential influence of *A. arbuscula*'s on infauna diversity. We show that 43% of the analyzed colonies had one or more associates, and a maximum of 18 individuals per colony. The sea anemone *Stephanauge acanellae* (Verrill, 1883) had the highest occurrence (28.6%), followed by the polychaete (scale worm) *Neopolynoe acanellae* (9.5%), nematodes (8.2%), sponges (4.8%), ophiuroids (4.2%), scalpellid barnacles (2.1%), and scallops (0.8%). Number of associates is likely underestimated due to possible specimen loss during sampling. Number of associates significantly increased with colony height, but not with depth or latitude. Analysis of $\delta^{15}\text{N}$ from *A. arbuscula* and hosts indicate that while the coral likely feeds on particulate organic matter, anemones, polychaetes and ophiuroids feed on higher trophic levels. Anemones, nematodes, and ophiuroids were more frequently found on samples collected in May, while scalpellid barnacles and polychaetes in October. From the limited number of samples available for the study, no significant differences in infauna diversity were found between samples with vs. without corals. Our study shows that *A. arbuscula* in the Northwest Atlantic consistently hosts several invertebrate species, but diversity likely varies in other locations hosting the coral.

Keywords *Acanella arbuscula* · Bamboo coral · Deep-sea coral · Functional role · Habitat · Northwest atlantic

Introduction

Acanella arbuscula (Johnson, 1862) is a widely distributed deep-water bamboo coral (Octocorallia, Family Keratoisidiidae) (Saucier et al. 2017). Different from most other gorgonian corals (i.e. sea fans), this bamboo coral has a root-like anchoring system, which allows it to grow directly on soft substrate (Saucier et al. 2017), although there are records of colonies living attached to hard substrate (Lapointe et al.

2020). The ability to successfully colonize soft substrates has allowed *A. arbuscula* to colonize extensive fields in soft bottom areas (e.g. Baker et al. 2012; Lapointe et al. 2020). While this might represent an advantage in terms of potential for habitat colonization, it has also likely made the species more vulnerable to fishing activities that concentrate in areas with “trawlable”, soft bottoms (van Denderen et al. 2013).

In the Northwest (NW) Atlantic, *A. arbuscula* numerically dominates the group of corals regionally categorized as “small gorgonians”, as colony height usually does not surpass 30 cm (e.g. Baker et al. 2012; this study), and are often caught as fishing bycatch in commercial and scientific fishing (Wareham and Edinger 2007). Colonies can be decades old with growth rates estimated at <2 cm y⁻¹ (Sherwood and Edinger 2009; Piccirillo et al. 2025) and are considered indicators of Vulnerable Marine Ecosystems (VME) (Fuller et al. 2008; Beazley and Kenchington 2012).

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As a VME indicator, better understanding the biology and ecological roles of *A. arbuscula* is important, which includes their role as habitat to other species and their potential role influencing benthic infauna dynamics in soft sediment areas. The presence of other invertebrates found in association with *A. arbuscula* has been reported in the literature, but usually as isolate observations. For example, the sea anemone *Stephanauge acanellae* (Verrill, 1883) has its specific epithet based on its host's genus, but little is known about the nature of this relationship. Endobiotic copepods have also been reported to live in association with this bamboo coral (Grygier 1983), and recently a new species of parasitic nematode was described from *A. arbuscula* specimens (living underneath the stem/branches tissue), believed to be the only described nematode parasitic of an octocoral (Westerman et al. 2021). Although the role of *A. arbuscula* in influencing benthic macrofauna (i.e. infauna) in soft sediment areas has not been studied, research on the cold-water bamboo coral *Keratoisis flexibilis* (Pourtales, 1868) (Pierrejean et al. 2020) and on sea pens (Miatta and Snelgrove 2022) have shown that the presence of these corals can be associated with macrofauna diversity and nutrient recycling. For instance, areas with dense bamboo corals have been shown to have enhanced infaunal density compared to nearby bare sediment areas, and acted as a source of nitrate and ammonium, enhancing nutrient release of the surrounding sediment (Pierrejean et al. 2020).

The objectives of this study were to describe and quantify the diversity of organisms living in association with *A. arbuscula* based on samples collected from Newfoundland to Baffin Bay (NW Atlantic), from depths of 79–1439 m, and to obtain additional insights into the nature of these relationships through $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotopes analysis of coral hosts and their associates. We also examined a small set of macrofauna from sediments around *A. arbuscula* to explore this species' potential role in soft-bottom infauna diversity.

Materials and methods

Specimen sampling

Colonies of *Acanella arbuscula* were collected during multispecies trawl surveys conducted by the Department of Fisheries and Oceans Canada (DFO, NL region) as well as DFO Arctic region surveys, the Fisheries Observer Program (FOP), and the Northern Shrimp Research Foundation (NSRF) between Newfoundland and Baffin Bay, from mean depths of 79–1439 m collected between 2003–2018 (Fig. 1). Trawl sets for the DFO and NSRF surveys took place using a Campelen 1800 shrimp trawl and a modified Campelen 1800 trawl (foot gear increased from 14" to 21" and the

fishing line floated, further extending the opening off bottom, Kenchington et al. 2010) respectively, with a codend mesh liner size of 12.7 mm, towed during 15 min at a vessel speed of 3 knots (Mccallum and Walsh 1996; Kenchington et al. 2010). The FOP samples were obtained from a variety of commercial fishing surveys including trawls, longlines and gillnets, and specific information is not readily available for each set. Depth was calculated using a sensor attached to the trawl and represents mean depths calculated between the beginning and end of each trawl set. Because bottom trawling is expected to dislodge mobile associated fauna, we expect that our account of diversity of associates is conservative and likely underestimated, particularly regarding highly mobile fauna (e.g. crustaceans), which might evade the coral during sampling.

Metrics were obtained for 733 colonies, but fragments, samples without tissue, and samples for which position data was not available were excluded from the quantitative (associates presence, abundance) analyses, leading to a total of 623 retained colonies (i.e. valid colonies). Samples with a mix of tissue and exposed skeleton were retained. We used the top part of the colony (distal to the stem) as a proxy for total colony height, to maximize the number of colonies included in the study, given the missing stems in multiple colonies. Some colonies were obtained from the same trawl set (i.e. same general position and depth). In addition to the valid colonies, where available, exceptional observations of epibionts not observed on those samples or other relevant information were also included for completeness.

Given the large number of samples, colonies were examined for the presence of associates that could be seen with the naked eye. In the case of nematodes (endobionts) we also inspected the underlaying stem and branch tissue where there was indication of tissue thickening (which is an indication of nematode presence, Westerman et al. 2021). Organisms were counted; in the case of ophiuroids, we also measured the distance between ophiuroid disc and the base of the colony (N measured=26, of 30) as well as ophiuroid disc diameter. Ophiuroid position was measured and divided by colony height. A value of zero would represent the base of the colony; therefore position was classified as base, middle-low, middle-high, and top regions for values of 0–0.25, 0.26–0.50, 0.51–0.75, and 0.76–1, respectively. Some associates and *A. arbuscula* fragments were randomly kept for stable isotopes analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, frozen at $-20\text{ }^{\circ}\text{C}$, described below) and other associates were preserved in 95–100% ethanol for DNA barcoding (see details on the next sections) and/or morphological identification. Although measuring specimens was not conducted consistently due to the large number of samples and logistical challenges, a small number of polychaetes ($N=13$) and

Fig. 1 Distribution of *Acanella arbuscula* and ROV sediment push-core samples included in this study. Map produced in Arc Pro 2.9.8 using the World Ocean Reference basemap

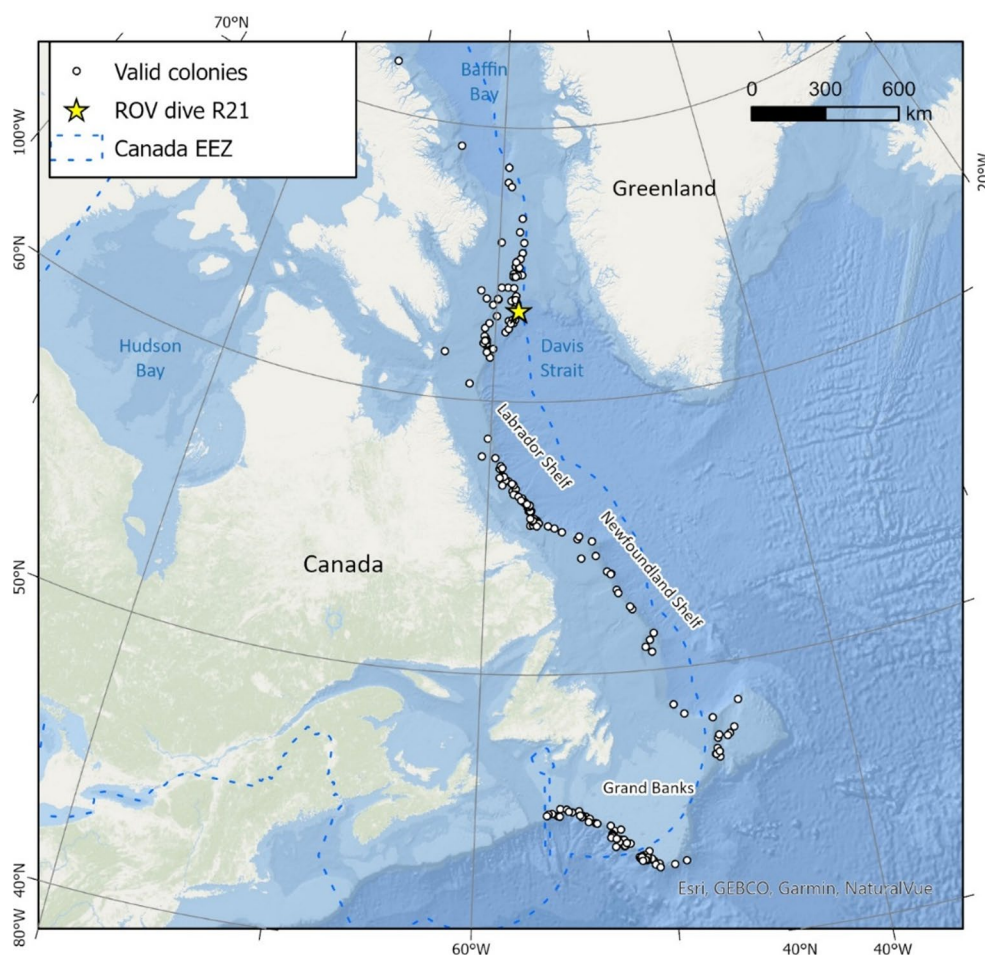


Table 1 Primers used for PCR and sequencing for polychaete DNA barcode identification (from Folmer et al. 1994; Palumbi 1996)

Primer name	Primer Sequence 5'–3'	Reference
<i>16S rDNA</i>		
ArL	CGCCTGTTTATCAAAAACAT	Palumbi (1996)
BrH	CCGGTCTGAACTCAGATCAC GT	Palumbi (1996)
cytochrome oxy- dase I (<i>COI</i>)		
LCO 1490	GGTCAACAAATCATAAAGATA TTGG	Folmer et al. (1994)
HCO 2198	TAAACTTCAGGGTGACCAAA AAATCA	Folmer et al. (1994)

anemones ($N=35$) was also measured (range, average, and SD provided; same used in the stable isotopes analysis).

Molecular analysis

Species identification of polychaete samples was determined using molecular techniques as they were too damaged for morphological identification. Polychaete specimens were stored in 95–100% ethanol before DNA extraction. DNA

was extracted using the DNeasy Blood and Tissue Kit (Qiagen) following manufacturer's protocol for tissue extraction.

Using PCR we amplified segments of *cytochrome oxidase I (COI)* and *16 S rDNA (16 S)*. Previously described primer pairs, LCO1490 and HCO 2198 for COI (Folmer et al. 1994) and *16S* arL/brH primer pair for *16S* (Palumbi 1996) were used (Table 1). The same PCR program was used for both sets of primer pairs as follows: initial denaturation of 95 °C for 5 min followed by 25 cycles of denaturation of 95 °C for 30 s, annealing of 42 °C for 30 s, and extension of 72 °C for 30 s followed by a final extension of 72 °C for 5 min. All markers were amplified in 25 µl reactions using 12.5 µl of DreamTaq Green PCR 2x Master Mix (ThermoFisher Scientific), 0.5 µl of each 10 µM forward and reverse primers, and 1 µl sample. PCR products were visualized using gel electrophoresis to ensure correct product size. Successful PCR products were cleaned to remove primers and PCR reagents using Agencourt AMPure XP beads (Beckman Coulter) and sequenced using Sanger sequencing at The Center for Applied Genomics (Sick Kids Hospital, Toronto, Ontario).

Sequences obtained were compared to *Neopolynoe* sequences available in GenBank database (<https://www.ncbi.nlm.nih.gov/genbank/>)

bi.nlm.nih.gov) as of 30 November 2020. Most sequences originating from a single study (Taboada et al. 2020). Percent identity within species was calculated using MEGA X (Kimura 1980). Phylogenetic analyses were completed with reference sequences with the family Polynoidae (Online Resource 1) with *Laetmonice flicornis* Kinberg, 1856 and *Aphrodita aculeata* Linnaeus, 1758 (family Aphroditidae), as outgroups. Sequences were aligned using Clustal W (Larkin et al. 2007) and *COI* and *16S* were concatenated to allow for longer sequence length and improved ability to resolve phylogeny. Phylogenetic inference was performed in IQTree (Nguyen et al. 2015). Trees were built using the maximum likelihood method (Felsenstein 1981) and the best model for distance estimation using ModelFinder (Kalyaanamoorthy et al. 2017) and applied using a partition model to allow for different models for each gene segment (Chernomor et al. 2016). Robustness of clades was tested using ultrafast bootstrap test (Hoang et al. 2018) with 1000 replicates. Sequences from this study have been submitted to GenBank with accession numbers OL792616–OL792628 (Online Resource 2).

Most nematodes included in this study were also part of the study published by Westerman et al. (2021), and their description as well as GenBank accession numbers for 36 individuals are provided therein.

Stable isotope analyses

A total of 21 *Acanella arbuscula* samples were prepared for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analysis. A different number of samples was available to examine the $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ relationship, versus only $\delta^{15}\text{N}$ for the associates. Samples of sea anemones ($N=35$ for $\delta^{15}\text{N}$, $N=29$ for both), polychaetes ($N=15$ for $\delta^{15}\text{N}$, $N=11$ for both), and ophiuroids ($N=7$) were also prepared for the analysis. Other associates were not included due to their small sizes and biomass. There were no sediment or seawater samples available. Samples were freeze-dried and crushed using an agate mortar and pestle. Approximately 1 mg of dry sample was weighed in tin capsules for analyses. Crushed samples of *A. arbuscula* (polyps) and ophiuroids (entire animal) intended for $\delta^{13}\text{C}$ analysis were acidified using 10% HCl to eliminate carbonates (Sherwood et al. 2008). In all cases, samples for $\delta^{15}\text{N}$ were not acidified, and were analyzed separately. In the case of samples with CaCO_3 , percent carbon and nitrogen were determined from the acidified samples. Samples were analyzed at the Stable Isotopes Laboratory at Memorial University (St. John's, Canada). We have opted for not lipid-correcting our $\delta^{13}\text{C}$ data using available equations because the recommended equations (e.g. Logan et al. 2008) have focused on marine invertebrates such as krill, with very different C/N ratios than our samples.

Sediment sampling

Sediment push-cores were collected using the remotely operated vehicle (ROV) ASTRID aboard the Canadian Coast Guard Ship (CCGS) *Amundsen* on July 29th 2021. We collected three pairs of push-cores, three on top of *A. arbuscula* colonies ("coral", Online Resource 3) and three near ("no coral") the corresponding colonies (~ 0.5 – 2.4 m apart), from an average depth of 1317 ± 0.47 m. The most distant core pairs were ~ 10 m apart. Push-cores were 6.6 cm in internal diameter and ~ 35 cm tall (Neves et al. 2023) (although only the first 10 cm of sediment was sub-sampled). Unfortunately, additional push-cores could not be collected during the expedition due to logistical limitations associated with deep-water ROV surveys.

Once aboard, cores were photographed and coral colonies were removed and utilized in another study (Piccirillo et al. 2025). Seawater was gently siphoned out of the cores and sediment samples were extruded and sectioned in three depth layers (0–2, 2–5, 5–10 cm), preserved in 10% buffered formalin for 48–72 h, then transferred to 70% ethanol. Sediment samples and siphoned seawater were sieved through a 500- μm mesh sieve, then the retained material was sorted, counted (biomass also determined) and identified to the lowest possible taxonomic level by a trained taxonomist. We recognize that the top layer of the cores may also contain epifauna, but we refer to the ensemble as infauna for simplicity. In some cases organism presence was noted, but not quantified (e.g. polychaete parts). Although we have attempted to identify nematodes based on the known parasitic nematode living in *A. arbuscula* (Westerman et al. 2021), they were mostly immature and could not be identified (pers. comm. Oleksandr Holovachov).

We analyzed infauna data as organisms cm^{-3} to account for the different thickness of sediment layers (Kornijów and Pawlikowski 2016). Individual volumes per layer were 68.4 cm^3 , 102.6 cm^3 , and 171.1 cm^3 (from 0–2, 2–5, 5–10 cm, respectively) and a combined total volume of 342.12 cm^3 and total surface area of 275.8 cm^2 . Information is also provided in cm^{-2} as a standard density metric.

Data analysis

Number of associates (abundance) vs. colony height, depth, latitude, and month

Data analysis was conducted using RStudio version 2025.05.1 (RStudio Team 2021). In order to assess whether number of associates (abundance) varied with colony height, depth, latitude, and month (see below), we ran a generalized linear mixed model (GLMM) to consider the count nature of the untransformed data and to include trawl set as a random

factor (given that multiple colonies came from the same set). We used the `glmmTMB` function of the `glmmTMB` package (Brooks et al. 2017) and a negative binomial distribution to account for overdispersion of residuals. We used the `simulateResiduals` function of the `DHARMA` package to test assumptions of normality and heterogeneity of residuals, overdispersion and zero-inflation (Hartig 2022).

To assess the potential influence of season, we examined the frequency of associates' occurrence by month for May and October only, which were the months with the highest number of samples in contrasting seasons ($N=178$ and $N=323$, respectively, for a total of 501 colonies). To compensate for the unbalanced number of samples for each month, we present the frequency data relative to the total number of sets per month.

Infauna analysis

Data analysis for infauna assessments was conducted using PRIMER 7. Total abundances per push-core were converted to density (abundance cm^{-2}), but metrics per layer of sediment (i.e. 0–2, 2–5, 5–10 cm) were converted to volume (Kornijów and Pawlikowski 2016). We excluded records where only organism parts were reported (e.g. ophiuroid arms, spicule clumps, polychaete parts) and proceeded with analysis at the lowest possible taxonomic level. In some cases organisms were pooled into higher taxonomic levels when there was uncertainty whether two taxa represented the same species (e.g. species level vs. genus level). However, we acknowledge that by doing so we might have also underestimated diversity in our samples. Sample R21-1 (5–10 cm) only contained polychaete parts and was excluded from the analyses.

The data were square-root transformed and a PERMANOVA was first applied on pooled core data (whole core) with type (coral vs. no coral) as a fixed factor. We used a Bray-Curtis similarity, type III sum of squares, and an unrestricted permutation of raw data, with 9999 permutations (Anderson et al. 2008). A second PERMANOVA was run to assess the influence of sediment depth layer (0–2, 2–5, 5–10 cm) on infauna patterns, listing core ID as a random factor to consider the dependence structure of layers within each core. However, a very small number of unique permutation values was obtained, so we used a random sampling from the asymptotic permutation distribution to obtain Monte Carlo p-values (Anderson et al. 2008). Simpson's index (d) was calculated, as it can be considered safer for small sample sizes (e.g. Clinton et al. 2024). Species accumulation curves were generated based on the S_{obs} estimator, using a 999 permutation for density per sediment layer and density per core.

Results

Polychaete DNA barcoding

Based on the results of our molecular analysis, the polychaete specimens found in association with *Acanella arbuscula* are genetically the Polynoidae scale worm *Neopolynoe acanellae* (Verrill, 1882). They showed a 98–100% identity to records on GenBank for the *COI* region over 491 bp, and 99.1–100% for the *16S* region over 426 bp (Online Resource 2). Phylogenetic analyses have all sequences from this study falling in monophyletic groups with previous sequences for *N. acanellae* (Online Resource 4).

General patterns

Out of the 623 valid colonies, 269 contained one or more associates (43%), for a maximum number of taxa and abundance of five and 18 per colony, respectively (Table 1). Colony size for valid colonies ranged between 6.6 and 30 cm. Number of associates significantly increased with colony height, but not with depth, latitude, or month (Fig. 3a; Table 3). A total of 10 taxa were found associated with *A. arbuscula* (Table 2), four of them more consistently found: the grasping sea anemone *Stephanauge acanellae*, the ophiuroid *Astrochele lymani* Verrill 1878, the polychaete *Neopolynoe acanellae*, and the nematode *Paraborjania corallicola* (Westerman et al., 2021) (Fig. 3b Table 2). The bathymetric distribution of *A. arbuscula* colonies with or without associates was not different (Fig. 4).

A total of 427 grasping sea anemones (*S. acanellae*) were found on 178 of the valid colonies, with an occurrence rate of 28.6%. Sea anemones were found on colonies collected between 98 and 1354 m (Fig. 4), from the SW Grand Banks to Davis Strait (Fig. 5). The sea anemone completely surrounds a portion of the coral branches, although the edges of the base do not fuse (Fig. 2). Most colonies with sea anemones contained a single individual (48%), although in one case a single colony 25 cm tall was found to host 15 sea anemones (Fig. 3; Table 4). A total of four tissue-less colonies (non-valid colonies) had sea anemones ($N=1-7$) growing on their skeletons. Sea anemone length for the measured specimens averaged 11.7 ± 3.1 mm (5.4–17.6 mm, $N=35$).

A total of 59 polychaetes were found on the valid colonies (9.5%). A single individual per colony was observed among all of the analyzed specimens (Tables 2 and 4; Fig. 2). Polychaetes were found on colonies collected between 252 and 1387 m (Fig. 4), from the SW Grand Banks to Davis Strait (Table 4; Fig. 5). Polychaete length for the measured specimens averaged 20.2 ± 6.1 mm (12–30.3 mm, $N=13$).

The nematode *P. corallicola* was found on 51 of the valid colonies (8.2%), for a total abundance of 110 individuals

Table 2 Invertebrates associated with *Acanella arbuscula* in the Northwest Atlantic. N col=number of colonies. Occ (%)=occurrence %. Mean abundance does not include colonies with zero specific associates

Associate	Species	N col	Total abundance	N per colony	Mean abundance±SE	Occ (%)	Depth (m)
Sea anemone	<i>Stephanauge acanellae</i>	178	427	1–15	2.4±0.16	28.6	98–1354
Polychaete	<i>Neopolynoe acanellae</i>	59	59	1	1±0	9.5	252–1387
Nematode	<i>Paraborjnia corallicola</i>	51	110	1–12	2.16±0.25	8.2	79–1354
Ophiuroid	<i>Astrochele lymani</i>	22	30	1–2	1.15±0.07	4.2	404–1027
	<i>Gorgonocephalus</i> sp.	3					
	<i>Ophiuroid</i> sp.	1					
Sponge	<i>Iophon</i> sp.	30	NA	Presence only	Presence only	4.8	573–1233
Scalpellid barnacle	NA	13	45	1–9	3.46±0.77	2.1	573–768 ¹
Scallop	<i>Delectopecten vitreus</i>	5	5	1 ²	1±0	0.8	224–768
Platyhelminth	? <i>Kronborgia</i> sp.	2	NA	Presence only	Presence only	0.8	573
Additional fauna observed outside of main dataset							
Feather star ³	Unidentified	2 ³	Presence only ⁴	Presence only ⁴	Presence only ⁴	NA ⁵	1286–1299
Pycnogonid	Unidentified	2	Presence only ⁴	Presence only ⁴	Presence only ⁴	NA ⁵	188–657

¹A specimen outside of the main dataset was collected from 382 m; ²We have observed >1 scallop per colony when examining old images of *Acanella arbuscula*, which were not included in this study (e.g. Figure 2); ³Includes one trawl and one in situ observation; ⁴Individuals not counted; ⁵Not included in calculations

Table 3 Summary statistics for generalized linear mixed model on the effects of colony height, depth, latitude, and month (May and October only) on number of associates (abundance) per *Acanella arbuscula* colony. N=501 colonies

Effect	Estimate	SE	z-value	p-value
(Intercept)	−1.64	1.015	−1.616	0.106
Colony height	0.016	0.002	8.605	<2e-16
Mean depth	0	0	−0.008	0.993
Latitude	−0.012	0.022	−0.538	0.591
Month	0.051	0.339	0.151	0.88
Random effects (Trawl set)				
(Intercept)	Variance	SD		
	0.6493	0.8058		
Model fit statistics				
Statistic	Value			
AIC	1274.5			
BIC	1304			
Log-likelihood	−630.3			

Values in bold represent significant p-values

(Table 2). Nematodes were found underneath the tissue of *A. arbuscula* colonies (Fig. 2), usually but not always restricted to the stem or trunk of the colonies. Most colonies had one or between 2 and 5 nematodes per colony, with a maximum of 12 nematodes found on a single colony (Table 4; Fig. 3b). Nematodes were found on colonies collected between 79 and 1354 m (Fig. 4), from the SW Grand Banks to Davis Strait (Table 2; Fig. 5).

Ophiuroids were found in 26 of the valid colonies (4.2%), generally solitary (N=22 colonies) but occasionally as a pair (N=4 colonies) (Tables 2 and 4), for a total of 30 ophiuroids encountered. They were found on colonies collected from mean depths ranging 404–1027 m (Fig. 4), and were restricted to the SW Grand Banks and East Newfoundland

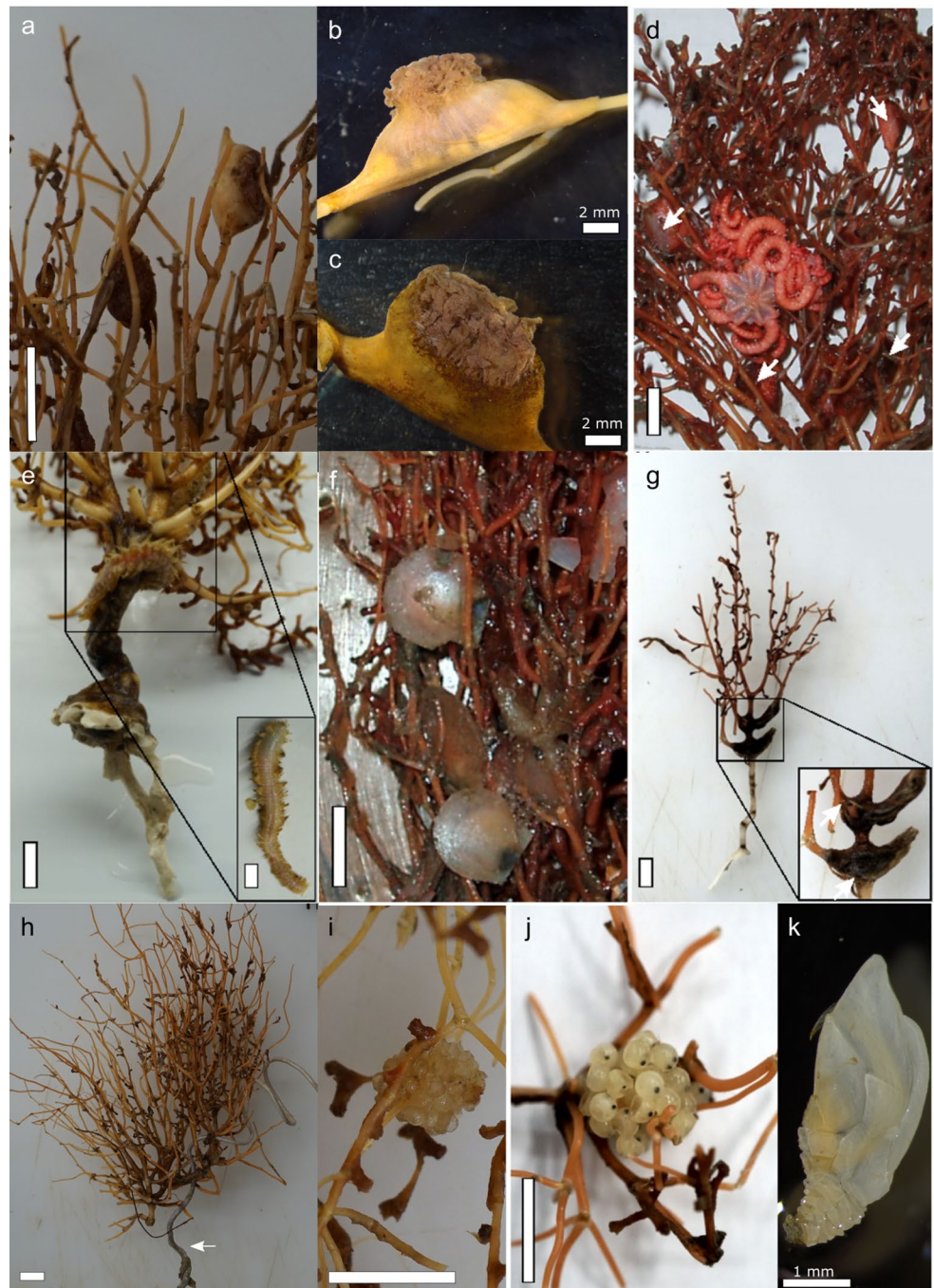
(Fig. 5; Table 2). Three ophiuroid species were recorded: *Astrochele lymani* (22 colonies, 84.6% of ophiuroid occurrences), *Gorgonocephalus* sp. (3 colonies, 11.5%), and one unidentified ophiuroid (1 colony, 3.8%). The East Newfoundland sample was a *Gorgonocephalus* sp. Ophiuroid disc diameters on valid colonies ranged between 2.7 and 17.1 mm (N=23). Of the 26 ophiuroids for which position on the colony was determined, most were located between the middle-high (N=14) and middle-low (N=7), followed by top (N=3), and base (N=2) regions. Ophiuroids have also been observed in situ on branches of *A. arbuscula* (Online Resource 3).

Sponges (*Iophon* sp.) were found on 30 colonies (4.8%, Online Resource 5) and seen on *A. arbuscula* observed in situ through ROPOS ROV imagery (Online Resource 3), although species identification cannot be confirmed from the image alone. They were found on colonies collected between 573 and 1233 m, from the SW Grand Banks to Davis Strait (Table 2). In addition, they were found on two colonies having no tissue, from the same general region and depth.

Scalpellid barnacles were found on 13 of the retained colonies (2.1%) collected between 573 and 768 m (Fig. 4; Table 2), restricted to the SW Grand Banks area (Online Resource 5). A total of 1–9 individuals per colony were noted. Scalpellid barnacles were also noted on three colonies having no tissue (N=4–6), one of which from a shallower depth than the colonies retained for analyses (382 m), but also in the SW Grand Banks.

An organism morphologically similar to cocoons of the platyhelminth *Kronborgia* sp. was found entangled on two *A. arbuscula* colonies (Fig. 2) collected from the same set in October from 573 m, SW Grand Banks (Table 2, Online Resource 5). Scallops were observed on five of the retained

Fig. 2 Photo-plate of *Acanella arbuscula* colonies with some of its common associates. **a–c)** the sea anemone *Stephanauge acanellae*; **d)** the ophiuroid *Astrocheile lymani* and sea anemones (white arrows); **e)** polychaete *Neopolynoe acanellae*; **f)** scallops; **g)** tissue mass with nematodes; **h)** Platyhelminth, possibly *Kronborgia* sp. (arrow); **i, j)** egg mass on bare *A. arbuscula* skeletons; **k)** scalpellid barnacle. Scale bars represent 1 cm, except where indicated



colonies (0.8%, Fig. 2), collected between 224 and 768 m, in the SW Grand Banks area (Table 2, Online Resource 5). Two of the specimens were identified as *Delectopecten vitreus* (Gmelin, 1791), but the other specimens were not examined. An unidentified unstalked feather star (Crinoidea) was observed in situ on a colony of *A. arbuscula* collected during the ROV push-core dive (Online Resource 3, Online Resource 5) in Davis Strait and on a trawl sample outside of the main dataset on the Labrador Shelf (Table 2). Two colonies with pycnogonids were also observed outside

of the main dataset, on the Labrador Shelf (Table 2). Egg masses from an unidentified organism were observed on two of the retained *A. arbuscula*, and on one tissue-less fragment (Fig. 2).

The relative number of colonies with associates was comparable between samples collected in May and October (Fig. 6). In most cases, the relative number of colonies with associates was slightly higher in May ($N=178$ colonies, anemones, nematodes, ophiuroids, and sponges), but colonies with polychaetes and scalpellid barnacles were more

Fig. 3 Invertebrates associated with *Acanella arbuscula* in the Northwest Atlantic: **(a)** associates' abundance in relation to colony height overlaid with GLMM fitted line and 95% confidence interval (shaded area); **(b)** frequency of occurrence of most frequent associates by abundance class (i.e. number of individuals per colony)

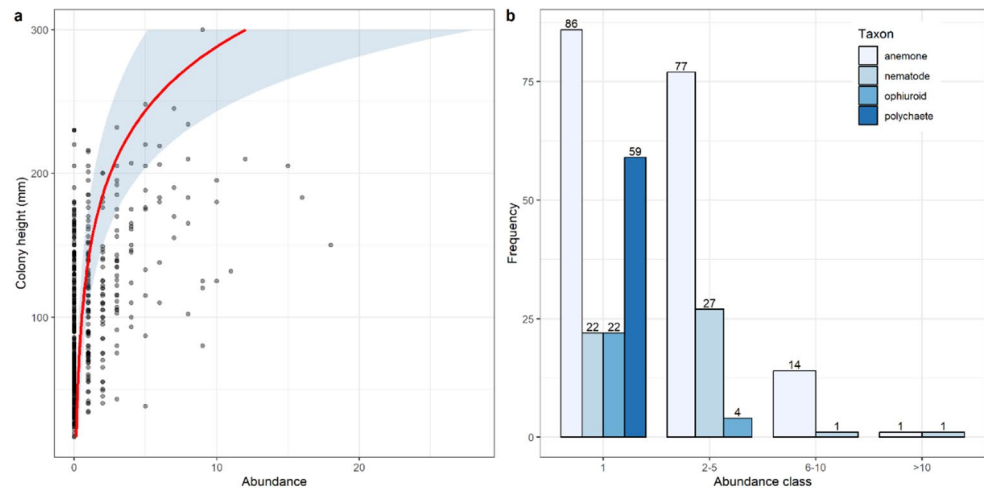


Table 4 Frequency of occurrence of invertebrates most frequently associated with *Acanella arbuscula* in the Northwest Atlantic by abundance class (i.e. Number of individuals per colony) and occurrence rate (%). Total=269 colonies, including taxa not listed on the table (total in table=314 because many colonies have >1 taxa)

Taxa	1	2–5	6–10	> 10	Total (col)	%
Sea anemones	86	77	14	1	178	28.6
Polychaetes	59	0	0	0	59	9.5
Nematodes	22	27	1	1	51	8.2
Ophiuroids	22	4	0	0	26	4.2

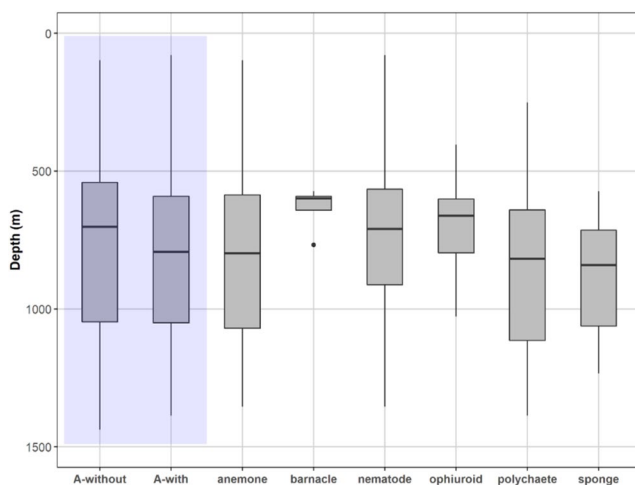


Fig. 4 Bathymetric distribution of *Acanella arbuscula* colonies with (A-with) and without (A-without) associates (shaded area), and most associates based on samples included in this study. The data presented in this plot did not consider duplicates in a same set (i.e. if an associate was present in a specific trawl set, its presence at that depth was counted only once even if found on more than one colony in that set). Total number of trawl sets=179, total number of *A. arbuscula* colonies=623, total number of *A. arbuscula* with associates=269 (including taxa not shown on figure). Other associates not included due to small N

common in October ($N=323$ colonies) (Fig. 6). The largest difference between the two months was seen for polychaetes, ophiuroids, and sponges (Fig. 6).

Stable isotope analyses

The results from the stable isotope analyses showed similar $\delta^{13}\text{C}$ levels for *A. arbuscula* and its associates (-22.5 to -18.45‰), with sea anemones showing the highest values (Fig. 7a). $\delta^{15}\text{N}$ levels were higher in the associates (10.6 – 13.8‰) than in *A. arbuscula* colonies (9.3 – 11.3‰) (Fig. 7). Polychaetes and sea anemones shared similar $\delta^{15}\text{N}$ values, with ophiuroids only slightly reduced (Fig. 7b). We excluded the ophiuroids from the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ plot because $\delta^{13}\text{C}$ values were too enriched in relation to the sea anemones, polychaetes and *A. arbuscula*. We attribute this to challenges involving the removal of CaCO_3 from those samples. Unfortunately, not enough material was available to allow a second acidification step.

Sediment samples

Infauna density ranged between 10 and 33 individuals per push-core (0.08 – 0.28 individuals cm^{-2} , 0.11 – 0.43 individuals cm^{-3}). Overall, infauna density across sediment depth layers was significantly different (Fig. 8; Table 5), although there were no differences between 0–2 vs. 5–10 cm or 2–5 vs. 5–10 cm. Densities were higher in the first layer of

Fig. 5 Spatial distribution of *Acanella arbuscula* samples included in this study and its most common associates: ophiuroids ($N=26$ colonies), anemones ($N=178$ colonies), polychaetes ($N=59$ colonies), and nematodes ($N=51$ colonies). Symbol sizes indicate abundance range per colony. Empty circles (valid *Acanella* colonies) represent stations where *A. arbuscula* was present but the specific associate was not. Total number of trawl sets=179, total number of *A. arbuscula* colonies=623, total number of *A. arbuscula* with associates=269 (including taxa not shown on map). See Fig. 1 for general locations mentioned in the text

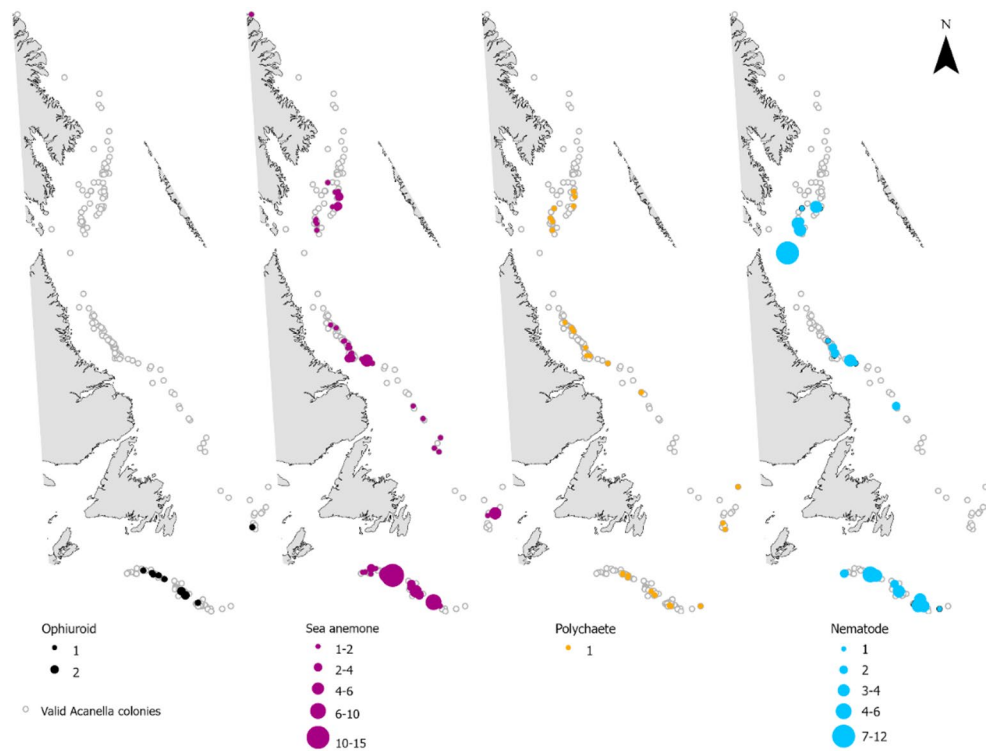
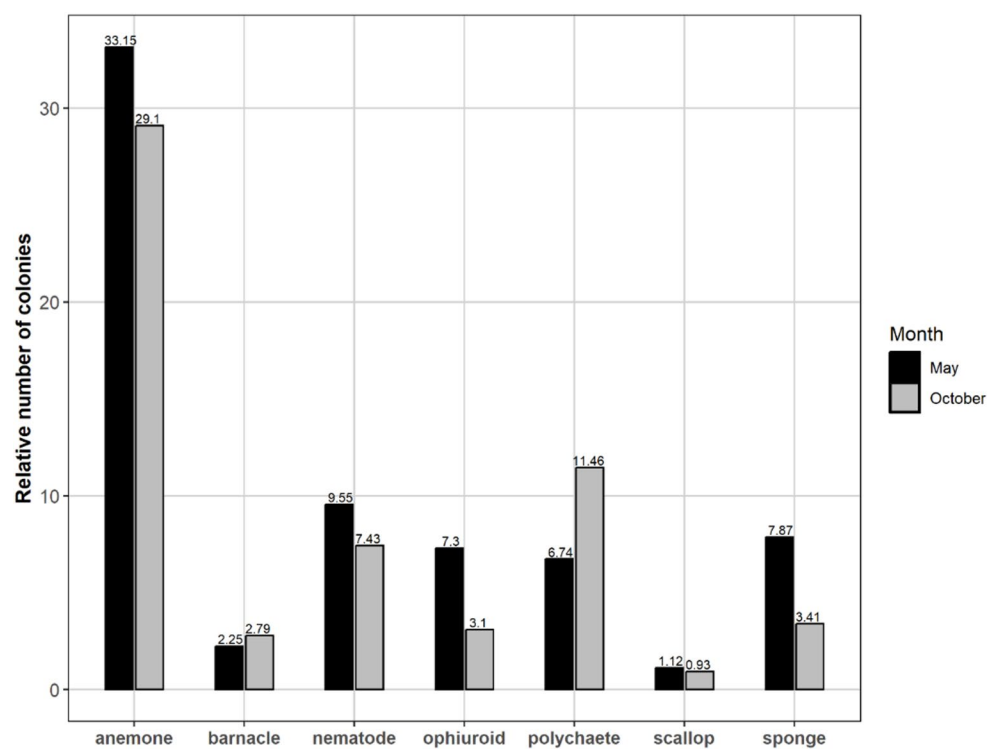


Fig. 6 Frequency of *Acanella arbuscula* colonies with specific associates relative to the total number of colonies per month, for May and October (spring and fall in the Northwest Atlantic, respectively)



sediment (0–2 cm) for both coral and no coral push-cores, followed by 2–5 and 5–10 cm (Fig. 8; Table 5).

Infau density was not significantly different between coral and no coral associated sediment samples (Fig. 9a; Table 5). It was higher at the no coral samples for the 0–2 and 5–10 cm layers, but twice as high at the coral samples

for the 2–5 cm layer (Fig. 8). Annelida (polychaetes) were the most dense taxa in the 0–2 cm layer closely followed by nematodes, which in turn were the most dense taxa for the 2–5 and 5–10 cm layers (Fig. 8b). The most abundant polychaete was *Prionospio* sp. followed by Cirratulidae sp. No nematodes were found on the *A. arbuscula* colonies

Fig. 7 Stable isotopic composition of *Acanella arbuscula* and some of its associates from the Northwest Atlantic: (a) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ relationship for *A. arbuscula*, sea anemones, and polychaetes, and (b) box-plot of $\delta^{15}\text{N}$ composition by taxon, including ophiuroids

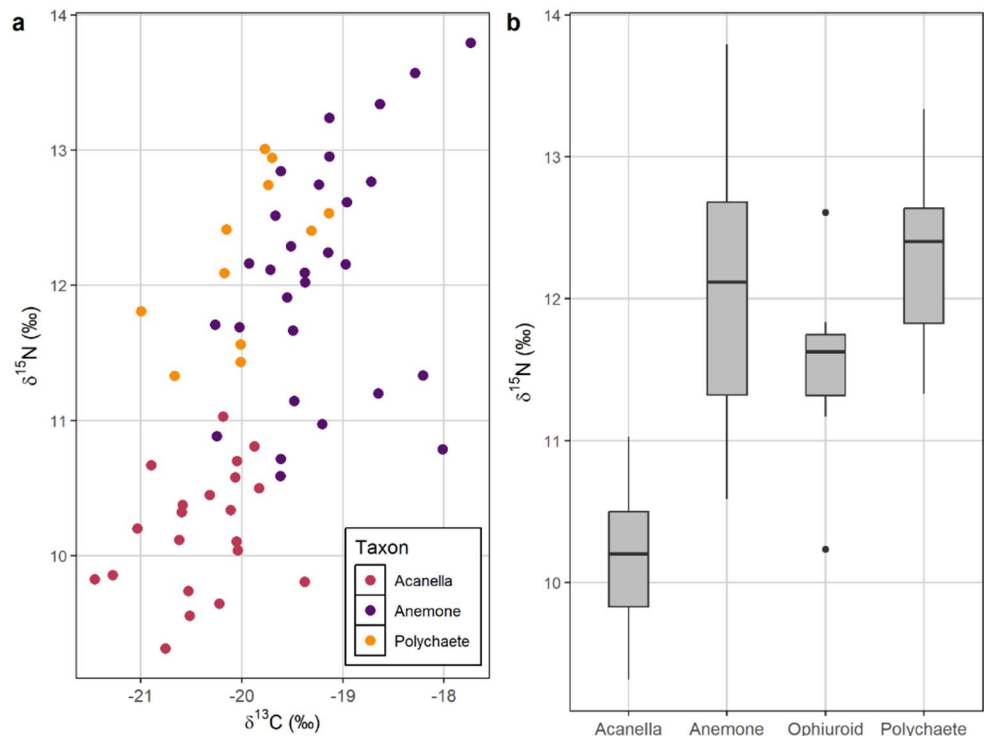
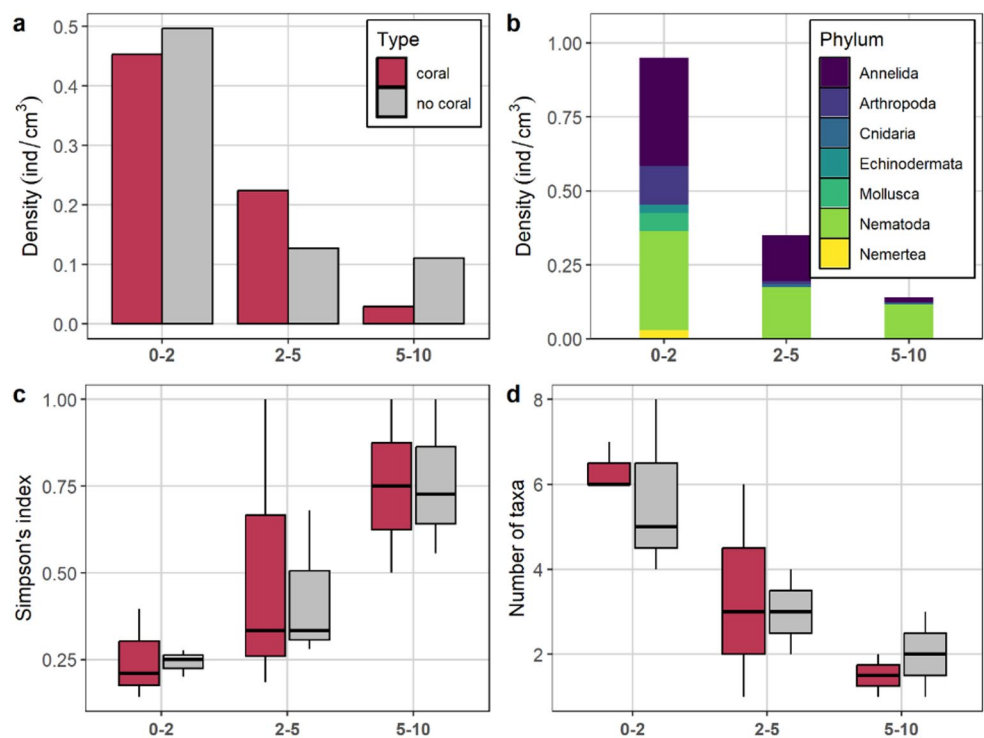


Fig. 8 Infauna from sediment push-core samples in *Acanella arbuscula* habitat by sediment depth layer (0–2, 2–5, 5–10 cm). (a) infauna density (individuals cm^{-3}) by type of sample: sediment collected on top of *A. arbuscula* (coral) or near *A. arbuscula* (no coral), (b) infauna density by phylum. (c–d) Simpson's index and number of taxa, displayed by type of sample (coral vs. no coral)



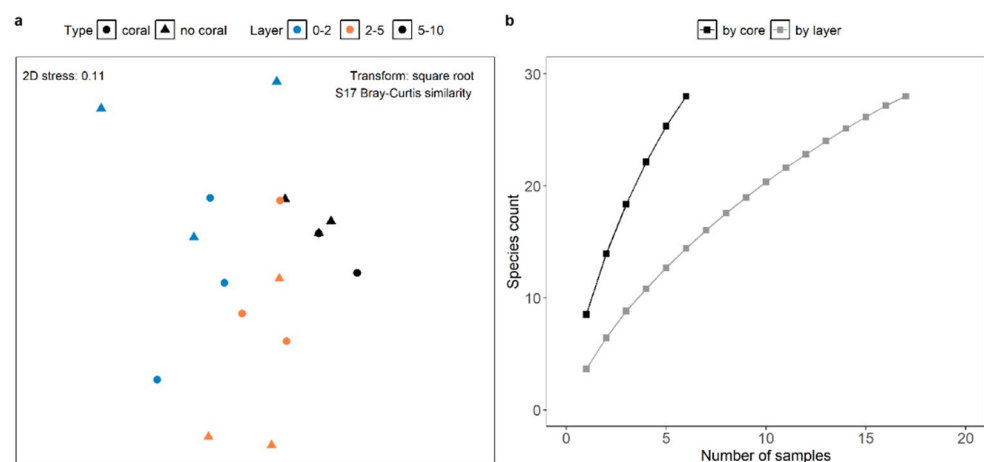
collected with the sediment push-cores. Number of taxa was highest in the surface layers for both coral and no coral samples, and higher for coral than no coral samples in the 2–5 cm layer. Simpson's index (d) showed the opposite pattern and it was highest in the 5–10 cm layer, followed by 2–5 and 0–2 cm, for both coral and no coral samples,

and slightly higher in the former samples (Fig. 8c–d). Species accumulation curves by core and by sediment depth layer indicated that our samples did not reach an asymptote (Fig. 9b).

Table 5 Results of PERMANOVA on infauna density in relation to sediment depth (0–2, 2–5, 5–10 cm) (pairwise and global) and type of push-core (coral vs. no coral)

Groups	t	P (perm)	Unique perms	P(MC)	-	-	-
0–2 × 2–5	1.3474	0.0813	9759	0.1409	-	-	-
0–2 × 5–10	1.8416	0.0148	9273	0.0326	-	-	-
2–5 × 5–10	2.1079	0.0103	9304	0.0242	-	-	-
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	P(MC)
Sediment depth	2	13,837	6918.6	3.1029	0.0012	9911	0.0049
Core (random)	5	12,556	2511.2	1.1262	0.3319	9912	0.3505
Residuals	9	20,068	2229.7	-	-	-	-
Total	16*	47,437	-	-	-	-	-
Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms	
Type (coral vs. no coral)	1	378.82	378.82	0.69946	0.6983	10	
Residuals	4	2166.4	541.59	-	-	-	
Total	5	2545.2	-	-	-	-	

*The number of samples (and df) is inflated by the fact that each depth layer is considered a sample, when in fact they are not independent from each other within a core

Fig. 9 (a) Non-metric MDS of square-root transformed infauna density in relation to sediment push-core type (coral vs. no coral) and sediment depth layer, and (b) species accumulation curves by core and by sediment layer

Discussion

Although many of the associates illustrated in this study have been previously reported with *Acanella arbuscula*, this is the first study to quantify the association and to examine this coral as habitat in a more comprehensive manner. Number of associates per colony significantly increased with colony height, which is expected given that larger colonies provide more space for organisms to settle, hide, or feed (Wahl 1989) and can host more individuals (Buhl-Mortensen and Mortensen 2004; Meretta et al. 2024). Nevertheless, species-specific needs or intra-specific interactions should be considered. For instance, we identified a maximum of one polychaete and two ophiuroids per colony, despite the small size of some ophiuroids (disc ranged 2.7–17.1 mm). Meanwhile, sea anemones ranged between 1 and 15 individuals per colony.

Bamboo corals have been considered to not often host symbionts, commensals, and parasites (Watling et al. 2011). These authors indicated that *A. arbuscula* may host anemones, scale worms (such as *Neopolynoe acanellae*),

ascothoracid barnacles, a shrimp and occasionally a parasitic copepod. They reported that out of 23 *A. arbuscula* specimens collected from the New England and Corner Rise Seamounts, 61% ($N=14$) hosted invertebrate commensals, of which the most common was a scale worm on the older colonies (Watling et al. 2011). This number is higher than the occurrence identified in our study (43%), which highlights potential regional differences or even sampling methods.

Since specimens in this study were collected using bottom trawling, we expect that individuals of mobile species found in association with *A. arbuscula* could have escaped, having an impact on the presence and abundance of epibionts. In fact, most epibionts reported here are either sessile or sedentary organisms. The ophiuroid *Astrochele lymani* can firmly wrap its arms around the host, and chances of evading the colony are smaller, like juvenile *Gorgonocephalus* sp. living on soft corals (e.g. Neves et al. 2020). The polychaetes might also be able to securely hide between branches during the process and stay on the colony (see discussion on polychaetes below). The in situ observation of

a unstalked feather star on an *A. arbuscula* colony (Online Resource 3) further illustrates the presence of mobile epibionts not often captured on trawl samples (also observed on one trawled colony, like pycnogonids). We also observed what appear to be amphipods in one in situ image (Online Resource 3). Therefore, our numbers should be taken conservatively, and it can be assumed that overall, the diversity of animals that live in association with *A. arbuscula* in this region can be higher than the portrayed here. Given the knowledge of additional known associates not encountered in our study, such as a parasitic copepod (Grygier 1983), gall-forming barnacle (Moysse 1983), and different species of ophiuroids (Pearson and Gage 1984), it becomes clear than *A. arbuscula* can host > 10 taxa.

In comparison to other corals living in soft bottom areas in this region, *A. arbuscula* appears to have a comparable diversity of associated taxa (epi and endobionts). For instance, Baillon et al. (2014) identified 14 species associated with the sea pen *Anthoptilum grandiflorum* (Verrill, 1879) and six to *Balticina finmarchica* (Sars, 1851) (Baillon et al. 2014), compared to 10 displayed here (plus the amphipods seen in situ).

Sea anemones

Sea anemones were the most common taxon found with *Acanella arbuscula*, with an occurrence rate of 28.6%. *Stephanauge acanellae* and *Stephanauge inornata* (published as *Amphianthus inornata*) have been reported in association with *A. arbuscula* (Bronsdon et al. 1997; Watling et al. 2011). In fact, these two species have been considered obligates on *A. arbuscula* in the North Atlantic (Buhl-Mortensen and Mortensen 2004). Although *S. acanellae* has been described in a specific association with *A. arbuscula*, Sebens (1998), following Carlgren (1942), suggested that the species might be a synonym of *Stephanauge nexilis* (Verrill, 1883), which is usually found on the gorgonians *Primnoa* sp. and *Paramuricea* sp., and also reported on the sea pen *Balticina finmarchica* (Baillon et al. 2014).

Polychaetes

Three polychaete species have been reported in association with *Acanella* spp. The polynoids *Eunoe spinulosa* Verrill, 1879 (Buhl-Mortensen and Mortensen 2004) also mentioned in Molodtsova et al. (2016), *Australaugeneria iberica* (Ravara and Cunha 2016), and *N. acanellae* (Ditlevsen 1917), also referred in Watling et al. (2011) and Taboada et al. (2021). Our molecular analysis indicates that the polychaete species found on *A. arbuscula* from the NW Atlantic has a very close (98–100%) match to *Neopolynoe acanellae*. Two specimens from our study collected from the same trawl

set between 244 and 265 m (mean depth 252 m, start position 55.6117, −57.0133) appear to represent the shallowest record of *N. acanellae* from the NW Atlantic (see Bock et al. 2010; Hamel et al. 2015). However, since these specimens were not included in the molecular analysis and due to our lack of morphological examination, this record remains to be confirmed.

The polychaete *N. acanellae* has been described to have an obligate relationship with the corals on which it lives. It has been reported in association with *Pseudoanthomastus agaricus* (Studer, 1890) (see Verrill 1881; Molodtsova 2013), *Anthomastus grandiflorus* Verrill 1878 (Ditlevsen 1917; likely also a *Pseudoanthomastus* species, see Molodtsova 2013), the sea pen *Ptilella grandis* (Ehrenberg, 1834) (Pettibone 1963; Hamel et al. 2015), and *Acanthogorgia armata* Verrill 1878 (Verrill 1881), indicating a non-exclusive relationship with *A. arbuscula*. While no other polychaetes were mentioned in association with *A. arbuscula* by Martin and Britayev (1998) in their first review of polychaete symbionts, two other species are listed in their updated 2018 review (Martin and Britayev 2018): the scale worm *A. iberica*, which was described in association with a colony of *Acanella* sp. (Ravara and Cunha 2016) and *E. spinulosa*. In addition, in the 2018 review, *N. acanellae* is only mentioned in association with the octocoral *Thouarella* (*Thouarella*) *variabilis* Wright & Studer, 1889.

In a hypothetical description of the potential relationship between the worm and the coral, Ditlevsen (1917) suggested that based on its anatomy *N. acanellae* (published as *Harmothoe acanellae*) would be able of “swimming” (our quotation marks), in addition to crawling on the coral. This “swimming” ability would allow the worm to move from one colony to another, in an analogy to a seahorse attaching its tail to a “plant” (our quotation marks): “*I imagine the H. acanellae only swimming from one coral-bush to another, where it then takes hold of a branch with its abdomen, f.i. as a Hippocampus with his tails takes hold of a plant*” (Ditlevsen 1917). It is still undocumented whether the polychaete does move between colonies as poetically described by Ditlevsen. Nevertheless, juveniles and adults of the symbiont polychaete *Paradyte crinoidicola* (Potts, 1910) have been found to migrate between crinoid hosts (Britayev and Mekhova 2014). These authors also found indication that males actively migrate more than females, and suggested searching for mating partners and intraspecific competition as potential causes for host migration in that species.

Stomach content analysis of polychaetes found on *P. grandis* indicated that they can feed on this sea pen (Hamel et al. 2015), pointing to a parasitic relationship. Similarly to what was documented for *P. grandis*, only one polychaete was found on each *A. arbuscula* colony. As suggested by Hamel et al. (2015) in their study, we cannot exclude

the possibility that additional specimens could have been lost during the trawl process. However, ours is at least the third study to report the presence of a single specimen of *N. acanellae* on different coral colonies of different species (see Molodtsova et al. 2016). In addition, occurrence rates for *A. arbuscula* were 9.5%, almost twice that found for *P. grandis* (5%, Hamel et al. 2015). Furthermore, single polychaete specimens (confirmed as *N. acanellae* based on genetics) were also found on colonies of both *P. grandis* and an Alcyoniidae mushroom coral collected using an ROV during an expedition to northern Labrador and Davis Strait (B. M. Neves, pers. obs.). Therefore, it is possible that this polychaete does not tolerate simultaneous sharing of coral hosts with intra-specific individuals, as Polynoidae scale worms can display aggressive territorial intra-specific interactions (Martin et al. 2021).

However, citing Verrill (year not identified) and Ditlevsen (1917), Pettibone (1963) mentioned that individuals of this polychaete “have been found living commensally among the branches of the horny coral *Acanella arbuscula* (J. Y. Johnson), where they are found among the close branches near the base of the coral, moving about among the branches and where they may be very abundant”. Based on Ditlevsen’s account and our sampling method, the possibility of multiple polychaetes sharing the same host cannot be excluded. Nevertheless, geographic factors could also be at play, and these dynamics could differ between regions where the species is found.

Nematodes

The family Marimermithidae is characterized by nematodes that are parasitic on other invertebrates, however, the association with *A. arbuscula* was only recently revealed (Westerman et al. 2021). The relationship between nematodes and deep-water corals, particularly species associated with soft sediments, might have been overlooked. It is now known that both adult and juvenile nematodes utilize the coral, particularly females (Westerman et al. 2021). Considering the importance of nematodes in the reworking of organic matter in marine sediments (Solan and Wigham 2005), the presence of these corals might enhance their presence. In a study examining the role of bamboo corals on infauna diversity in the Eastern Canadian Arctic, Pierrejean et al. (2020) found nematodes as the most abundant infaunal organism in the soft bottom areas where another bamboo coral (*Keratois flexibilis*) forms dense forests. In this study, nematodes were found in sediment samples collected both near and underneath *A. arbuscula* colonies. Although it was not possible to determine the species, we confirmed that the specimens do not belong to *P. corallicola*, the species found on *A. arbuscula* (Oleksandr Holovachov, pers.

comm.). This suggests that *P. corallicola* is indeed restricted to the coral (as a parasite would) and does not venture the coral-sediment interface.

Ophiuroids

Remarkably, published records of *Astrochele lymani* in association with *A. arbuscula* are uncommon. In fact, to our knowledge the only record of the association was provided by Verrill (1878) when describing *A. lymani* as a new species (and new genus), based on specimens collected from the Southeastern slope of Le Have (LaHave) Bank (NW Atlantic, Nova Scotia), at ~365 m. Verrill referred to the coral as *Acanella normani*, which has been synonymized with *A. arbuscula* (Saucier et al. 2017).

Other ophiuroid species have been reported in association with *A. arbuscula*. In the Rockall Trough (NE Atlantic), the ophiuroids *Ophiacantha bidentata* (Bruzellius, 1805) and *Ophiactis abyssicola* (M. Sars, 1861) have been reported on both *A. arbuscula* and on the solitary scleractinian *Flabellum (Ulocyathus) alabastrum* Moseley, 1876 (see Pearson and Gage 1984). These authors reported that most *A. arbuscula* trawled from station “M” carried at least one *O. bidentata* on the coral branches. *Ophiacantha bidentata* has a distribution range much wider than *A. lymani* (Stöhr et al. 2024, 2025). Verrill (1884) also mentioned that *A. lymani* was often found on *A. arbuscula* with several *Ophiacantha* sp. ophiuroids. This is a good example of how the specific taxa associated with *A. arbuscula* may vary depending on location. For instance, Pearson and Gage’s samples were collected in the Rockall Trough (NE Atlantic), which is outside of the known range of *A. lymani* (Stöhr et al. 2025). Indeed, all records of *A. lymani* in our study were from the SW Grand Banks area with no records in more northern waters, despite the wide latitudinal range of our samples. These samples were also restricted to depths of 404–1027 m.

It is remarkable that no other ophiuroid taxa were found on our *A. arbuscula* samples beyond the range of *A. lymani*, with the exception of one colony which had a basket star (*Gorgonocephalus* sp.) juvenile on it, which are often found in association with soft corals (families Alcyoniidae and Capnellidae), common in the study area (Neves et al. 2020). The soft coral *Duva florida* (Rathke, 1806), one of the species known to host juveniles of *Gorgonocephalus* sp. (Neves et al. 2020), was also collected at the station where this *A. arbuscula* colony was collected (46.7067, −47.2483).

In addition to individuals living on *A. arbuscula*, ophiuroids are commonly seen in seafloor imagery near the base of *A. arbuscula* colonies. For instance, *Ophiomusium lymani* Wyville-Thomson, 1873 (now accepted as *Ophiomusa lymani*) was almost always observed in close association with *A. arbuscula* colonies (Hughes and Gage 2004), and an

unidentified ophiuroid has also been noticed often near *A. arbuscula* in Davis Strait, NW Atlantic (B.M. Neves, pers. comm., Online Resource 3).

Asteronyx loveni Müller & Troschel, 1842 was also reported in association with *A. arbuscula* (Packer et al. 2007). However, this species has also been considered an obligate to sea pens (Buhl-Mortensen et al. 2010), such as *Funiculina quadrangularis* (Pallas, 1766) (see De Clippele et al. 2015), *Distichoptilum gracile* Verrill, 1882 (see de Castro Manso et al. 2018) and *Pennatula phosphorea* Linnaeus, 1758 (Buhl-Mortensen et al. 2010), and also reported associated with the gorgonian *Radicipes* sp. (Fujita and Ohta 1988).

Information on ontogeny of *Astrochele lymani* is not published, although the World Register of Marine Species' (WoRMS) database lists body size in this species (as qualitative data) as ranging between 2 and 200 mm (Stöhr et al. 2025). The range of disc diameters of individuals found on *A. arbuscula* (2.7–17.1 mm) indicates different life stages present on the coral, including juveniles and young ophiuroids. The potential to host juveniles is an important characteristic of corals as habitat to other species (e.g. Baillon et al. 2012; Neves et al. 2020). The specimen originally described by Verrill had a disc diameter of 7 mm (Verrill 1878).

Most of ophiuroids for which location was measured were found on the middle-high part of the colony. It is possible that this observation reflects a strategy to stay higher on the water column for better food access, which has been suggested for other organisms living in association with corals (e.g. Buhl-Mortensen and Mortensen 2005; De Clippele et al. 2015; Eichsteller et al. 2022; Schmidt et al. 2024). Specimens of *Gorgonocephalus* sp. were more common at the top of the colony on the gorgonians *Paramuricea placomus* (Linnaeus, 1758) and *Primnoa resedaeformis* (Gunnerus, 1763) (De Clippele et al. 2015), and mostly found on the upper half of soft coral colonies (Neves et al. 2020).

Other associates

Scalpellid barnacles were also reported in our study, with some *A. arbuscula* colonies hosting up to nine individuals. These barnacles were present at a low occurrence rate (2.1%), and were the only crustacean reported, possibly due to their sessile nature (i.e. not being removed during trawling). Unpublished molecular analysis of two specimens yielded a 95% match to *Weltnerium stroemii* (M. Sars, 1859). However, the relatively weak match suggests that the species is likely not *W. stroemii*. Watling et al. (2011) noted that barnacles are generally not abundant on octocorals, with few individuals usually found on the host. A gall-forming barnacle, different from the species reported here, is known to live in association with *A. arbuscula* (Moyse 1983), and

other barnacles have been reported in association with other octocorals including *P. resedaeformis* and *P. arborea* (Buhl-Mortensen and Mortensen 2005), a plexaurid and species of *Chrysogorgia* (references in Watling et al. 2011). Watling et al. (2011) observed that many bamboo corals are colonized by other invertebrates, including barnacles, when their tissue has died and the skeleton is exposed. We did notice that in some cases colonies had exposed tissue where the barnacle was attached to. Sponges were attached to bare parts of the skeleton and likely colonize the coral when some exposed skeleton is available. One of the colonies depicted in situ in Online Resource 3 is extensively covered by a white sponge, but it is unclear whether the sponge was growing solely on bare skeleton or whether it took over healthy tissue and polyps, as the rest of the colony appears healthy. There are cases of sponges that grow on octocorals without killing them, but affecting colony morphology (Calcinai et al. 2004). In the case of the specimens observed here, the sponges were indeed growing on bare skeleton, and no polyps were seen underneath them.

While the scallop *Delectopecten vitreus* is often found attached to dead skeletons of gorgonian and scleractinian corals (Dijkstra et al. 2009), in our specimens they were also found on live colonies, although utilizing apparently bare skeleton parts. To our knowledge this is the first report of the species on *A. arbuscula*. The unstalked feather star observed during the ROV dive might be more successful at evading the coral or being lost during trawling and perhaps this explains why this taxon was not observed in our samples, with the exception of one colony not included in the main dataset. Nevertheless, our in situ observation confirms this group as another taxon that utilizes *A. arbuscula* as substrate. Interestingly, the two feather star observations came from depths of 1286 m (Newfoundland Shelf) and 1299 m (Davis Strait) (Online Resource 5), and could indicate a species found in deeper habitats. Nevertheless, this would not explain its rare occurrence on our samples, as 113 (18%) *A. arbuscula* colonies were collected from mean depths > 1000 m.

Kronborgia caridicola Kannevorff and Christensen 1966 is a platyhelminth endoparasitic of shrimps, whose females construct a long coiled cocoon (46–71 cm) to deposit reproductive material (i.e. egg and yolk cells) (Kannevorff and Christensen 1966). While it was not possible to confirm the identity of the two specimens included in our study, these do have the same coiled morphology with a “silky surface-sheen” observed by authors studying this turbellarian genus (Kannevorff and Christensen 1966). We note that the cocoon-like individuals could have ended up on *A. arbuscula* as a result of the trawling process, and may not represent a real association, as these cocoons are often observed directly on the seafloor. In fact, Kannevorff and Christensen

(1966) indicated that the cocoon of *K. caridicola* must be anchored in the seafloor, due to the fact that specimens were embedded with “bottom” material.

Observations on seasonality

Although the relative number of colonies with associates slightly varied between May and October, those differences were not statistically significant when taken as a whole, which is not surprising given that most of the individuals are sea anemones, for which the difference in occurrence between May and October was small (29 vs. 33%, respectively). On the other hand, the frequency of polychaetes was almost doubled in October (fall in the NW Atlantic) in comparison to May (spring in the NW Atlantic). We expect that at least some of the associates found on *A. arbuscula* are perennial and therefore we would not see a clear impact of seasonality on their presence on the coral. To our knowledge there is no published data on the lifespans of the fauna associated to *A. arbuscula*. It is known that some Polynoidae polychaetes (Britayev et al. 2002), ophiuroids (Ravelo et al. 2017), sea anemones (Shick 1991), and nematodes (Gems 2000) can live for several years. But without taxon-specific life span data and more information on their behavior, we can only hypothesize that at least some of the associates live > 1 year. We would expect that while sessile animals such as sea anemones would have a more consistent occurrence on *A. arbuscula*, mobile animals such as polychaetes and ophiuroids could be more variable. Our results indicated no statistical effect of month on total associate abundance, but higher occurrence of colonies with specific fauna was observed in May or October. While we are not aware of published studies on the reproduction of *Neopolynoe acanellae*, most Polynoidae scale worm species are known to have seasonal breeding, such as *Gorgoniapolynoe caeciliae* (Fauvel, 1913) which is a spring breeder (Eckelbarger et al. 2005). Therefore, a peak in their occurrence during the fall could be a result of recruitment events taking place earlier in the year.

Ophiuroids showed the opposite pattern, where individuals were most common in May. There are also no published studies on the reproduction of *Astrochele lymani*, but Neves et al. (2020) working in the same region, reported that individuals of *Gorgonocephalus* sp. (same family as *A. lymani*) found on the cold-water soft coral *Drifa glomerata* (Verrill, 1869) were significantly larger in the spring than in the summer and fall, and that the relative number of *D. glomerata* colonies with basket stars peaked during the spring, which is a similar pattern to the observed here. Ophiuroids were not particularly small (2.7–17.1 mm in disc diameter), in comparison to juveniles of *Gorgonocephalus* sp. found on those soft corals (< 1 mm in disc diameter) (Neves et al.

2020). This could indicate that these higher occurrences in May are the result of recruitment events taking place the previous year, but this has yet to be confirmed. Nevertheless, our data indicate that seasonality likely plays a role on the occurrence of *A. lymani* on *A. arbuscula* colonies.

Stable isotopes remarks

The results of the $\delta^{15}\text{N}$ analysis indicated that polychaetes and sea anemones were mostly on the same trophic level, which was higher than *Acanella arbuscula*'s. This finding indicates that these associates do not compete for food items with their host, which is likely feeding on particulate organic matter (POM) based on comparatively low $\delta^{15}\text{N}$ levels (Sherwood et al. 2008). Our findings are supported by Taboada et al. (2021) whose stable isotopes data also suggests the polychaete *Neopolynoe acanellae* occupying a higher trophic level than its host *A. arbuscula*. It is interesting that polychaetes and sea anemones were on a more comparable trophic level, with polynoid polychaetes being considered mostly carnivores (Fauchald and Jumars 1979; Jumars et al. 2015), and likely indicating a similar feeding habit for these sea anemones. The sea anemones are much larger than *A. arbuscula*'s polyps, and therefore are able to feed on larger particles than the coral host. Sea anemones are polyphagous opportunists, with their feeding behaviors including both carnivory and the ingestion of dissolved and particulate organic matter (Shick 1991).

Sea anemones showed the highest range in $\delta^{13}\text{C}$ values (−21.6 to −18.45‰), indicating the potential for a more varied diet that could include pelagic and benthic organisms (France 1995). Nevertheless, the variation seen in $\delta^{13}\text{C}$ among samples could also be a result of the large spatial scope of our samples. For instance, Sherwood et al. (2008) reported that coral $\delta^{13}\text{C}$ increased slightly (< 1‰) from the Hudson Strait to the southern Grand Banks.

Sediment samples

Like other corals, *Acanella arbuscula* may influence water flow, retain nutrients and entrain plankton near the sediment (Tissot et al. 2006). Therefore, our expectation was that there would be a clear difference in infauna diversity patterns between coral vs. no coral sediment samples. Nevertheless, results indicated no difference in infauna density between coral vs. no coral samples.

Infauna density was the highest at the 0–2 cm sediment layer for both core types. However, when comparing coral vs. no coral samples, density was highest for corals only at the 2–5 cm sediment layer. Number of taxa was also higher in coral samples at the 2–5 cm layer. We hypothesize that the presence of a coral such as *A. arbuscula* at the sediment

surface, with a rootlike system which can be 1–2 cm tall, could be a deterrent for animals to live close to the surface. But collection and analysis of additional samples are needed to assess this hypothesis.

We recognize that our number of samples was small (only three pairs of sediment push-cores), as also highlighted by the species accumulation curves, which did not reach an asymptote. When examining density by core instead of by sediment depth layer, the curve was quite steep and even farther from reaching an asymptote. Nevertheless, we could still observe clear trends associated with sediment depth, which are expected in many benthic systems (e.g. Celenzano et al. 2019; Clinton et al. 2024), indicating that accurate patterns could still be drawn despite our small sample size. We find that due to the lack of strong community patterns for coral vs. no coral sediment samples, it would be risky to make a conclusive statement about the role played (or not) by *A. arbuscula* on sediment infauna diversity. Nevertheless, we believe that these data are still useful as this has not been assessed before. It is possible that a follow-up study that includes a larger sample size, cores of different diameters (Clinton et al. 2024), and considers meiofauna diversity (i.e. smaller mesh size) would yield more conclusive results. Given the depth of our study site (1317 m), it is possible that a considerable part of the infaunal organisms was <500 µm, and hence not retained in the used sieve. In addition, comparing *A. arbuscula* habitats (independently of distance to *A. arbuscula*) to “bare” soft sediment areas might also provide a better picture about the species’ potential role on infauna dynamics at the habitat level (Demopoulos et al. 2014; Bourque and Demopoulos 2018; Miatta and Snelgrove 2022). Miatta and Snelgrove (2022) identified that scale is important to consider when investigating these dynamics. These authors reported higher macrofaunal density and diversity when comparing sediment samples from sea pen habitats (fields) vs. “other sedimentary habitats”. But when examining sediment cores collected with vs. without sea pens (fine scale) in both habitats, macrofaunal metrics were only different for one station, located in the “other sedimentary habitat”. The authors suggested that in areas where sea pens are sparse, their direct effect on underlying macrofauna diversity might be more substantial than in areas where they are more abundant. Cúrdia et al. (2015) identified that scale (i.e., individual colony vs. coral garden) also influences the associated epibiota to the gorgonians *Eunicella gazella* and *Leptogorgia lusitanica*, suggesting a more relevant effect of colony complexity at the coral garden level than at the individual coral level. It is possible that examining the influence of *A. arbuscula* on sediment infauna from a large scale habitat perspective will yield more conclusive results.

Conclusions

Colonies of *Acanella arbuscula* provide habitat to a fauna that is quite consistent, and in some cases likely obligate (e.g. sea anemones) and parasitic (e.g., nematodes), and for both juveniles and adults (e.g. nematodes). We believe that future investigation of other corals found on soft sediment areas as well as *A. arbuscula* from regions outside of the NW Atlantic will yield additional discoveries (e.g. Vinha et al. 2023).

While the role played by most corals as habitat for other species is generally assumed to be innate due to their often arborescent morphologies, the relationship between host and associates is often not understood. Whether relationships are facultative or obligate is often unknown, but taxa that are frequently seen in association with other taxa and rarely seen on others, are often considered to be in obligate relationships. Parasites and symbionts are often recognized as such due to presence of traits adapted for the relationship. For instance, evidence of the symbiosis between the polychaete *Neopolynoe chondrocladiae* (Fauvel, 1943) and the carnivorous sponge *Chondrocladia* (*Chondrocladia*) *grandis* (Verrill, 1879) was revealed based on a combination of methods that included molecular connectivity, microbial, stable isotopes and morphological analyses of host and polychaete (Taboada et al. 2021). These authors proposed that the bioluminescence produced by the polychaete attracts prey to the host, providing food for both sponge and polychaete. But while such specific studies are not conducted for *A. arbuscula*, the nature of most associations remains presumed.

In conclusion, *A. arbuscula* is host to several species like many other corals, but is expected to play a particularly important role in soft sediment areas, where habitat availability for sessile and other epifaunal organisms is more limited. Their effect on infauna dynamics in the study area could not be confidently established, and we believe that further studies are required to elucidate this question.

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Data availability Data can be made available on request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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References

- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ Primer V7: user manual. Prim Ltd, Plymouth, UK, p 93
- Baillon S, Hamel J-F, Mercier A (2014) Diversity, distribution and nature of faunal associations with deep-sea pennatulacean corals in the Northwest Atlantic. *PLoS One* 9:e111519
- Baillon S, Hamel JF, Wareham VE, Mercier A (2012) Deep cold-water corals as nurseries for fish larvae. *Front Ecol Environ* 10:351–356. <https://doi.org/10.1890/120022>
- Baker KD, Wareham VE, Snelgrove PVR, Haedrich RL, Fifield DA, Edinger EN, Wilkinson KD (2012) Distributional patterns of deep-sea coral assemblages in three submarine canyons off Newfoundland, Canada. *Mar Ecol Prog Ser* 445:235–249. <https://doi.org/10.3354/meps09448>
- Beazley LI, Kenchington EL (2012) Reproductive biology of the deep-water coral *Acanella arbuscula* (Phylum cnidaria: class anthozoa: order Alcyonacea), Northwest Atlantic. *Deep Sea Res Part I Oceanogr Res Pap* 68:92–104. <https://doi.org/10.1016/j.dsr.2012.05.013>
- Bock G, Fiege D, Barnich R (2010) Revision of *Hermadion* Kinberg, 1856, with a redescription of *Hermadion magalhaensi* Kinberg, 1856, *Adyte hyalina* (GO Sars, 1873) n. comb. and *Neopolynoe acanellae* (Verrill, 1881) n. comb. (Polychaeta: Polynoidae). *Zootaxa* 2554:45–61
- Bourque JR, Demopoulos AWJ (2018) The influence of different deep-sea coral habitats on sediment macrofaunal community structure and function. *PeerJ* e5276. <https://doi.org/10.7717/peerj.5276>
- Britayev TA, Mekhova ES (2014) Do symbiotic polychaetes migrate from host to host? *Mem Mus Vic* 71:21–25. <https://doi.org/10.24199/j.mmv.2014.71.03>
- Britayev TA, Plyuscheva MV, Bujanovskij AI (2002) Size and age structure of scaleworms *Lepidonotus squamatus* and *Harmothoe imbricata* (Polychaeta, Polynoidae) in the white sea. *Zool Zh* 81:285–291
- Bronsdon SK, Rogers AD, Tyler PA, Rice AL, Gage JD (1997) Genetic study of the extent and consequences of sexual and asexual reproduction in the deep-sea epizoidic anemones *Amphianthus inornata* and *Kadosactis commensalis* (Cnidaria: Anthozoa). *Mar Biol* 128:231–239. <https://doi.org/10.1007/s002270050087>
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400. <https://doi.org/10.32614/rj-2017-066>
- Buhl-Mortensen L, Mortensen PB (2004) Symbiosis in deep-water corals. *Symbiosis* 37:33–61
- Buhl-Mortensen L, Mortensen PB (2005) Distribution and diversity of species associated with deep-sea gorgonian corals off Atlantic Canada. In: Freiwald A, Roberts JM (eds) *Cold-Water Corals and Ecosystems*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 849–879
- Buhl-Mortensen L, Vanreusel A, Gooday AJ, Levin LA, Priede IG, Buhl-Mortensen P, Gheerardyn H, King NJ, Raes M (2010) Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Mar Ecol* 31:21–50. <https://doi.org/10.1111/j.1439-0485.2010.00359.x>
- Calcinai B, Bavestrello G, Cerrano C (2004) Dispersal and association of two alien species in the Indonesian coral reefs: the octocoral *Carijoa riisei* and the demosponge *Desmapsamma anchorata*. *J Mar Biol Assoc U K* 84:937–941. <https://doi.org/10.1017/S0025315404010227h>
- Carlgren O (1942) Actiniaria part II. Danish Ingolf-Exped
- Celentano E, Lercari D, Maneiro P, Rodríguez P, Gianelli I, Ortega L, Orlando L, Defeo O (2019) The forgotten dimension in sandy beach ecology: vertical distribution of the macrofauna and its environment. *Estuar Coast Shelf Sci* 217:165–172. <https://doi.org/10.1016/j.ecss.2018.11.008>
- Chernomor O, von Haeseler A, Minh BQ (2016) Terrace aware data structure for phylogenomic inference from supermatrices. *Syst Biol* 65:997–1008. <https://doi.org/10.1093/sysbio/syw037>
- Clinton ME, Snelgrove PVR, Bates AE (2024) Macrofaunal diversity patterns in coastal marine sediments: re-examining common metrics and methods. *Mar Ecol Prog Ser* 735:1–26. <https://doi.org/10.3354/meps14576>
- Cúrdia J, Carvalho S, Pereira F, Guerra-García JM, Santos MN, Cunha MR (2015) Diversity and abundance of invertebrate epifaunal assemblages associated with gorgonians are driven by colony attributes. *Coral Reefs* 34:611–624. <https://doi.org/10.1007/s00338-015-1283-1>
- de Castro Manso CL, Prata J, Araya JF (2018) Deep-water ophiuroids (Echinodermata) associated with anthozoans and hexactinellid

- sponges from Northern Chile. *Thalassas* 34:93–102. <https://doi.org/10.1007/s41208-017-0042-1>
- De Clippele LH, Buhl-Mortensen P, Buhl-Mortensen L (2015) Fauna associated with cold water gorgonians and sea pens. *Cont Shelf Res* 105:67–78. <https://doi.org/10.1016/j.csr.2015.06.007>
- Demopoulos AWJ, Bourque JR, Frometa J (2014) Biodiversity and community composition of sediment macrofauna associated with deep-sea *Lophelia pertusa* habitats in the Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers* 93:91–103. <https://doi.org/10.1016/j.dsr.2014.07.014>
- Dijkstra HH, Warén A, Gudmundsson G (2009) Pectinoidea (Mollusca: Bivalvia) from Iceland. *Mar Biol Res* 5:207–243. <https://doi.org/10.1080/1745100802425643>
- Ditlevsen H (1917) Annelids. I. Danish Ingolf-Exped 4:1–71
- Eckelbarger KJ, Watling L, Fournier H (2005) Reproductive biology of the deep-sea polychaete *Gorgoniapolyneae caeciliae* (Polynoidae), a commensal species associated with octocorals. *J Mar Biol Assoc United Kingdom* 85:1425–1433. <https://doi.org/10.1017/S0025315405012609>
- 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* 14:358
- Fauchald K, Jumars PA (1979) The diet of worms: a study of polychaete feeding guilds. *Oceanogr Mar Biol Annu Rev* 17:193–284
- Felsenstein J (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. *J Mol Evol* 17:368–376. <https://doi.org/10.1007/BF01734359>
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol Mar Biol Biotechnol* 3:294–299
- France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Mar Ecol Prog Ser* 124:307–312
- Fujita T, Ohta S (1988) Photographic observations of the life style of a deep-sea ophiuroid *Asteronyx loveni* (Echinodermata). *Deep Sea Res Part Oceanogr Res Pap* 35:2029–2043. [https://doi.org/10.1016/0198-0149\(88\)90123-9](https://doi.org/10.1016/0198-0149(88)90123-9)
- Fuller SD, Murillo Perez FJ, Wareham V, Kenchington E (2008) Vulnerable marine ecosystems dominated deep-water corals and sponges in the NAFO convention Area. Ser no N5524 NAFO Scientific Council Research Document sci Counc res doc 2408/22, 24 pp <https://www.nafo.int/Portals/0/PDFs/sc/2008/scr08-022.pdf>
- Gems D (2000) Longevity and ageing in parasitic and free-living nematodes. *Biogerontology* 1:289–307. <https://doi.org/10.1023/A:1026546719091>
- Grygier MJ (1983) An endoparasitic lamippid copepod in *Acanella* from the North Atlantic. *Crustaceana* 45:176–182. <https://doi.org/10.1163/156854083X00604>
- Hamel JF, Montgomery EM, Barnich R, Mercier A (2015) Range extension of the deep-sea polychaete worm *Neopolyneae acanelae* in Canada. *Mar Biodivers Rec* 8:10–13. <https://doi.org/10.1017/S1755267214001444>
- Hartig F (2022) Package DHARMA Title Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. *Cran* 1–65
- Hoang DT, Chernomor O, von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: improving the ultrafast bootstrap approximation. *Mol Biol Evol* 35:518–522. <https://doi.org/10.1093/molbev/msx281>
- Hughes DJ, Gage JD (2004) Benthic metazoan biomass, community structure and bioturbation at three contrasting deep-water sites on the Northwest European continental margin. *Prog Oceanogr* 63:29–55. <https://doi.org/10.1016/j.pocan.2004.09.002>
- Jumars PA, Dorgan KM, Lindsay SM (2015) Diet of worms emended: an update of polychaete feeding guilds. *Annu Rev Mar Sci* 7:497–520. <https://doi.org/10.1146/annurev-marine-010814-020007>
- Kalyaanamoorthy S, Minh BQ, Wong TKF, von Haeseler A, Jermini LS (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat Methods* 14:587–589. <https://doi.org/10.1038/nmeth.4285>
- Kanneworff B, Christensen AM (1966) *Kronborgia caridicola* sp. nov., an endoparasitic turbellarian from North Atlantic shrimps. *Ophelia* 3:65–80. <https://doi.org/10.1080/00785326.1966.10409633>
- Kenchington E, Lirette C, Cogswell A, Archambault D, Archambault P, Benoit H, Bernier D, Brodie B, Fuller S, Gilkinson K, Lévesque M, Power D, Siferd T, Treble M, Wareham V (2010) Delineating coral and sponge concentrations in the biogeographic regions of the East Coast of Canada using Spatial analyses. *DFO Can Sci Adv Sec Res Doc* 2010/041:vi–
- Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *J Mol Evol* 16:111–120. <https://doi.org/10.1007/BF01731581>
- Kornijów R, Pawlikowski K (2016) A common error in calculating density of invertebrates in sediment core sections of unequal lengths. *Ann Limnol* 52:301–306. <https://doi.org/10.1051/limn/2016017>
- Lapointe AE, Watling L, France SC, Auster PJ (2020) Megabenthic assemblages in the lower bathyal (700–3000 m) on the New England and Corner Rise Seamounts, Northwest Atlantic. *Deep Sea Res Part I Oceanogr Res Pap* 165:103366. <https://doi.org/10.1016/j.dsr.2020.103366>
- Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higgins DG (2007) Clustal W and clustal X version 2.0. *Bioinformatics* 23:2947–2948. <https://doi.org/10.1093/bioinformatics/btm404>
- Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lutcavage ME (2008) Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *J Anim Ecol* 77:838–846. <https://doi.org/10.1111/j.1365-2656.2008.01394.x>
- Martin D, Aguado MT, Álamo MAF, Britayev TA, Böggemann M, Capa M, Faulwetter S, Fukuda MV, Helm C, Petti MAV, Ravara A, Teixeira MAL (2021) On the diversity of Phyllocladocida (Annelida: Errantia), with a focus on Glyceridae, Goniadidae, Nephtyidae, Polynoidae, Sphaerodoridae, Syllidae, and the holoplanktonic families. *Diversity* 13(3):65. <https://doi.org/10.3390/d13030131>
- Martin D, Britayev TA (1998) Symbiotic polychaetes: review of known species. *Oceanogr Mar Biol Annu Rev* 36:217–340
- Martin D, Britayev TA (2018) Symbiotic polychaetes revisited: an update of the known species and relationships (1998–2017). *Oceanogr Mar Biol* 56:371–448. <https://doi.org/10.1201/9780429454455-6>
- Mccallum BR, Walsh SJ (1996) Groundfish survey trawls used at the Northwest Atlantic Fisheries Center, 1971–present. *NAFO SCR Doc*. 96/50
- Meretta PE, Sirito SM, Schejter L, Tapia AP, Bremec C, Genzano G (2024) Sea fans and their associated fauna in the marine animal forests of Burdwood Bank at 54°S, SW Atlantic Ocean. *Mar Biodivers* 54:79. <https://doi.org/10.1007/s12526-024-01471-3>
- Miatta M, Snelgrove PVR (2022) Sea pens as indicators of macrofaunal communities in deep-sea sediments: evidence from the Laurentian channel marine protected Area. *Deep Res Part I Oceanogr Res Pap* 182(103702):1–25. <https://doi.org/10.1016/j.dsr.2022.103702>
- Molodtsova TN (2013) Deep-sea mushroom soft corals (Octocorallia: alcyonacea: Alcyoniidae) of the Northern Mid-Atlantic ridge.

- Mar Biol Res 9:488–515. <https://doi.org/10.1080/17451000.2012.750427>
- Molodtsova TN, Britayev TA, Martin D (2016) Cnidarians and their polychaete symbionts. In: Goffredo S, Dubinsky Z (eds) *The Cnidaria, past, present and future*. Springer, pp 387–413
- Moyse J (1983) *Isidascus bassindalei* gen.nov., sp.nov. (Ascothoracida: Crustacea) from north-east Atlantic with a note on the origin of barnacles. *J Mar Biol Assoc United Kindg* 63:161–180. <https://doi.org/10.1017/S0025315400049869>
- Neves BM, Wareham Hayes V, Herder E, Hedges K, Grant C, Archambault P (2020) Cold-water soft corals (Cnidaria: Nephtheidae) as habitat for juvenile basket stars (Echinodermata: Gorgonocephalidae). *Front Mar Sci* 7:1–21. <https://doi.org/10.3389/fmars.2020.547896>
- Neves BM, Auger V, Edinger E, Lockhart P, Morrissey C (2023) Preparing for remotely operated vehicle (ROV) seafloor surveys: a descriptive checklist for ocean scientists and managers Canadian Technical Report of Fisheries and Aquatic Sciences 3578. Can Tech Rep Fish Aquat Sci 3578 ix+37 p
- Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Mol Biol Evol* 32:268–274. <https://doi.org/10.1093/molbev/msu300>
- Packer DB, Boelke D, Guida V, McGee L-A (2007) State of deep coral ecosystems in the Northeastern US Region: Maine to Cape Hatteras. In: Lumsden S, Hourigan T, Bruckner A, Dorr G (eds) *The State of Deep Coral Ecosystems of the United States*. NOAA Technical Memorandum CRCP-3. Silver Spring MD 365 pp
- Palumbi SR (1996) What can molecular genetics contribute to marine biogeography? An urchin's tale. *J Exp Mar Bio Ecol* 203:75–92. [https://doi.org/10.1016/0022-0981\(96\)02571-3](https://doi.org/10.1016/0022-0981(96)02571-3)
- Pearson M, Gage JD (1984) Diets of some deep-sea brittle stars in the Rockall trough. *Mar Biol* 82:247–258. <https://doi.org/10.1007/BF00392406>
- Pettibone MH (1963) Marine polychaete worms of the new England region. I. Aphroditidae through trochochaetidae. *Bull United States Natl Museum* 1–356. <https://doi.org/10.5479/si.0362923.6.227.1>
- Piccirillo LF, Edinger E, de Moura Neves B, Burchell M, Layne GD, Hayes VE (2025) Growth rates and ages of the small bamboo coral <Emphasis Type="Italic">Acanella arbuscula</Emphasis> in the Northwest Atlantic. *Deep Sea Res Part II Top Stud Oceanogr*. <https://doi.org/10.1016/j.dsr2.2025.105485>
- Pierrejean M, Grant C, Neves B, Chaillou G, Edinger E, Blanchet FG, Maps F, Nozais C, Archambault P (2020) Influence of deep-water corals and sponge gardens on infaunal community composition and ecosystem functioning in the Eastern Canadian Arctic. *Front Mar Sci* 7:1–19. <https://doi.org/10.3389/fmars.2020.00495>
- Ravara A, Cunha MR (2016) Two new species of scale worms (Polychaeta: Aphroditiformia) from deep-sea habitats in the Gulf of Cadiz (NE Atlantic). *Zootaxa* 4097:442–450
- Ravelo AM, Konar B, Bluhm B, Iken K (2017) Growth and production of the brittle stars <Emphasis Type="Italic">Ophiura sarsii</Emphasis> and <Emphasis Type="Italic">Ophiocten sericeum</Emphasis> (Echinodermata: Ophiuroidea). *Cont Shelf Res* 139:9–20. <https://doi.org/10.1016/j.csr.2017.03.011>
- RStudio Team (2021) RStudio: Integrated Development Environment for R
- Saucier EH, Sajjadi A, France SC (2017) A taxonomic review of the genus *Acanella* (Cnidaria: Octocorallia: Isididae) in the North Atlantic Ocean, with descriptions of two new species. *Zootaxa* 4323:359–390. <https://doi.org/10.11646/zootaxa.4323.3.2>
- Schmidt LA, Brix S, Rossel S, Forster S, Eichsteller A (2024) Unveiling ophiuroid biodiversity across North Atlantic habitats via an integrative perspective. *Sci Rep* 14:20405. <https://doi.org/10.1038/s41598-024-71178-9>
- Sebens KP (1998) Marine flora and fauna of the Eastern united States. Anthozoa: Actiniaria, Corallimorpharia, Ceriantharia, and zoanthidea. NOAA Tech Rep NMFS 68
- Sherwood OA, Edinger EN (2009) Ages and growth rates of some deep-sea gorgonian and antipatharian corals of Newfoundland and Labrador. *Can J Fish Aquat Sci* 66:142–152
- Sherwood OA, Jamieson RE, Edinger EN, Wareham VE (2008) Stable C and N isotopic composition of cold-water corals from the Newfoundland and Labrador continental slope: examination of trophic, depth and spatial effects. *Deep Res Part I Oceanogr Res Pap* 55:1392–1402. <https://doi.org/10.1016/j.dsr.2008.05.013>
- Shick JM (1991) *A functional biology of sea anemones*. Springer Netherlands, Dordrecht, 420 pp
- Solan M, Wigham BD (2005) Biogenic particle reworking and bacterial–invertebrate interactions in marine sediments. In: *Interactions between macro- and microorganisms in marine sediments*. pp 105–124
- Stöhr S, O'Hara T, Thuy B (2024) World Ophiuroidea Database. *Ophiacantha bidentata* (Bruzellius, 1805). Accessed through: World Register of Marine Species at: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=124978> on 2024-08-07
- Stöhr S, O'Hara T, Thuy B (2025) World Ophiuroidea Database. *Astrochele lymani* Verrill, 1878. Accessed through: World Register of Marine Species at: <https://www.marinespecies.org/aphia.php?p=taxdetails&id=182992> on 2025-12-22
- Taboada S, Serra Silva A, Díez-Vives C, Neal L, Cristobo J, Ríos P, Hestetun JT, Clark B, Rossi ME, Junoy J (2021) Sleeping with the enemy: unravelling the symbiotic relationships between the scale worm *Neopolynoe chondrocladiae* (Annelida: Polynoidae) and its carnivorous sponge hosts. *Zool J Linn Soc* 193:295–318
- Taboada S, Silva AS, Neal L, Cristobo J, Ríos P, Álvarez-Campos P, Hestetun JT, Koutsouveli V, Sherlock E, Riesgo A (2020) Insights into the symbiotic relationship between scale worms and carnivorous sponges (Cladorhizidae, Chondrocladia). *Deep Sea Res Part I Oceanogr Res Pap*. <https://doi.org/10.1016/j.dsr.2019.103191>
- Tissot BN, Yoklavich MM, Love MS, York K, Amend M (2006) Benthic invertebrates that form habitat on deep banks off Southern California, with special reference to deep sea coral. *Fish Bull* 104:167–181
- van Denderen PD, van Kooten T, Rijnsdorp AD (2013) When does fishing lead to more fish? Community consequences of bottom trawl fisheries in demersal food webs. *Proc R Soc Lond B Biol Sci* 280:20131883
- Verrill AE (1878) Notice on recent marine fauna of the eastern coast of North America; part II. *Am J Sci* 16:371–378. <https://doi.org/10.2475/ajs.s3-16.95.371>
- Verrill AE (1881) New England annelida. Part I. Historical sketch, with annotated lists of the species hitherto recorded. *Trans Conn Acad Arts Sci* 4:285–324
- Verrill AE (1884) Results of Dredgings in the Gulfstream Region by the U. S. Fish-Commission. *Science* (80-) ns-4:8–10. <https://doi.org/10.1126/science.ns-4.74>
- Vinha B, Gori A, Rossi S, Piraino S, Huvenne V, Orejas C (2023) Trophic ecology of cold-water coral habitats of the Cabo Verde islands (NW Africa). In: *8th International Deep-Sea Coral Symposium*. Edinburgh
- Wahl M (1989) Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Mar Ecol Prog Ser* 58:175–189
- Wareham VE, Edinger EN (2007) Distribution of deep-sea corals in the Newfoundland and Labrador region, Northwest Atlantic Ocean. *Bull Mar Sci* 81:289–313
- Watling L, France SC, Pante E, Simpson A (2011) Chapter Two - Biology of Deep-Water Octocorals. In: Lesser M (ed) *Advances in Marine Biology*. Academic Press, pp 41–122
- Westerman R, Neves B, Ahmed M, Holovachov O (2021) *Aborjinia Corallicola* sp. n., a new nematode species (Nematoda :

Marimermithidae) associated with the bamboo coral *Acanella arbuscula* (Johnson). Syst Parasitol. <https://doi.org/10.1007/s11230-021-09996-y>

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