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Occurrence and biogeography of hydroids (Cnidaria: Hydrozoa) from deep-water coral habitats off the southeastern United States

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ABSTRACT

Deep-water coral habitats off the southeastern USA (SEUS) support diverse fish and invertebrate assemblages, but are poorly explored. This study is the first to report on the hydroids collected from these habitats in this area. Thirty-five species, including two species that are likely new to science, were identified from samples collected primarily by manned submersible during 2001–2005 from deep-water coral habitats off North Carolina to east-central Florida. Eleven of the species had not been reported since the 19th to mid-20th century. Ten species, and one family, the Rosalindidae, are documented for the first time in the SEUS. Latitudinal ranges of 15 species are extended, and the deepest records in the western North Atlantic for 10 species are reported. A species accumulation curve illustrated that we continue to add to our knowledge of hydroid diversity in these habitats. Sexually mature individuals were collected for 19 species during the summer to early autumn months. Most of the observed species (89%) liberate planula larvae as part of their life cycles, suggesting that these species exhibit a reproductive strategy that reduces the risk of dispersal to sub-optimal habitats. Hydroids occurred across various substrata including coral rubble, live corals, rock and other animal hosts including hydroids themselves. All observed species were regionally widespread with typically deep-neritic to bathyal sub-tropical/tropical distributions. Hydroid assemblages from deep-water SEUS coral habitats were most similar to those from adjacent deep-water habitats off the SEUS (17 shared species), and those in the Straits of Florida/Bahamas and Caribbean/West Indian regions (14 and 8 shared species, respectively). The similarity to sub-tropical and tropical assemblages and the richness of plumularioids in the SEUS deep-water coral habitats support the idea of a Pleistocene intrusion of tropical species northwards following an intensification of the Gulf Stream from the Caribbean.

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1. Introduction

Deep-water coral habitats, composed mostly of *Lophelia pertusa*, are abundant on the southeastern US (SEUS)

continental shelf and slope (Stetson et al., 1962; Paul et al., 2000; Popenoe and Manheim, 2001; Reed, 2002; Reed et al., 2006; Ross and Nizinski, 2007). Because of their depths of occurrence, presence of strong currents and associated rugged bottom topography, these habitats have remained largely unexplored. Our data from North Carolina to east-central Florida indicate that deep-water coral habitats on the continental shelf and slope of the SEUS support highly diverse ichthyofaunal and invertebrate

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assemblages (Ross and Nizinski, 2007; Ross and Quattrini, 2007). Deep-water coral habitats are focal points of biodiversity in the SEUS in part because of the apparent high productivity around reefs and the habitat complexity conferred by the framework-building scleractinian corals *L. pertusa*, *Enallopsammia* spp., *Madrepora oculata* and *Oculina varicosa* (Reed and Ross, 2005; Reed et al., 2006; Ross and Nizinski, 2007). Sophisticated and non-destructive technologies, such as submersibles, have been employed recently to sample the fauna inhabiting these deep-water coral habitats. Using this targeted, discrete collection methodology, we have made large collections of high quality, intact invertebrate material, comprising many phyla. This paper examines the occurrence and biogeography of the hydroid assemblages found in deep-water coral habitats off the SEUS.

Historical collections of deep-water hydroids from the SEUS region (e.g., Allman, 1877; Clarke, 1879; Fewkes, 1881; Nutting, 1900; Cain, 1972; Wenner et al., 1984) used traditional sampling methods, including trawls and dredges. But these gears frequently fragment and destroy delicate hydroids (Henry and Kenchington, 2004a,b), particularly the anthoathecates, which possess virtually no protective chitinous perisarc over their hydranths and gonophores. Dredging and trawling tend to intentionally avoid highly rugose areas (e.g., such as those found on *Lophelia* banks) to prevent gear from being damaged. Hydroids are also often small (<5 mm), not commercially important, and have many unresolved taxonomic problems. Therefore, deep-water hydroids have not been as rigorously studied as their shallow-water counterparts in the SEUS, and even less is known about hydroids living in deep-water coral habitats.

Current knowledge suggests that hydroids are richly represented in hard-bottom communities in the subtropical/tropical western North Atlantic (Allman, 1877; Clarke, 1879; Fewkes, 1881; Nutting, 1900; Fraser, 1944; Pearse and Williams, 1951; Vervoort, 1968, 1972; Cain, 1972; Wenner et al., 1984; Knott and Wendt, 1985; Calder, 1993a,b, 1998, 2000), particularly as one moves from inshore to mid- and off-shore areas (Wenner et al., 1984; Knott and Wendt, 1985). Elsewhere in the North Atlantic, hydroids collected from deep-water *Lophelia* habitats can be very species rich; 27 species from the Norwegian coast (Dons, 1944; Burdon-Jones and Tambs-Lyche, 1960; Mortensen and Fosså, 2006), 31 species from the SW Irish coast (Henry and Roberts, 2007), and 24 species from the Bay of Biscay (Browne, 1907; Le Danois, 1948). These accounts and the growing evidence for rich megafaunal assemblages associated with the deep-water coral habitats off the SEUS (Reed et al., 2006; Ross and Quattrini, 2007) prompted us to examine the hydroid fauna from our collections.

A sort through primarily submersible-based collections from the continental slope of the SEUS generated a large number of well-preserved whole hydroids, including the more delicate anthoathecates. Many hydroid specimens had complete intact reproductive structures, which is uncommon among deep-water hydroids collected by trawl or dredge. The rarity of such intact specimens, coupled with the infrequent sampling of hydroids from

this region (and deep-water coral habitats in general) warranted further examination and assessment of these unique collections. Our overall goals were to: (1) document the local and regional occurrence of hydroid species from SEUS deep-water coral habitats and (2) compare the biogeographical affinity of the hydroids from SEUS deep-water coral habitats with adjacent bathyal regions. We also discuss reproductive timing and dispersal modes of the species, given that these features of deep-water hydroids are rarely discussed and relate to the geographic distributions and biology of the species.

2. Materials and methods

2.1. Fieldwork

Hydroids were collected incidentally with other invertebrates from 31 dives and one trawl on deep-water reefs and coral banks along the SEUS shelf edge (82–103 m) and slope (368–770 m) during six (2001–2005) summer-fall cruises (Table 1; Fig. 1).

Benthic sampling was conducted using the Johnson-Sea-Link (JSL) submersibles I and II (Harbor Branch Oceanographic Institute). Usually two daytime dives (ranging from ca. 1.5–3 h each) were made with the JSL each day on or near reef areas (Table 1). Depth, temperature, date and time were logged at 1 scans⁻¹ intervals (data were overlain on video) using a real-time data logger (Sea-Bird SBE 25 or 19plus) attached to the submersible. Submersible position was tracked from the surface support ship using a Trackpoint II system.

When the JSL stopped, time, exact location and depth were recorded. During these frequent stops, objects or specimens to be collected were first videotaped, the video camera variously set from wide-angle to close-up views depending on subject matter and objectives, and then collected using a suction device or grab. Specimens were preserved at sea in 10% formalin-buffered seawater solution or 70% ethanol.

Otter trawls were deployed around reef areas to supplement JSL benthic data (Fig. 1; Table 1). Prior to trawling, the area was surveyed with single beam sonar to ensure that trawls avoided major coral or high profile areas; however, the trawling objective was to tow as close to reef areas as possible. The otter trawl (4.9 m head rope, 38.1 mm mesh) was towed for 29–45 min at ~2 knot (3.7 km/h) ground speed. Trawl catches were preserved as above.

2.2. Sorting and identification

In total, 25 fragments of dead scleractinian coral, 15 other invertebrate hosts, 7 fragments of live scleractinian coral, and 2 rocks were examined. Additionally, in 12 instances, hydroids were discovered loose within our collections, and thus represented samples with unknown substrata. In total, these 61 samples represented the geographic and bathymetric ranges of deep-water coral habitats in the SEUS.

Hydroids were carefully scraped or chipped from substrata, taking care that the attachment sites remained

Table 1
List of hydroid species and their corresponding station data from deep-water coral habitats off the SEUS (n/a = no data available)

Sample	Hydroid species	Date	Latitude (N)	Longitude (W)	Depth (m)	Bottom temperature (°C)	Bottom current speed (Kn)
<i>Cape laakout</i>							
CH-01-113-trawl	<i>Cladocarpus sigma</i>	8/29/2001	34.3425	−75.8031	378	n/a	n/a
JSLI-01-4361-bucket 11	<i>Halecium beanii</i> , <i>H. macrocephalum</i>	9/22/2001	34.3275	−75.7911	398	9.3	0.1–0.2
JSLI-01-4362-bucket 8	<i>Stegopoma plicatile</i>	9/22/2001	34.3237	−75.7919	368	10.2	n/a
JSLI-04-4692-bucket 4	<i>Clytia</i> sp., <i>Stegopoma plicatile</i>	6/15/2004	34.3240	−75.7866	401	9.7	n/a
JSLI-04-4693-bucket 6	<i>Clytia</i> sp., <i>Plumularia</i> cf. <i>attenuata</i>	6/15/2004	34.3248	−75.7858	416	9.3	0.7
JSLI-04-4694-basket	<i>Plumularia</i> cf. <i>attenuata</i> , <i>Zygophylax convallarius</i>	6/16/2004	34.1876	−75.8966	389	10.6	0.5–0.6
JSLI-04-4695-front bucket 3	<i>Campanularia macroscypha</i> , <i>Halecium beanii</i> , <i>Plumularia attenuata</i>	6/16/2004	34.1908	−75.8953	411	9.8	0.3–0.4
JSLI-05-4890-basket	<i>Eudendrium exiguum</i> , <i>Nemertesia geniculata</i>	10/17/2005	34.3247	−75.7870	387	8.5	0.8
JSLI-05-4891-front bucket 2	<i>Eudendrium</i> sp., <i>Zygophylax convallarius</i>	10/17/2005	34.3232	−75.7923	369	9.2	1.1
JSLI-05-4891-basket	<i>Halecium beanii</i> , <i>Nemertesia geniculata</i>	10/17/2005	34.3232	−75.7923	368	9.2	1.1
JSLI-05-4892-bucket 5	<i>Campanularia macroscypha</i> , <i>Eudendrium exiguum</i> , <i>Halecium beanii</i> , <i>Nemertesia geniculata</i>	10/18/2005	34.2343	−75.8723	381	9.0	0.6
<i>Cape fear</i>							
JSLI-04-4696-front bucket 1	<i>Aglaophenopsis hirsuta</i>	6/17/2004	33.5728	−76.4616	396	9.1	1
JSLI-04-4696-front bucket 3	<i>Halecium macrocephalum</i> , <i>Nemertesia geniculata</i>	6/17/2004	33.5728	−76.4616	396	9.0	1
JSLI-04-4696-bucket 10	<i>Nemertesia geniculata</i> , <i>Plumularia</i> cf. <i>attenuata</i>	6/17/2004	33.5727	−76.4613	402	9.2	1
<i>North Carolina outer shelf</i>							
JSLII-02-3312-bucket 9	<i>Cryptolaria pectinata</i>	8/15/2002	33.2300	−77.2656	82	17.9	0.5
JSLII-02-3312-bucket 11	<i>Acryptalaria conferta</i>	8/15/2002	33.2301	−77.2656	79	17.7	n/a
JSLII-03-3422-bucket 9	<i>Athecata</i> sp. 1, <i>Campanularia hincksii</i> , <i>Sertulariidae</i> sp.	8/19/2003	33.4149	−77.0777	99	17.7	0.3
<i>Stetson Banks</i>							
JSLI-04-4689-bucket 7	<i>Cryptolaria pectinata</i> , <i>Diplapteroides grandis</i> , <i>Halecium macrocephalum</i>	6/13/2004	31.8195	−77.6152	668	12.2	0.7
JSLI-04-4698-basket	<i>Acryptalaria conferta</i>	6/18/2004	31.8258	−77.6144	684	11.0	n/a
JSLI-04-4699-bucket 6	<i>Aglaophenopsis hirsuta</i> , <i>Campanularia macroscypha</i> , <i>Nemertesia geniculata</i>	6/18/2004	31.8466	−77.6103	694	10.9	0.3–0.4
JSLI-04-4699-bucket 9	<i>Cladocarpus flexilis</i> , <i>Halecium macrocephalum</i> , <i>Nemertesia geniculata</i> , <i>Plumularia</i> cf. <i>attenuata</i> , <i>Sertularella catena</i>	6/18/2004	31.8457	−77.6116	670	11.0	0.3–0.4
JSLI-05-4898-bucket 10	<i>Zygophylax convallarius</i>	10/21/2005	32.2689	−77.4746	582	8.5	0.1–0.2
JSLI-05-4904-bucket 4	<i>Sertularella gayi robusta</i> , <i>Cladocarpus paradiseus</i>	10/27/2005	31.8462	−77.6134	651	9.6	1
<i>Savannah Banks</i>							
JSLI-05-4900-bucket 5	<i>Eudendrium fruticosum</i>	10/22/2005	31.7415	−79.0942	500	9.2	0.5
JSLI-05-4902-bucket 2	<i>Nemertesia geniculata</i> , <i>Sertularella gayi robusta</i>	10/26/2005	31.7045	−79.1238	501	8.1	0.7–0.8
JSLI-05-4902-front bucket 3	<i>Sertularella</i> sp.	10/26/2005	31.4827	−79.6414	501	8.1	0.7–0.8
JSLI-05-4902-bucket 8	<i>Aglaophenopsis hirsuta</i> , <i>Halapteris geminata</i> , <i>Zygophylax convallarius</i>	10/26/2005	31.7042	−79.1233	551	8.1	0.7–0.8
JSLI-05-4902-bucket 12	<i>Campanularia macroscypha</i>	10/26/2005	31.7046	−79.1243	502	8.1	0.7–0.8
<i>Jacksonville lithaherms</i>							

JSLI-04-4683-basket	<i>Acryptalaria conferta</i> , <i>Aglaophenopsis hirsuta</i> , <i>Cladocarpus sigma</i> , <i>Zygophylax convallarius</i>	6/10/2004	30.5168	-79.6618	548	10.6	0.6-0.7	
JSLI-04-4684-bucket 1	<i>Eudendrium eximium</i> , <i>Halopteris geminata</i>	6/10/2004	30.5156	-79.6605	550	10.1	0.5-0.6	
JSLI-04-4684-bucket 3	<i>Calvinia mirabilis</i> , <i>Plumularia cf. attenuata</i>	6/10/2004	30.5133	-79.6627	551	9.1	0.5-0.6	
JSLI-04-4684-basket ^a	<i>Athecata sp. 1</i> , <i>Athecata sp. 2</i> , <i>Halecium macrocephalum</i> , <i>Halopteris geminata</i>	6/10/2004	30.5141	-79.6624	561	9.2	0.5-0.6	
JSLI-04-4685-front bucket 3	<i>Campanulinidae sp.</i>	6/11/2004	30.8122	-79.6320	636	7.9	0.5	
JSLI-04-4686-front bucket 3	<i>Athecata sp. 1</i> , <i>Cryptalaria pectinata</i> , <i>Nemertesia geniculata</i> , <i>Zygophylax convallarius</i>	6/11/2004	30.5016	-79.6531	593	9.9	0.4	
JSLI-04-4701-front bucket 2	<i>Sertularella gayi robusta</i>	6/19/2004	30.4827	-79.6418	647	7.4	1.0	
JSLI-04-4701-bucket 3	<i>Acryptalaria conferta</i> , <i>Aglaophenopsis hirsuta</i>	6/19/2004	30.4824	-79.6408	669	7.4	0.3-0.4	
JSLI-05-4907-basket	<i>Aglaophenopsis hirsuta</i> , <i>Cryptalaria pectinata</i> , <i>Nemertesia</i> <i>geniculata</i> , <i>Zygophylax convallarius</i>	11/1/2005	30.8008	-79.6420	538	7.9	0.1	
JSLI-05-4907-bucket 1	<i>Cladocarpus paradiseus</i>	11/1/2005	30.8033	-79.6458	541	8.1	n/a	
JSLI-05-4907-bucket 9	<i>Aglaophenopsis hirsuta</i> , <i>Carymarpha sp.</i> , <i>Schizatricha profunda</i> , <i>Sertularella gayi robusta</i>	11/1/2005	30.8023	-79.6401	523	7.8	0.1	
JSLI-05-4907-bucket 10	<i>Eudendrium eximium</i>	11/1/2005	30.8023	-79.6401	523	7.8	0.1	
JSLI-05-4907-bucket 12	<i>Aglaophenopsis hirsuta</i> , <i>Athecata sp. 2</i> , <i>Eudendrium distichum</i> , <i>Eudendrium eximium Stegopama plicatile</i>	11/1/2005	30.8007	-79.6421	534	8.0	0.1	
JSLI-05-4907-front tray	<i>Cladocarpus paradiseus</i> , <i>Nemertesia geniculata</i>	11/1/2005	30.8005	-79.6421	535	8.0	0.1	
JSLI-05-4908-bucket 1	<i>Aglaophenopsis hirsuta</i> , <i>Eudendrium distichum</i> , <i>Eudendrium sp.</i> , <i>Halopteris geminata</i> , <i>Nemertesia geniculata</i> , <i>Plumularia cf.</i> <i>attenuata</i> , <i>Sertularella gayi robusta</i> , <i>Zygophylax convallarius</i>	11/1/2005	30.5191	-79.6597	585	7.6	0.3-0.4	
JSLI-05-4908-bucket 9	<i>Eudendrium sp.</i> , <i>Halopteris geminata</i> , <i>Kirchenpaueriidae sp.</i> , <i>Zygophylax convallarius</i>	11/1/2005	30.5186	-79.6603	590	7.3	0.3-0.4	
JSLI-05-4908-bucket 10	<i>Athecata sp. 1</i> , <i>Athecata sp. 2</i> , <i>Cladocarpus paradiseus</i> , <i>Nemertesia</i> <i>geniculata</i> , <i>Rosalinda sp.</i>	11/1/2005	30.5192	-79.6586	595	7.4	0.3-0.4	
JSLI-05-4908-bucket 11	<i>Aglaophenopsis hirsuta</i> , <i>Plumularia cf. attenuata</i>	11/1/2005	30.5201	-79.6577	621	7.4	0.3-0.4	
<i>Cape Canaveral</i>								
JSLI-04-4681- front basket (port)	<i>Cladocarpus carinatus</i>	6/9/2004	28.7931	-79.6210	761	6.8	0.4-0.5	
JSLI-04-4681- front basket (starboard)	<i>Halecium beanii</i> , <i>Lafaea coalescens</i>	6/9/2004	28.7940	-79.6214	737	6.7	0.4-0.5	
JSLI-04-4682-bucket 1	<i>Plumularia cf. attenuata</i>	6/9/2004	28.7962	-79.6210	770	n/a	0.4	
JSLI-04-4702-basket	<i>Aglaophenopsis hirsuta</i> , <i>Cladocarpus paradiseus</i>	6/20/2004	28.7944	-79.6230	714	6.5	0.3-0.4	
JSLI-04-4703-front bucket 1	<i>Zygophylax convallarius</i>	6/20/2004	28.7771	-79.6161	748	6.7	0.3-0.4	
JSLI-04-4705-bucket 1	<i>Cladocarpus paradiseus</i>	6/21/2004	28.0393	-79.6130	686	6.3	1	
JSLI-04-4705-bucket 2	<i>Zygophylax convallarius</i>	6/21/2004	28.0393	-79.6130	686	6.3	n/a	

^a Three samples were collected into the JSL basket during this dive. The hydroid collected detached from one of these samples, but it was impossible to determine which one. Depth was similar for all three samples. The samples were fairly close together, and the location and time are given for the first sample.

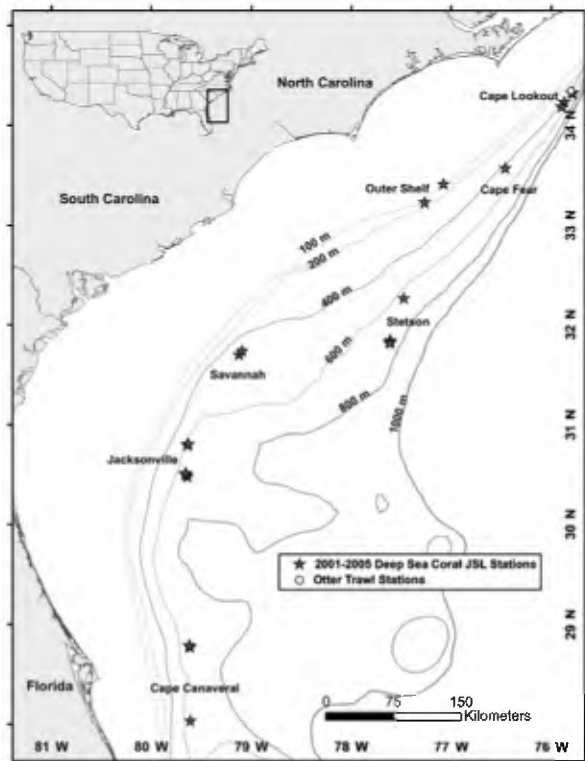


Fig. 1. Stations containing the hydroids examined in this study. Note that overlapping dive stations are simply artefacts of plotting these stations to show the latitudinal range of this study, from Cape Lookout to Cape Canaveral.

intact. Individual hydroid colonies were then transferred to separate vials and stored in 95% ethanol. Hydroids were identified using a Zeiss Stemi 2000 stereoscope fitted with an AxioCam MRC5 digital camera. Digital photographs of whole animals and characteristic features were taken for each species. Voucher specimens of each species were deposited at the National Museum of Natural History, Smithsonian Institution (see Appendix).

2.3. Analyses

All species recorded from each sample were compiled into the presence/absence format in PRIMER (version 6, Clarke and Gorley, 2006). A species accumulation curve was generated using the Species–Area Plot function that chronologically ordered samples. Specimens with fully intact reproductive structures (gonophores) were noted.

The local occurrence of species was reported by recording all species found on a given substratum, which included live scleractinian coral (denuded polyp internodes on live colonies), other invertebrate hosts, coral rubble or dead coral fragments, rock, or unknown sources.

Regional occurrence was examined by cross-referencing published distribution records of each species with latitudinal and depth records generated from the present study of deep-water coral habitats off the SEUS. Biogeo-

graphic affinities were examined by comparing published accounts of deep-water hydroids (excluding styliasterids) from adjacent areas in the western North Atlantic (Fraser, 1944; Vervoort, 1968, 1972; Bogle, 1984; Calder, 1988, 1991a, 1993b, 1997a, b, 1998; Marques and Calder, 2000; Calder and Cairns, in press) with those collected during the present study. For our purposes, “deep-water” hydroids refer to bathyal species following Calder’s (1998) ordination (i.e., 200–2000 m), which revealed a grouping of species with wide bathymetric ranges within this bathyal zone. Thus, we have excluded the samples from the North Carolina outer shelf (Table 1) from the biogeographic analysis as these were obtained <200 m. Five regions were delineated *a priori* roughly following Calder’s (1992) ordination of the shallow-water hydroid fauna of the western Atlantic: (1) Nova Scotia to Cape Hatteras, (2) SEUS (Cape Hatteras to southern Florida, excluding the Florida Keys), (3) Bermuda, (4) Caribbean/West Indies, and (5) Straits of Florida (including the Dry Tortugas and the Florida Keys) to the Bahamas. Species lists were compiled for each region. The Gulf of Mexico was not included in our analysis as its bathyal hydroid fauna is not well known (Fraser, 1944; Calder and Cairns, in press), although many species exist in the deeper neritic (50–200 m) waters of coral banks in the northwestern region of the Gulf of Mexico (Defenbaugh, 1974; Rezak et al., 1985) and the southeastern region (Calder and Cairns, in press). We delineated the southeast as region (5), above. All taxonomy and synonymies followed those of Calder (1988, 1991a, 1993b, 1997a), Peña Cantero and Vervoort (1999), Svoboda and Stepanjants (2001), Bouillon et al. (2004) and Ramil and Vervoort (2006). A group-averaged cluster plot was generated from the Bary–Curtis similarities between regions, estimated from the presence–absence data in PRIMER.

3. Results

3.1. Richness

Thirty-six taxa, belonging to 12 families and 23 genera, were identified from the collections (Table 1). Athecata sp. 1 was excluded from further analysis because of its close resemblance to *Eudendrium fruticosum*; therefore, only 35 species were actually recognized. Future revision of the genus *Eudendrium* will likely place the eudendriids from the present study in synonymy with other known members of this genus (A. Marques, personal communication). The number of species steadily increased chronologically, with approximately one species recorded after each successive dive (Fig. 2). The species accumulation curve illustrated a progressive increase in stepwise fashion to sample 28; after 29 samples, the curve climbed dramatically without approaching an asymptote.

Nearly one-quarter (8/35) of the hydroid species were anthoathecates, a group of hydroids united by the almost universal absence of protective perisarc around the hydranths and gonophores. The JSL submersibles, therefore, have proven valuable since hydroids collected by submersibles are relatively pristine and delicate structures

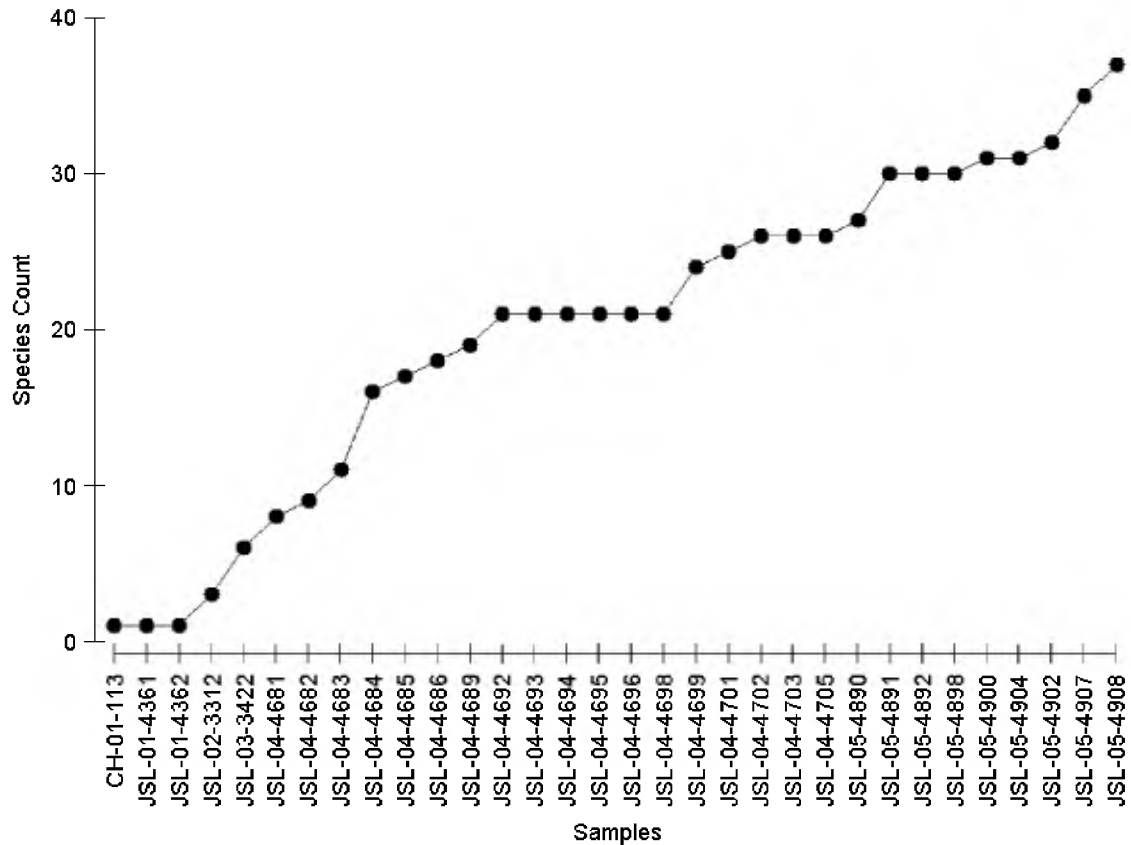


Fig. 2. Species accumulation curve for the number of new hydroid species encountered on SEUS deep-water coral habitats from samples chronologically ordered (2001–2005).

remain undamaged. Thus, species identification can be made with greater certainty.

Two of the species may be new to science. The first, a single encrusting colony of *Rosalinda* sp., was attached basally to a single large colony of the hydroid *Cladocarpus paradiseus* collected at 595 m depth on the Jacksonville lithoherms. Although sexually reproductive, the gonophore contents of the *Rosalinda* sp. could not be discerned, and thus the presence of a medusa versus a planula stage could not be determined. Because crucial information regarding the life cycle is lacking, the specimen cannot be described as a new *Rosalinda* species (N. Boero and C. Gravili, personal communication), and may be conspecific with *Rosalinda incrustans*, found in the northern Gulf of Mexico (Calder and Cairns, in press). Nevertheless, the family Rosalindidae is recorded here for the first time in the SEUS and for the first time on another hydroid. The second possible new species, *Corymorpha* sp., was collected at 523 m, also on the Jacksonville lithoherms. Two specimens of *Corymorpha* sp. were wrapped around a single dead fragment of the scleractinian coral *Enllopsammia profunda*. The developing medusae within the gonophores were not mature, and precluded the assignment of a new species (A. Svoboda, personal communication). Although unlikely, *Corymorpha* sp. could be either of two shallow-water species: *Corymorpha pendula*, a boreal species inhabiting sandy to muddy bottoms from Atlantic

Canada to Massachusetts (Fraser, 1944; Calder, 1975) or *Corymorpha januarii*, a species otherwise endemic to south Brazil (Da Silveira and Migotto, 1992).

Eleven species recorded in the present study had not been collected since the late 19th to approximately the mid-20th century: *Eudendrium distichum*, *Eudendrium exiguum*, *E. fruticosum*, *Holecium macrocepholum*, *Halopteris geminata*, *Nemertesia geniculata*, *Plumularia* cf. *attenuata*, *Schizotricha profundo*, *Calvinia mirabilis*, *Diplopteroides grandis*, and *Cladocarpus flexilis*.

3.2. Reproduction

Over half of the species (19/35) collected between June and November were sexually reproductive, with slightly more reproductive specimens collected during autumn (October–November; Table 4). Only four of the 35 species (*Corymorpha* sp., *Clytia* sp., Campanulinidae sp., and *Stegopoma plicatile*) liberate medusae as part of their life cycles (although this is implicitly assumed for the latter two taxa), while the remaining species possess fixed gonophores that release planula larvae.

Several male and female specimens of *H. macrocepholum* were collected with intact gonophores. However, the gonophores on males appeared more sigmoidal in our specimens, while somewhat truncated in the type

Table 2

Latitudinal and depth ranges of hydroids identified to species level found on SEUS deep-water reefs

	Latitudinal range in western North Atlantic	Bathymetric range in western North Atlantic	Source(s)
<i>Eudendrium distichum</i>	Jacksonville lithoherms* to Florida Keys	529*–585 m*	Fraser (1944)
<i>Eudendrium exiguum</i>	Cape Lookout* to Florida Keys	294–387 m*	Fraser (1944)
<i>Eudendrium eximium</i>	Jacksonville lithoherms* to Florida Keys	15–550 m*	Fraser (1944)
<i>Eudendrium fruticosum</i>	Savannah Banks* to Key West	405–500 m*	Fraser (1944)
<i>Campanularia hincksii</i>	Nova Scotia to Florida	15–110 m	Fraser (1944)
<i>Campanularia macroscypha</i>	Cape Lookout* to Yucatan Peninsula	84–1119 m	Fraser (1944)
<i>Stegapoma plicatile</i>	Atlantic Canada to Jacksonville lithoherms*	18–1939 m	Fraser (1944); Calder (1997b)
<i>Halecium beanii</i>	New Brunswick to Cape Canaveral*	9–737 or 761 m*	Fraser (1944)
<i>Halecium macrocephalum</i>	Delaware Bay to West Indies	Typically bathyal, down to 670 m*	Fraser (1944); Vervoort (1972)
<i>Acryptolaria conferta</i>	Nantucket to Antigua	Typically neritic-abyssal, from ~70 to 2394 m	Fraser (1944); Calder (1997b)
<i>Cryptolaria pectinata</i>	Cape Fear* to West Indies	82*–668 m*	Fraser (1944)
<i>Lafoea coalescens</i>	Bermuda to Florida Keys	60–737 or 761 m*	Fraser (1944); Calder (1998)
<i>Zygophylax convallarius</i>	Cape Lookout* to West Indies	139–748 m*	Fraser (1944); Vervoort (1972)
<i>Sertularella catena</i>	Bermuda to Puerto Rico	660–713 m	Fraser (1944); Calder (1998)
<i>Sertularella gayi robusta</i>	Nantucket to West Indies	29–958 m	Fraser (1944); Vervoort (1972)
<i>Nemertesia geniculata</i>	Cape Lookout* to Florida	499–805 m	Fraser (1944)
<i>Plumularia cf. attenuata</i>	Cape Lookout* to West Indies	192–1053 m	Fraser (1944)
<i>Schizotricha profunda</i>	Georgia to Jacksonville lithoherms*	534–1320 m	Fraser (1944)
<i>Calvinia mirabilis</i>	Georgia to Florida	457–805 m	Fraser (1944)
<i>Diplapteraides grandis</i>	Stetson* to Florida	750–882 m	Fraser (1944)
<i>Halapteris geminata</i>	Savannah Banks* to West Indies	228–1056 m	Fraser (1944)
<i>Aglaophenopsis hirsuta</i>	Cape Fear* to West Indies	413–805 m	Fraser (1944); Vervoort (1972)
<i>Cladocarpus carinatus</i>	Georgia to Dry Tortugas	750–1320 m	Fraser (1944)
<i>Cladocarpus flexilis</i>	Nova Scotia to North Carolina, Gulf of Mexico	49–670 m*	Fraser (1944)
<i>Cladocarpus paradiseus</i>	Georgia to West Indies	183–805 m	Fraser (1944)
<i>Cladocarpus sigma</i>	Chesapeake Bay to Cuba	66–1572 m	Fraser (1944)

The symbol "*" refers to a new record for the western North Atlantic.

specimen described by Allman (1877). In all other aspects, our specimens are similar to those of Allman. Given the pristine condition of the gonophores and the importance of a detailed morphological description of reproductive structures, these new specimens from deep-water coral habitats off the SEUS will thus permit a future species re-description for *H. macrocephalum* (W. Vervoort, personal communication).

3.3. Local occurrence

3.3.1. Live scleractinian coral (n = 7)

Only five species, *E. fruticosum*, *Zygophylax convallarius*, *Sertularella gayi robusta*, *N. geniculata* and *P. cf. attenuata* (Table 3), were observed on live scleractinians, specifically *Lophelia*. Calcified coral skeleton was sometimes observed overgrowing the hydrorhiza (i.e., root system; Fig. 3) of hydroids. Assuming that *Athecata* sp. 1 was possibly *E. fruticosum*, then no species occurred exclusively on live coral.

3.3.2. Dead scleractinian coral (n = 25)

A total of 25 species was recorded on dead scleractinian coral substrata (Table 3). These included larger



Fig. 3. Colony of *Eudendrium fruticosum* illustrating live coral overgrowth of the basal hydrorhiza attachment.

(>10 cm) species such as *S. gayi robusta*, *C. paradiseus* and *Aglaophenopsis hirsuta*, as well as smaller (<1 cm) species such as *Campanularia macroscypha* and *Clytia* sp. Ten species were found exclusively on dead corals, including *E. exiguum*, *Eudendrium eximium*, *Corymorpha* sp., *Clytia* sp., *Lafoea coalescens*, *Kirchenpaueriidae* sp., *S. profunda*, *D. grandis*, *Cladocarpus carinatus* and *C. flexilis*.



Fig. 4. Dead antipatharian host for large fertile plumulariid colonies and other smaller hydroid species. The antipatharian was collected dead (Stetson Banks, JSLI 4904, 671 m; photographed in ship-board aquarium).

3.3.3. Other animal hosts ($n = 15$)

Eighteen species of hydroids colonized fauna other than scleractinians (Table 3). Other hydroids, sponges, barnacles, bryozoans, gorgonians and antipatharians (Fig. 4) supported numerous large hydroids (*E. eximium*, *S. gayi robusta*, *A. hirsuta*, *C. carinatus* and *C. paradiseus*) that were often themselves colonized by many smaller species (e.g., *Athecata* sp. 2, *Campanularia hincksii*, *E. distichum*, *Halecium beanii*, *H. geminata*, *N. geniculata*, *S. plicatile*, *Rosalinda* sp.) and small colonies of *Z. convallarius*. Four taxa, *Rosalinda* sp., *C. hincksii*, *Campanulinidae* sp. and *C. mirabilis*, were found exclusively on these other animal hosts, and not on scleractinians.

3.3.4. Rock ($n = 2$)

Two species, *Sertularella* sp. and a small colony of *C. paradiseus*, were observed on rock substrata (Table 3). Only *Sertularella* sp. was found exclusively on this substratum.

3.4. Regional occurrence

Characteristic species of the SEUS deep-water coral habitats (i.e., those occurred in more than half of the stations) were *H. macrocephalum*, *Z. convallarius*, *N. geniculata*, *P. cf. attenuata* and *A. hirsuta* (Table 1). The plumulariids *N. geniculata* and *S. profunda* are recorded here for the first time since Nutting's original descriptions from specimens collected from the coast of Georgia, USA (Nutting, 1900).

Ten species are recorded in the SEUS for the first time (Table 2), including *E. distichum*, *E. exiguum*, *E. eximium*, *E. fruticosum*, *H. beanii*, *Cryptolaria pectinata*, *L. coalescens*, *Sertularella catena*, and *C. flexilis*. *S. plicatile*, a bipolar species, is recorded for the first time in the south of Cape Hatteras in the western North Atlantic.

Twelve species were recorded northward of their known latitudinal ranges in the western Atlantic (Table 2):

Table 3

Hydroid occurrence across various substrata in the SEUS deep-water coral habitats (n/a refers to an unknown substratum i.e., the hydroid became detached)

Species	Live coral	Dead coral	Other fauna	Rock	n/a
<i>Athecata</i> sp. 2		X	X		
<i>Eudendrium</i> sp.		X			X
<i>Eudendrium distichum</i>		X	X		
<i>Eudendrium exiguum</i>		X			
<i>Eudendrium eximium</i>		X			
<i>Eudendrium fruticosum</i>	X				
<i>Corymarpha</i> sp.		X			
<i>Rosalinda</i> sp.			X		
<i>Campanularia hincksii</i>			X		
<i>Campanularia macroscypha</i>		X	X		
<i>Clytia</i> sp.		X			
<i>Campanulinidae</i> sp.			X		
<i>Stegapama plicatile</i>		X	X		
<i>Halecium macrocephalum</i>		X	X		X
<i>Halecium beanii</i>		X	X		X
<i>Acryptalaria conferta</i>		X	X		
<i>Cryptolaria pectinata</i>		X	X		X
<i>Lafaea coalescens</i>		X			
<i>Zygophylax convallarius</i>	X	X	X		X
<i>Sertulariidae</i> sp.					X
<i>Sertularella</i> sp.				X	
<i>Sertularella catena</i>					X
<i>Sertularella gayi robusta</i>	X	X	X		
<i>Kirchenpaueriidae</i> sp.		X			
<i>Nemertesia geniculata</i>	X	X	X		X
<i>Plumularia cf. attenuata</i>	X	X			X
<i>Schizatricha profunda</i>		X			
<i>Calvinia mirabilis</i>			X		
<i>Diplopteraides grandis</i>		X			
<i>Halopteris geminata</i>		X	X		
<i>Aglaaphenopsis hirsuta</i>		X	X		X
<i>Cladacarpus carinatus</i>		X			
<i>Cladacarpus flexilis</i>		X			
<i>Cladacarpus paradiseus</i>		X	X	X	X
<i>Cladacarpus sigma</i>					X
Total number of species	5	25	18	2	12

E. distichum, *E. exiguum*, *E. eximium*, *E. fruticosum*, *C. macroscypha*, *C. pectinata*, *Z. convallarius*, *N. geniculata*, *P. cf. attenuata*, *D. grandis*, *H. geminata* and *A. hirsuta*. Known geographic distributions of *S. plicatile*, *H. beanii* and *S. profunda* in the western North Atlantic were extended southwards to include Florida (Table 2). Only six of the species reported here (*C. hincksii*, *S. plicatile*, *H. beanii*, *C. pectinata*, *S. gayi robusta* and *Cladacarpus sigma*) have more cosmopolitan distributions and occur outside the western Atlantic. A single Pacific record of *H. macrocephalum* off the coast of California (Fraser, 1948) is considered doubtful but awaits confirmation (W. Vervoort, personal communication). With the possible exception of the two potentially new species, no species was endemic to the SEUS coral habitats.

All species of hydroids examined in this study typically occur in deep-neritic to bathyal habitats (i.e., below 200 m). However, *E. distichum*, *E. exiguum*, *E. eximium*, *E. fruticosum*, *H. beanii*, *H. macrocephalum*, *C. pectinata*, *L. coalescens*, *Z. convallarius*, and *C. flexilis* were collected at depths deeper than their previously reported bathymetric

ranges. *E. distichum* and *C. pectinata* were collected at depths more shallow than those previously reported (Table 2). Thus, from the taxa identified to species, 69% (18/26) represent new range records (latitude, depth or both).

3.5. Biogeography

Data pooled from published accounts and the present study revealed 171 deep-water (200–2000 m) hydroid species ranging from Atlantic Canada to the Caribbean/West Indies region. The richest deep-water hydroid assemblages occur in the Straits of Florida/Bahamas region (64 species) and the Caribbean/West Indies (51 species). Other deep-water habitats off the SEUS and the NE USA/Canada were similarly diverse with 47 and 48 species of hydroids, respectively. The deep-water hydroid fauna of Bermuda was less speciose with 20 species. The SEUS deep-water coral habitats, therefore, support relatively rich (35 species) hydroid assemblages, considering

that our collections contained hydroids collected incidentally during sampling of deep-water corals and associated substrata.

The hydroid assemblages from deep-water coral habitats off the SEUS were mostly similar to those from other deep-water habitats off the SEUS (45% similarity, 17 species in common; Fig. 5). Hydroids from the SEUS deep-water coral habitats were also similar to the Straits of Florida/Bahamas assemblage (14 shared species) and the Caribbean/West Indies assemblage (8 shared species). The SEUS reef assemblage was less similar to those from NE USA/Canada (six shared species) and Bermuda (four shared species).

4. Discussion

4.1. Hydroid richness in deep-water coral habitats

Deep-water corals were discovered off the SEUS in the late 1800s, and since that time several deep-water reefs

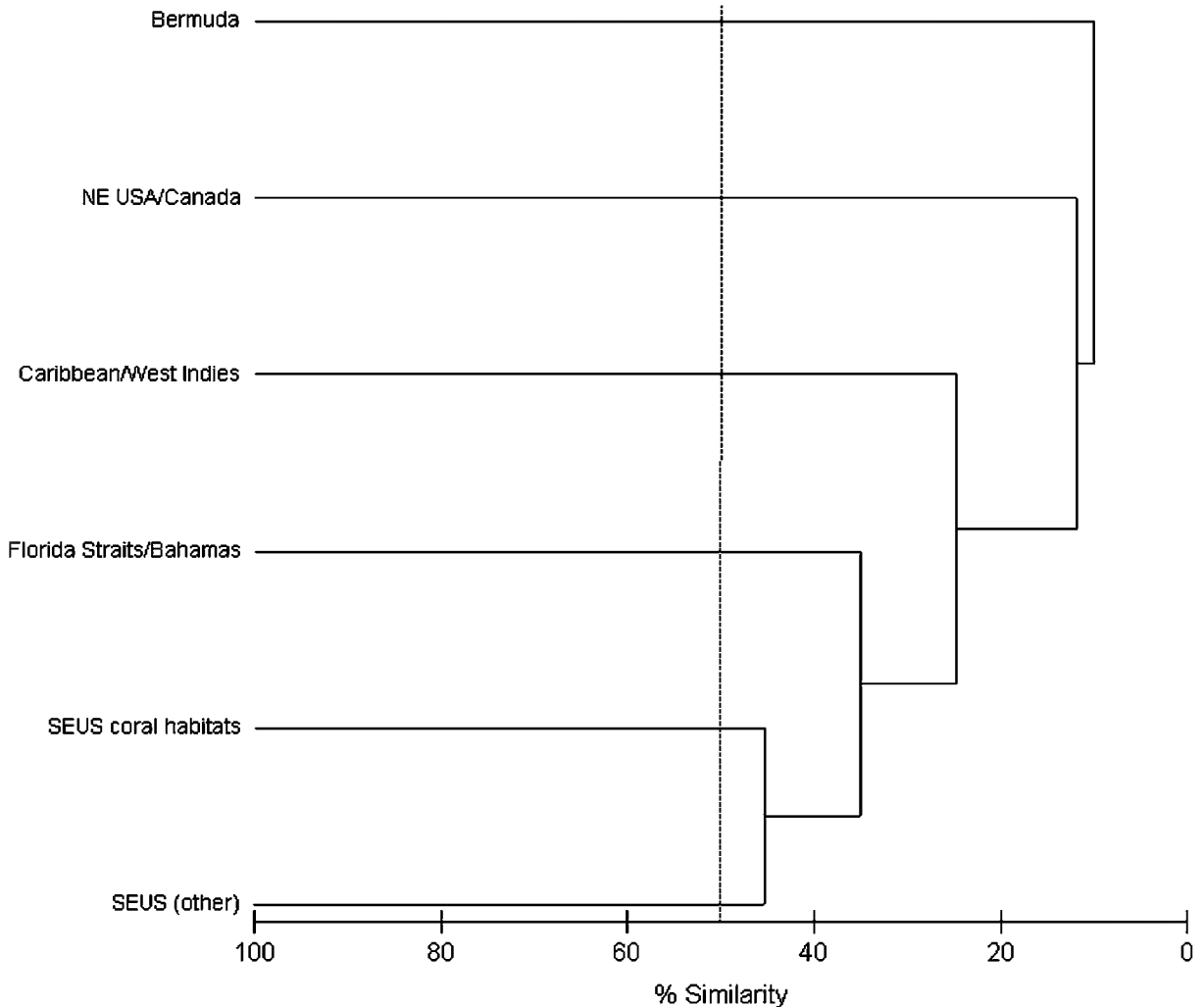


Fig. 5. Similarity of deep-water (200–2000 m) hydroid assemblages across regions adjacent to the SEUS coral habitats. The vertical line delineates 50% similarity.

have been characterized geologically (e.g., Stetson et al., 1962; Ayers and Pilkey, 1981; Paull et al., 2000; Popenoe and Manheim, 2001). Biological data on these reefs have been lacking, but recent studies (Messing et al., 1990; Reed et al., 2006; Ross and Quattrini, 2007) indicate that these habitats support rich invertebrate and ichthyofaunal assemblages. The present study shows that a rich hydroid assemblage is found among the SEUS deep-water coral habitats, and that much basic natural history information, such as reproductive timing and modes, still remains to be gleaned from these samples.

Similar *Lophelia* habitats in the NE Atlantic harbor more than 1300 species of fishes and invertebrates (Roberts et al., 2006), including new hydroid species, genera and families (e.g., Henry and Roberts, 2007; Moura et al., 2007). *Lophelia* habitats in the NE Atlantic, ranging from cooler waters of Norway to warmer temperate waters of Portugal, are better known faunistically: 71 hydroid species (excluding stylasterids) have been recorded (from Browne, 1907; Dons, 1944; Le Danois, 1948; Burdon-Jones and Tambs-Lyche, 1960; Jensen and Frederiksen, 1992; Mortensen and Fosså, 2006; Henry and Roberts, 2007; Moura et al., 2007), 51 of which are ampho-Atlantic species (L.-A. Henry, unpublished data). Seven of these 51 species were also found in our study from the SEUS. Because hydroid species are generally widespread between North America and the western European shelf (Medel and López-González, 1998), we can expect further studies of hydroids across western Atlantic *Lophelia* habitats to lead to a higher proportion of ampho-Atlantic species.

Generally, hydroid species richness decreases with increasing depth (Calder, 1998; Genzano and Zamponi, 2003; Altuna, 2007). However, increased exploration, collection, taxonomic effort and genetic analyses in deep-water habitats of the North Atlantic have revealed many hydroid species, some cryptic or new to science, particularly on seamounts and other coral habitats (e.g.,

Vervoort, 1966; Ramil and Vervoort, 1992; Calder, 1993b, 1996, 1997b, 1998; Calder and Vervoort, 1998; Henry, 2001; Henry and Roberts, 2007; Moura et al., 2007, 2008). Such hydroid discoveries are unlikely to refute the overall trend of decreasing hydroid richness with depth, but they will moderate what appears to be an otherwise steep decline in species richness and point to the importance of deep-water coral habitats in enhancing biodiversity.

Hydroid richness from the SEUS deep-water coral habitats seems to rival that observed on shallow-water coral reefs in the western North Atlantic. For example, 43 hydroid species were reported from tropical reefs of Carrie Bow Cay, Belize (Spracklin, 1982; Puce et al., 2005), while 11 hydroid species inhabit the coral reefs of Bermuda (Calder, 1993a). Although these comparisons highlight the potential richness of deep-water coral habitats, such comparisons should be made cautiously since quantitative analyses are hampered by a lack of standardization in sampling methodology (e.g., aerial extent sampled versus biomass/area of coral analyzed).

4.2. Reproduction in deep-water hydroids

Knowledge of species' life histories and the collection of fertile individuals provided us with some preliminary information regarding the reproductive ecology of hydroids from deep-water coral habitats of the SEUS. Most of the hydroids (30/35 species) collected here release planula larvae, instead of medusae, during their sexually reproductive stage. Planulae were also the predominant dispersal mode used by hydroids from deep-water seamounts off Bermuda (Calder, 2000).

Our specimens exhibited slightly more reproductive maturity in samples collected from autumn months (Table 4). But, since sampling did not occur year round, we cannot speculate further as to reproductive timing in hydroids from the SEUS deep-water coral habitats.

Table 4
Reproductive timing of sexually mature hydroids collected from deep-water coral habitats in the SEUS

Species	June–July	August–September	October–November
<i>Eudendrium distichum</i>			●
<i>E. exiguum</i>			●
<i>E. eximium</i>	●		
<i>E. fruticosum</i>			●
<i>Carymarpha</i> sp.			●
<i>Rosalinda</i> sp.			●
<i>Halecium beanii</i>	●	○	○
<i>H. macrocephalum</i>	●	○	
<i>Cryptolaria pectinata</i>		●	○
<i>Zygophylax convallarius</i>	○		●
<i>Sertularella gayi robusta</i>	○		●
<i>Nemertesia geniculata</i>	●		●
<i>Plumularia</i> cf. <i>attenuata</i>	●		○
<i>Calvinia mirabilis</i>	●		
<i>Halopteris geminata</i>	●		●
<i>Aglaophenopsis hirsuta</i>	●		●
<i>Cladocarpus carinatus</i>	●		
<i>C. paradiseus</i>	○		●
<i>C. sigma</i>	○	●	

The symbol "●" denotes a mature specimen, while the symbol "○" refers to a specimen that was immature.

Seasonal changes in water temperature control reproductive timing in shallow-water coastal hydroids of the mid-SEUS (Calder, 1990), but temperature variability on the SEUS deep-water coral habitats is not well known. Alternatively, reproductive timing may track variation in other environmental factors, such as food supply. Organic flux is temporally variable over other deep-water coral habitats (Kiriakoulakis et al., 2007), and appears to be critical in the life cycle of hydromedusae in Mediterranean canyon habitats (Gili et al., 2000). Continuous monitoring of physico-chemical properties in the SEUS deep-water coral habitats is required before we can understand reproductive timing in hydroids and other fauna inhabiting these environments.

4.3. Local occurrence of hydroids

Since most hydroids are hard substratum generalists (Gili and Hughes, 1995), no substratum affinities were expected. However, the local occurrence of hydroids on various substrata is controlled by a combination of biological, physical and stochastic factors (Calder, 1991b). Dead scleractinian and gorgonian corals often support the most diverse hydroid assemblages in shallow- and deep-water coral habitats (Reed et al., 1982; Spracklin, 1982; Jensen and Frederiksen, 1992; Buhl-Mortensen and Mortensen, 2005; Mortensen and Fosså, 2006) as these represent hard inert substrata that continuously become available during the life cycle of a deep-water reef (Roberts et al., 2006). We demonstrated that other animal hosts also harbor rich hydroid assemblages, and thus their availability and diversity is intimately linked to hydroid diversity in deep-water coral habitats. Few species occurred on live corals in our study, and this may suggest that deep-water corals possess anti-fouling mechanisms, such as mucus secretion, that effectively restrict settlement to polyp internodes. Those hydroids that did colonize live corals risked being at least partially overgrown by the encroaching coral skeleton (e.g., Fig. 3).

4.4. Regional occurrence and biogeographical affinities of hydroids

Our data extend the latitudinal and depth ranges of 69% of the species identified in this study, with most of these hydroid species typically bathyal in distribution. Hydroids from the SEUS deep-water coral habitats were mostly similar to hydroids from adjacent bathyal areas of the SEUS and in the sub-tropical/tropical western North Atlantic in general (Fig. 5). Calder (1992) also noted high similarity between hydroid assemblages from deep neritic waters offshore from the SEUS and those from the tropical western North Atlantic. In both cases, the offshore hydroid fauna of the SEUS and those in the sub-tropical/tropical Atlantic appear unified by the effects of the Gulf Stream system.

The sub-tropical/tropical affinity of the SEUS hydroids is probably facilitated by present-day south to north larval dispersal via the Gulf Stream (including the Loop Current and Florida Current). Additionally, this affinity may be

explained by historical oceanographic events. Western boundary currents including the Florida Current/Gulf Stream that initiated and intensified during the middle Miocene to early Pleistocene may have transported a suite of hydroid species northward from the Caribbean/West Indian region where deep-water hydroids are very diverse (Briggs, 2005; Vermeij, 2005). Successful Caribbean/West Indian “invaders” should exhibit traits selected to improve their fitness in highly competitive habitats such as tropical coral reefs, making them highly likely to successfully invade new areas where selection pressure is not as high (Vermeij, 2005). For hydroids, such traits could include the presence of stinging nematocysts bundled into nematophores found all over the colony. Members of the superfamily Plumularioidea characteristically have nematophores, and are particularly rich in the tropical Caribbean/West Indian region (Fraser, 1944, 1946). Thirty-four percent (12/35) of hydroids collected in the present study were plumularioids, a speciose taxon comprising 67 deep-water (200–2000 m) species in the western North Atlantic. Thus, the defensive/competitive capabilities of plumularioids may have allowed them to successfully invade deep-waters of the SEUS from tropical waters during the early Pleistocene.

5. Conclusions

This study revealed rich hydroid assemblages with sub-tropical/tropical affinities inhabiting deep-water coral habitats off the SEUS. This richness, and the potential to find many more ampho-Atlantic species and undescribed species, suggests that further examination of the biodiversity and biogeography of hydroids and other epifauna of the SEUS deep-water coral habitats is warranted. Such investigations will lead to an improved understanding of the connectivity of deep-water coral habitats within the North Atlantic, but will require sustained resources and particularly the use of more sophisticated sampling technology, such as submersibles and ROVs, and more rigorous standardized methods to systematically collect fauna.

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Appendix

List of cataloged specimens of hydroids collected during this study and deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

USNM Cat. no.	Species
1110641	<i>Halecium macrocephalum</i>
1110798	<i>Acryptolaria conferta</i>
1110799	<i>Lofoea coalescens</i>
1110803	<i>Clodocarpus sigma</i>
1110804	<i>Calvinia mirabilis</i>
1110805	<i>Halecium macrocephalum</i>
1110806	<i>Clytia</i> sp.
1110807	<i>Sertularella catena</i>
1110808	<i>Campanularia macroscypha</i>
1110809	<i>Clodocarpus flexilis</i>
1110815	<i>Halecium macrocephalum</i>
1110816	<i>Diplopteroides grandis</i>
1110822	<i>Eudendrium exiguum</i>
1110823	<i>Cryptolaria pectinato</i>
1110824	<i>Clodocarpus paradiseus</i>
1110825	<i>Corymorpha</i> sp.
1110826	Athecata sp. 1
1110827	Athecata sp. 2
1110860	<i>Eudendrium</i> sp.
1110861	Kirchenpaueriidae sp.
1110862	Sertulariidae sp. 1
1111140	<i>Schizotricho profundo</i>
1111142	<i>Agloophenopsis hirsuta</i>
1111143	<i>Sertularella goyi robusta</i>
1111144	<i>Agloophenopsis hirsuta</i>
1111145	<i>Stegopomo plicatile</i>
1111146	<i>Eudendrium eximium</i>
1111147	<i>Nemertesio geniculato</i>
1111148	<i>Sertularella</i> sp.
1111149	<i>Sertularella goyi robusta</i>
1111150	<i>Rosalinda</i> sp.
1111151	<i>Haploteris geminata</i>
1111152	<i>Agloophenopsis hirsuta</i>
1111153	<i>Zygophylax convallorius</i>
1111154	<i>Eudendrium distichum</i>
1111155	<i>Plumularia</i> cf. <i>attenuata</i>
1111156	<i>Sertularella goyi robusta</i>
1111157	<i>Clodocarpus carinatus</i>
1111158	<i>Halecium beanii</i>
1111159	<i>Clodocarpus paradiseus</i>
1111160	<i>Rosalinda</i> sp.

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