PERGAMON

Deep-Sea Research I 45 (1998) 1843–1860

DEEP-SEA RESEARCH
PART I

Hydroid diversity and species composition along a gradient from shallow waters to deep sea around Bermuda

Dale R. Calder*

Department of Zoology, University of Toronto, Toronto, Ont., Canada M5S 3G5

Received 5 February 1997; received in revised form 16 March 1998; accepted 24 May 1998

Abstract

Hydroids were examined in 88 qualitative samples from a depth range of 0–4550 m in the Bermuda area. Of 89 species represented overall, 54 were present in samples from 0 to 25 m. Thirty-one of these 54 taxa were found only within that bathymetric zone. Hydroid species numbers remained relatively high (36) in collections from shallow neritic bottoms (26–100 m), although the faunal assemblage of the zone was quite distinct from that of overlying waters. Numbers of species dropped to 23 in the 101–200 m range and declined further from 21 to three in samples from the 201–500 and 501–1000 m zones. Only seven species (*Tubularia* sp., *Eudendrium* sp. 2, *Egmundella superba*, *Opercularella* sp., *Acryptolaria longitheca*, *Filellum serratum*, *Lafoea coalescens*) were collected at depths exceeding 1000 m in the study area. Mean numbers of species per sample likewise indicated that the hydroid fauna was richest in shallow waters (< 100 m) of the Bermuda Platform and poorest in the deep sea, and that changes in diversity along the bathymetric gradient were greatest over the upper 500 m. From submersible observations and collections between 730 and 3550 m, hydroids appeared to be scarce at great depths on the slope of the Bermuda Pedestal, even where hard substrates (rocky outcrops, calcareous rubble, megafaunal invertebrates) were present. *Thecocodium brieni*, an infrequently collected anthoathecate species, is reported from Bermuda and the western Atlantic for the first time. © 1998 Elsevier Science Ltd. All rights reserved.

1. Introduction

One of the most imposing ecological gradients on earth is that extending from the surface to the abyss of the ocean (Gage and Tyler, 1991). Changes in species

* Correspondence address: Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ont., Canada M5S 2C6. Fax: 001 416 586 5863; e-mail: dalec@rom.on.ca.

PII: S0967-0637(98)00044-2

composition of benthos may be pronounced over relatively short distances with depth (see Vinogradova, 1962; Sanders and Hessler, 1969; Menzies *et al*., 1973; Hecker, 1990), particularly in comparison with certain horizontal marine gradients (e.g. latitudinal and estuarine ecoclines). Vertical zonation patterns of intertidal biota and the factors regulating distributional limits of species there (Mathieson and Nienhuis, 1991) have been extensively studied. Much less is known about biodiversity and bathymetric zonation of benthos in the deep sea because of the remoteness and relative inaccessibility of the environment.

Evidence suggests that diversity of some benthic taxa, especially of infauna (e.g. peracarid crustaceans, polychaetes, bivalve mollusks) is exceptionally high at great depths (Hessler and Sanders, 1967; Sanders and Hessler, 1969; Grassle and Maciolek, 1992). However, deep-sea diversity varies considerably among major invertebrate groups, and Sanders (1979) contrasted the rich peracarid fauna with the much lower numbers of ophiuroid species in the abyss. Among the epifauna, species numbers of Bryozoa per station were shown by Schopf (1969) to decrease with increasing depth on a world-wide basis. Hydroids, generally well represented in neritic epibenthos of all oceans (Fraser, 1944; Naumov, 1960; Millard, 1975; Stepanjantz, 1979; Hirohito, 1988, 1995; Cornelius, 1995), appear to be a relatively minor component of abyssal and hadal fauna (Kramp, 1951, 1956; Vervoort, 1966; Calder, 1996, 1997b).

Objectives of this study were to examine hydroid species assemblages in samples along a depth gradient, extending from sea surface to deep-ocean floor, in waters around the oceanic island of Bermuda.

2. Materials and methods

Hydroids were examined in 88 qualitative samples from the Bermuda region, extending over a depth range from 0 to 4550 m (Table 1, Fig. 1). Shallow-water collecting (0–100 m) was undertaken by diving (snorkeling, SCUBA), dredging, manual collecting, and use of fouling panels. Species inhabiting the upper slope (101–500 m) of the Bermuda Pedestal were sampled by dredging, tangle netting, trapping (i.e. collection of hydroids on gastropod shells inhabited by pagurid crabs), and submersible (SDL-1). Most specimens from the 501–1500 m depth range were obtained by dredging, trapping, tangle netting, and grab sampling (Van Veen grab). Eight stations between 730 and 3550 m along the northwest slope of the Bermuda Pedestal were sampled by submersible (DSV Alvin) during March 1993. Substrates at these stations were scanned visually for hydroids during stops averaging 22 min per station (ranging from 65 min at 3550 m to 8 min at 730 m). In addition, rocks, rubble, megafaunal invertebrates, and other substrates were collected and placed either in an insulated and compartmentalized chest or in plastic boxes for transport to the surface. These substrates were preserved aboard ship and examined for hydroids in the laboratory. The deepest sample was a set of five oak fouling panels secured over a six-month period to an open ocean mooring SE of Bermuda (ALTOMOOR–2, 31°44′00′N, 64°10′00′W, 4550 m). These panels, 12.5×6.5 cm each, were identical with a set immersed in shallow waters of Castle Harbour, Bermuda. Of the 88 samples

Table 1
Data on 88 samples for hydroids, at depths between 0 and 4550 m, in waters around Bermuda

Zone	Location	Date	Depth (m)	Method	No. species
0–25 m	Argus Bank (Argus tower)	23-IV-76	20	SCUBA	8
	North Lagoon (tanker mooring A)	5-X-76	13	SCUBA	2
	Ferry Reach	2-IX-77	0.5–1.5	Snorkel	5
	Ferry Reach	5-IX-77	0–2	Snorkel	2
	Castle Hbr (Walsingham Pond)	5-IX-77	0–2	Snorkel	1
	Hungry Bay	6-IX-77	0–1.5	Snorkel	2
	Whalebone Bay (ledges @ mouth)	7-IX-77	0–2	Snorkel	13
	Whalebone Bay, (*Thalassia* bed)	8-IX-77	0–2	Snorkel	4
	Flatts Inlet	13-IX-77	0–2	Snorkel	9
	North Rock	19-IX-77	1–3	Snorkel	3
	Harrington Sd (Hall's Island)	20-IX-77	0–2	Snorkel	11
	Flatts Inlet	21-IX-77	0–2	Snorkel	20
	Flatts Inlet	27-II-82	0–0.5	Manual	10
	Harrington Sd (Green Bay Cave)	3-III-82	0–5	SCUBA	3
	Whalebone Bay (ledges @ mouth)	4-III-82	0–4	SCUBA	9
	Flatts Inlet	5-III-82	0–3	Snorkel	14
	Harrington Sd (Green Bay)	8-III-82	0–2	Snorkel	3
	Castle Hbr (Castle Grotto)	20-VII-82	0–2	Snorkel	7
	Ferry Reach, (*Thalassia* bed)	26-VII-82	0–1.5	Snorkel	5
	Castle Hbr (Tucker's Town)	27-VII-82	0–1	Snorkel	4
	Harrington Sd (Hall's Island)	27-VII-82	0–1.5	Snorkel	4
	Harrington Sd (Stream Passage Cave)	27-VII-82	0–1.5	Snorkel	10
	Whalebone Bay (ledges @ mouth)	28-VII-82	0–4	Snorkel	11
	Castle Harbour (nr Castle Roads)	30-VII-82	0–3	Snorkel	8
	Flatts Inlet	1-VIII-82	0–3	Snorkel	12
	Flatts Inlet	2-VIII-82	0–3	Snorkel	17
	Castle Hbr (Tucker's Town reef)	3-VIII-82	0–7	SCUBA	7
	Castle Hbr (Wreck @ Nonsuch Is)	3-VIII-82	0–3	SCUBA	13
	Harrington Sd (Hall's Island)	5-VIII-82	0–2	Snorkel	6

(*continued on next page*)

Table 1 (*continued*)

Zone	Location	Date	Depth (m)	Method	No. species
	Harrington Sd (Flatts Inl duct)	29-IX-86	0.5	Snorkel	16
	Flatts Inlet area (Burchall's Cove: *Sargassum*)	23-XI-89	0	Manual	9
	Flatts Inlet	25-XI-89	0–2	Snorkel	10
	Pilchard Bay (mangrove system)	28-XI-89	0–1	Snorkel	6
	Castle Hbr (Walsingham Bay)	1-XII-89	0–1	Snorkel	3
	Castle Hbr (Walsingham Pond)	25-V-91	0–1	Snorkel	1
	Castle Hbr (Longbird Bridge)	28-VIII-95 to 13-XII-95	2	Fouling panels	9
26–100 m	BDA Platform, S Castle Roads	3-IX-77	60–90	Dredge	13
	BDA Platform, S Castle Roads	1-VII-83	73	Dredge	16
	Challenger Bank	3-X-84	70	Dredge	7
	BDA Platform, S Castle Roads	13-V-91	70–90	Dredge	9
	BDA Platform, S Castle Roads	14-V-91	90	Dredge	6
	BDA Platform, S Castle Roads	14-V-91	80	Dredge	4
	Challenger Bank	17-V-91	60	Dredge	5
	BDA Platform, S Castle Roads	22-V-91	70	Dredge	11
	BDA Platform, S Castle Roads	23-V-91	60–100	Dredge	3
	BDA Platform, S Castle Roads	26-V-91	65–85	Dredge	9
	BDA Platform, ENE Castle Roads	27-V-91	85	Dredge	8
	BDA Platform, NW North Rock	28-V-91	62–73	Dredge	11
	BDA Platform, SW North Rock	28-V-91	70–82	Dredge	1
	BDA Platform, S Castle Roads	8-IV-92	91	Dredge	10
	BDA Platform, S Castle Roads	9-IV-92	91	Dredge	3
	BDA Platform, S Castle Roads	10-IV-92	91	Dredge	1
	BDA Platform, S Castle Roads	19-IV-92	82	Dredge	6
101–200 m	BDA Pedestal, S Castle Roads	1-VII-83	119	Dredge	5
	BDA Pedestal, S Castle Roads	14-V-91	105	Dredge	4
	BDA Pedestal, S Castle Roads	22-V-91	105	Dredge	7
	BDA Pedestal, S Castle Roads	26-V-91	110	Dredge	2
	BDA Pedestal, S Castle Roads	12-IV-92	119	Dredge	4

	BDA Pedestal, SW Chub Heads	6-X-94	101	Dredge	3
	BDA Pedestal, SW Chub Heads	6-X-94	146	Dredge	4
	BDA Pedestal, SW Chub Heads	19-X-94	110	Dredge	11
	BDA Pedestal, Hungry Bay Bight	3-III-97	195	Submersible (SDL-1)	10
201–500 m	BDA Pedestal, S Castle Roads	24-VII-82	256	Crab trap	2
	BDA Pedestal, S Castle Roads	27-V-91	325	Crab trap	5
	BDA Pedestal, S Castle Roads	4-IV-92	274–329	Crab trap line	14
	BDA Pedestal, SW Chub Heads	10-X-94	281	Tangle net	1
	BDA Pedestal, Hungry Bay Bight	25-II-97	376	Submersible (SDL-1)	1
	BDA Pedestal, Hungry Bay Bight	25-II-97	244	Submersible (SDL-1)	5
	BDA Pedestal, Hungry Bay Bight	3-III-97	283	Submersible (SDL-1)	3
	BDA Pedestal, Hungry Bay Bight	3-III-97	221	Submersible (SDL-1)	0
501–1000 m	BDA Pedestal, ENE Castle Roads	14-IV-92	549	Dredge	1
	BDA Pedestal, NW Bermuda	18-III-93	730	Submersible (Alvin)	1
	BDA Pedestal, SW Chub Heads	10-X-94	713	Crab trap	2
	BDA Pedestal, SW Chub Heads	19-X-94	914	Tangle net	0
	BDA Pedestal, SE Hungry Bay Bight	2-VI-96	699–752	Chain sack dredge	0
	BDA Pedestal, SE Hungry Bay Bight	2-VI-96	562–624	Chain sack dredge	0
1001–2000m	BDA Pedestal, NW Bermuda	18-III-93	1770	Submersible (Alvin)	0
	BDA Pedestal, NW Bermuda	18-III-93	1506	Submersible (Alvin)	1
	Bowditch Seamount	31-V-96	1329	Van Veen grab	0
	Bowditch Seamount	31-V-96	1322	Van Veen grab	2
	Bowditch Seamount	31-V-96	1321–1381	Bucket dredge	0
	Bowditch Seamount	31-V-96	1302–1324	Chain sack dredge	4
2001–3000 m	BDA Pedestal, NW Bermuda	17-III-93	2523	Submersible (Alvin)	0
	BDA Pedestal, NW Bermuda	17-III-93	2216	Submersible (Alvin)	0
3001–4000 m	BDA Pedestal, NW Bermuda	17-III-93	3550	Submersible (Alvin)	2
	BDA Pedestal, NW Bermuda	17-III-93	3403	Submersible (Alvin)	0
	BDA Pedestal, NW Bermuda	17-III-93	3011	Submersible (Alvin)	2
> 4000 m	Bermuda Rise, SE Bermuda	29-VIII-95 to 17-III-96	4550	Fouling panels	0

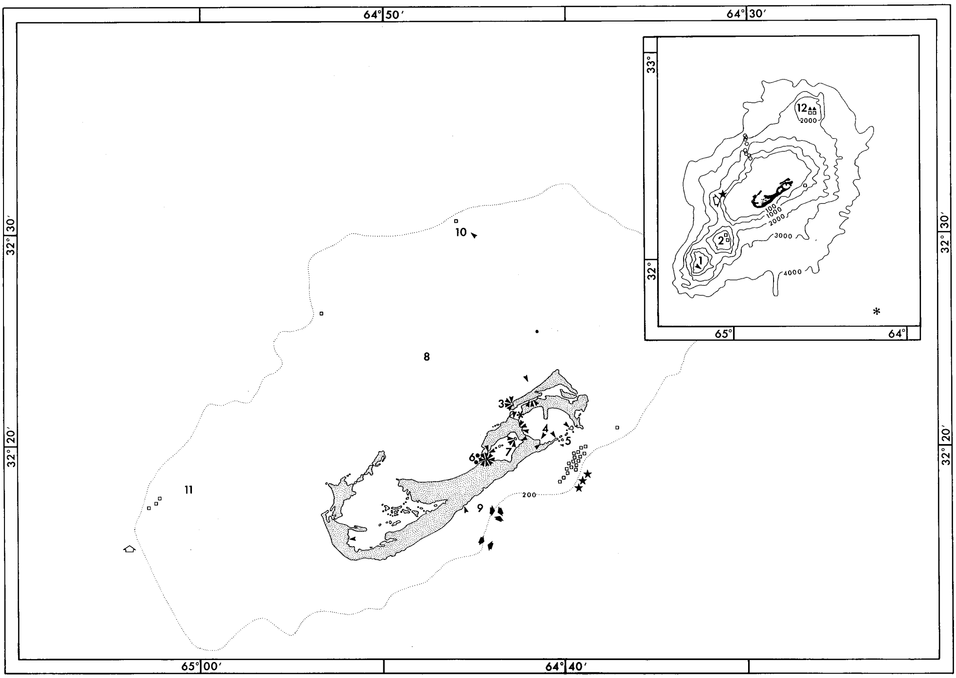

Fig. 1. Sampling sites around the oceanic island of Bermuda, and on three nearby seamounts as shown in inset. Isobaths in meters. 1 = Argus Bank; 2 = Challenger Bank; 3 = Whalebone Bay–Ferry Reach area; 4 = Castle Harbour; 5 = Castle Roads; 6 = Flatts Inlet area; 7 = Harrington Sound; 8 = North Lagoon; 9 = Hungry Bay Bight; 10 = North Rock; 11 = Chub Heads; 12 = Bowditch Seamount. Arrowheads = diving sites; closed triangles = Van Veen grab sites; closed circles = manual collecting sites; open squares = dredging sites; open arrows = tangle net sites; stars = crab trap sites; closed arrows = submersible (SDL-1) sites; open circles = submersible (DSV Alvin) sites; asterisks = fouling panel sites.

examined, seven were from seamounts flanking the Bermuda Pedestal (one from Argus Bank, two from Challenger Bank, and four from Bowditch Seamount).

Data from comprehensive hydroid collections only were included in this study. Specific searches for individual species as part of taxonomic studies (e.g. Calder, 1988, 1991a, 1997a) of the shallow-water fauna (0–100 m) were omitted. Moreover, only one of 16 collections of pelagic *Sargassum*, made during investigations of hydroids associated with those seaweeds (e.g. Calder, 1993, 1995), was considered. As a result, of the 110 species currently known from Bermuda, 21 from surface and near-surface (0–25 m) collections have not been included here.

To aid in assessing changes in hydroid diversity and species composition with depth, nine essentially arbitrary bathymetric zones were recognized: 0–25 m (surface and nearsurface), 26–100 m (shallow neritic), 101–200 m (deep neritic), 201–500 m (uppermost bathyal), 501–1000 m (upper bathyal), 1001–2000 m (mid-bathyal), 2001–3000 m (lower bathyal), 3001–4000 m (upper abyssal), and >4000 m (mid-abyssal). Principal components analysis of data from these depth zones was computed using the program PRINCOMP, employing a correlation matrix of variables (Podani, 1988).

3. Results

Eighty-nine species of hydroids (including *Thecocodium brieni*, new to Bermuda and to the western Atlantic) were identified in the samples. Changes in species numbers and composition were most pronounced over the upper 500 m (Table 2). Only 10 of the 89 species reported here were collected below that depth. Six of the deep-water hydroids (*Stylactaria* sp., *Leuckartiara* sp., *Opercularella* sp., *Acryptolaria longitheca*, *Filellum serratum*, *Lafoea coalescens*) were found over vertical distances exceeding 500 m. Sampling was not extensive enough to adequately define bathymetric ranges of most species off Bermuda.

The most taxonomically rich assemblage (54 species) was identified in collections from the surface and nearsurface zone (0–25 m). Species with the highest frequency of occurrence in samples from this depth (Table 2) included an anthoathecate (*Pennaria disticha*) and five leptothecates (*Obelia dichotoma*, *Halecium bermudense*, *Dynamena disticha*, *Cnidoscyphus marginatus*, *Dynamena crisioides*). Hydroid diversity was also moderately high (36 species) in the shallow neritic zone (26–100 m). However, faunal composition in this region was distinct from that in overlying waters (Table 2), with six leptothecates (*Plumularia setacea*, *Macrorhynchia allmani*, *Antennella secundaria*, *Synthecium tubithecum*, *Aglaophenia dubia*, *Dynamena dalmasi*) exhibiting highest frequency in the samples. Hydroids were less diverse, and less frequent, in samples from the deep neritic zone (101–200 m) and from the uppermost bathyal region (201–500 m). Specimens were typically scarcest, and diversity lowest, in collections from depths exceeding 500 m.

In addition to differences in numbers of species reported from different bathymetric zones (Table 2), numbers of species in individual samples also tended to be highest (maximum of 20) in shallow collections (Table 1, Fig. 2), although there was considerable variation from one sample to another at a given depth. In contrast, the maximum number in samples from depths greater than 500 m was only four, and more than half of samples (10 of 18) from such stations contained no hydroids.

Mean numbers of species per sample (Table 3) from each of the various depth zones likewise indicated greatest hydroid species richness in shallow waters. Both the highest mean number of species per sample ($x = 7.5$) and maximum number of species per sample (20) were recorded from the surface and nearsurface zone (0–25 m). Samples from greater than 500 m had the lowest mean numbers of species ($x = 1.3$ or fewer).

Observations and collections during two deep submersible dives in DSV Alvin provided further evidence of low hydroid diversity and abundance in the deep-sea compared with the fauna of shallow waters off Bermuda, even where hard substrates were present. During close visual examinations of the bottom (at distances of 1–3 m and occasionally less) at each of eight stations between 3550 and 730 m on the Bermuda Pedestal, hydroids were seen only at the uppermost site. At that location,

Table 2
Species of hydroids reported from different bathymetric zones in the Bermuda area, and the number and percent of samples from each zone in which each was present

Bathymetric zone	Species	# samples	% of samples
0–25 m	*Pennaria disticha* Goldfuss, 1820[a]	18	50
	Obelia dichotoma (Linnaeus, 1758)[a]	18	50
	Halecium bermudense Congdon, 1907[b]	17	47
	Dynamena disticha (Bosc, 1802)[b]	17	47
	Cnidoscyphus marginatus (Allman, 1877)[b]	13	36
	Dynamena crisioides Lamouroux, 1824[b]	12	33
	Tridentata turbinata (Lamouroux, 1816)[b]	10	28
	Halopteris alternata (Nutting, 1900)[b]	10	28
	Plumularia strictocarpa Pictet, 1893[b]	10	28
	Turritopsis nutricula McCrady, 1857[a]	9	25
	Eudendrium carneum Clarke, 1882[b]	9	25
	Millepora alcicornis Linnaeus, 1758[a]	8	22
	Clytia hemisphaerica (Linnaeus, 1767)[a]	8	22
	Clytia linearis (Thornely, 1900)[a]	8	22
	Dynamena quadridentata (Ellis and Solander, 1786)[b]	8	22
	Myrionema amboinense Pictet, 1893[b]	7	19
	Ventromma halecioides (Alder, 1859)[b]	7	19
	Bimeria vestita Wright, 1859[b]	6	17
	Zyzzyzus calderi Petersen, 1990[b]	6	17
	Sertularella conica Allman, 1877[b]	6	17
	Tridentata distans (Lamouroux, 1816)[b]	6	17
	Bougainvillia muscus (Allman, 1863)[a]	5	14
	Lafoeina amirantensis (Millard and Bouillon, 1973)[a]	5	14
	Halecium nanum Alder, 1859[b]	5	14
	Clytia gracilis (M. Sars, 1850)[a]	5	14
	Cladonema radiatum Dujardin, 1843[a]	3	8
	Clytia noliformis auct.[a]	3	8
	Macrorhynchia philippina Kirchenpauer, 1872[a]	3	8
	Corydendrium parasiticum (Linnaeus, 1767)[b]	2	6
	Eudendrium capillare Alder, 1856[b]	2	6
	Ectopleura mayeri Petersen, 1990[a]	2	6
	Halecium tenellum Hincks, 1861[b]	2	6
	Orthopyxis sargassicola (Nutting, 1915)[c]	2	6
	Clytia macrotheca (Perkins, 1908)[a]	2	6
	Obelia bidentata Clark, 1875[a]	2	6
	Symmetroscyphus intermedius (Congdon, 1907)[b]	2	6
	Tridentata marginata (Kirchenpauer, 1864)[b]	2	6
	Monotheca margaretta Nutting, 1900[b]	2	6
	Pachycordyle napolitana Weismann, 1883[a]	1	3
	Eudendrium bermudense Calder, 1988[b]	1	3
	Coryne sargassicola Calder, 1988[b]	1	3
	Zanclea alba (Meyen, 1834)[a]	1	3
	Sagamihydra dyssymetra (Billard, 1929)[b]	1	3
	Halecium lightbourni Calder, 1991[b]	1	3
	Hebellopsis scandens (Bale, 1888)[a]	1	3
	Scandia mutabilis (Ritchie, 1907)[b]	1	3

Table 2 (*continued*)

Bathymetric zone	Species	# samples	% of samples
	Clytia hummelincki (Leloup, 1935)[a]	1	3
	Synthecium tubithecum (Allman, 1877)[b]	1	3
	Diphasia tropica Nutting, 1904[b]	1	3
	Tridentata tumida (Allman, 1877)[b]	1	3
	Antennella secundaria (Gmelin, 1791)[b]	1	3
	Plumularia setacea (Linnaeus, 1758)[b]	1	3
	Plumularia floridana Nutting, 1900[b]	1	3
	Aglaophenia latecarinata Allman, 1877[b]	1	3
26–100 m	*Plumularia setacea* (Linnaeus, 1758)[b]	13	76
	Macrorhynchia allmani (Nutting, 1900)[b]	13	76
	Antennella secundaria (Gmelin, 1791)[b]	12	71
	Synthecium tubithecum (Allman, 1877)[b]	8	47
	Aglaophenia dubia Nutting, 1900[b]	7	41
	Dynamena dalmasi (Versluys, 1899)[b]	6	35
	Filellum serratum (Clarke, 1879)[b]	5	29
	Acryptolaria conferta (Allman, 1877)[b]	4	24
	Lafoea coalescens Allman, 1877[b]	4	24
	Sertularella conica Allman, 1877[b]	4	24
	Sagamihydra dyssymetra (Billard, 1929)[b]	3	18
	Campanularia macroscypha Allman, 1877[b]	3	18
	Dynamena disticha (Bosc, 1802)[b]	3	18
	Sertularella diaphana (Allman, 1885)[b]	3	18
	Antennella quadriaurita Ritchie, 1909[b]	3	18
	Gymnangium speciosum (Allman, 1877)[b]	3	18
	Corydendrium parasiticum (Linnaeus, 1767)[b]	2	12
	Turritopsis nutricula McCrady, 1857[a]	2	12
	Halecium tenellum Hincks, 1861[b]	2	12
	Hincksella cylindrica (Bale, 1888)[b]	2	12
	Tridentata tumida (Allman, 1877)[b]	2	12
	Plumularia floridana Nutting, 1900[b]	2	12
	Monotheca margaretta Nutting, 1900[b]	2	12
	Aglaophenia latecarinata Allman, 1877[b]	2	12
	Eudendrium bermudense Calder, 1988[b]	1	6
	Plicatotheca anitae Calder and Vervoort, 1986[b]	1	6
	Lafoeina amirantensis (Millard and Bouillon, 1973)[a]	1	6
	Halecium bermudense Congdon, 1907[b]	1	6
	Hebella dyssymetra Billard, 1933[b]	1	6
	Hebellopsis communis Calder, 1991[c]	1	6
	Hebellopsis michaelsarsi (Leloup, 1935)[c]	1	6
	Clytia nr. *latitheca* Millard and Bouillon, 1973[c]	1	6
	Obelia dichotoma (Linnaeus, 1758)[a]	1	6
	Cnidoscyphus marginatus (Allman, 1877)[b]	1	6
	Diphasia tropica Nutting, 1904[b]	1	6
	Gymnangium sinuosum (Fraser, 1925)[b]	1	6
101–200 m	*Antennella secundaria* (Gmelin, 1791)[b]	9	100
	Plumularia setacea (Linnaeus, 1758)[b]	7	78

(*continued on next page*)

Table 2 (*continued*)

Bathymetric zone	Species	# samples	% of samples
	Filellum serratum (Clarke, 1879)[b]	4	44
	Lafoeina amirantensis (Millard and Bouillon, 1973)[a]	3	33
	Halecium tenellum Hincks, 1861[b]	3	33
	Lafoea coalescens Allman, 1877[b]	3	33
	Eudendrium sp. 1[b]	2	22
	[d]Operculate 2 (undet.)[c]	2	22
	Campanularia macroscypha Allman, 1877[b]	2	22
	Clytia linearis (Thornely, 1900)[a]	2	22
	Synthecium tubithecum (Allman, 1877)[b]	2	22
	Turritopsis fascicularis Fraser, 1943[b]	1	11
	Bougainvillia aberrans Calder, 1993[a]	1	11
	Leuckartiara sp.[a]	1	11
	Filifera (undet.)[c]	1	11
	[d]*Thecocodium brieni* Bouillon, 1967[b]	1	11
	Eudendrium carneum Clarke, 1882[b]	1	11
	Plicatotheca anitae Calder and Vervoort, 1986[c]	1	11
	Acryptolaria conferta (Allman, 1877)[b]	1	11
	Clytia gracilis (M. Sars, 1850)[a]	1	11
	Dynamena dalmasi (Versluys, 1899)[b]	1	11
	Aglaophenia dubia Nutting, 1900[b]	1	11
	Macrorhynchia allmani (Nutting, 1900)[b]	1	11
201–500 m	*Eudendrium* sp. 1[b]	4	50
	Stylactaria sp.[a]	3	38
	Lafoea coalescens Allman, 1877[b]	3	38
	Turritopsis fascicularis Fraser, 1943[b]	2	25
	Clytia linearis (Thornely, 1900)[a]	2	25
	Corydendrium parasiticum (Linnaeus, 1767)[b]	1	13
	Bougainvillia aberrans Calder, 1993[a]	1	13
	Leuckartiara sp.[a]	1	13
	Filifera (undet.)[c]	1	13
	Eudendrium bermudense (Calder, 1988)[b]	1	13
	Lafoeina amirantensis (Millard and Bouillon, 1973)[a]	1	13
	Cuspidella sp.[b]	1	13
	Operculate (undet.)[c]	1	13
	Halecium tenellum Hincks, 1861[b]	1	13
	Scandia mutabilis (Ritchie, 1907)[b]	1	13
	Clytia gracilis (M. Sars, 1850)[a]	1	13
	Clytia nr. *latitheca* Millard and Bouillon, 1973[a]	1	13
	Clytia sp.[a]	1	13
	Sertularella gayi unituba Calder, 1991[b]	1	13
	Antennella secundaria (Gmelin, 1791)[b]	1	13
	Plumularia setacea (Linnaeus, 1758)[b]	1	13
501–1000 m	*Sertularella catena* (Allman, 1877)[b]	2	33
	Leuckartiara sp.[a]	1	17
	Stylactaria sp.[a]	1	17
1001–2000 m	*Egmundella superba* Stechow, 1921[b]	2	33
	Lafoea coalescens Allman, 1877[b]	2	33

Table 2 (*continued*)

Bathymetric zone	Species	# samples	% of samples
	[d]*Eudendrium* sp. 2[b]	1	17
	[d]*Tubularia* sp.[b]	1	17
	Filellum serratum (Clarke, 1879)[b]	1	17
2001–3000 m	None		
3001–4000 m	*Opercularella* sp.[c]	2	67
	Acryptolaria longitheca (Allman, 1877)[b]	2	67
> 4000 m	None		

[a]Species with free medusa or medusoid.
[b]Species with fixed gonophores.
[c]Species with gonophore type unknown.
[d]Species not previously reported from Bermuda.

small colonies of a leptothecate species (*Sertularella catena*, 3 cm high) were observed and collected. Specimens not seen during the dives, but sorted later from bottom samples, included two leptothecate species (*Acryptolaria longitheca*, *Opercularella* sp.) on stalks of hexactinellid sponges from 3011 and 3550 m, and an anthoathecate (*Tubularia* sp.) on calcareous rubble from 1506 m. Collections of bottom samples from four (3403, 2523, 2216, 1770 m) of the eight deep submersible stations did not contain any hydroids.

The relationships of hydroid faunal assemblages identified from various bathymetric zones around Bermuda was apparent in a principal components analysis of the data (Fig. 3). The surface and nearsurface zone (0–25 m), with a comparatively rich and faunistically distinct assemblage, occurred by itself in the upper left quadrant of the diagram. Shallow neritic (26–100 m) and deep neritic (101–200 m) zones were located quite close together in the upper right quadrant, an indication of the similarity of their faunas. Zones in bathyal waters (201–500, 501–1000, 1001–2000 m), having moderately related assemblages, occurred in the lower right quadrant. The upper abyssal zone (3001–4000 m), with its unique species composition, appeared alone in the lower left quadrant. Both lower bathyal (2001–3000 m) and mid-abyssal (> 4000 m) zones were excluded from the analysis because no hydroids were collected in samples from either depth.

4. Discussion

Differences observed in diversity and species composition of hydroids from one bathymetric area to another in waters around Bermuda must be attributed in part to the unequal numbers of samples from different zones, to differences in sampling methods used, and to the increased difficulty of collecting these cnidarians at greater

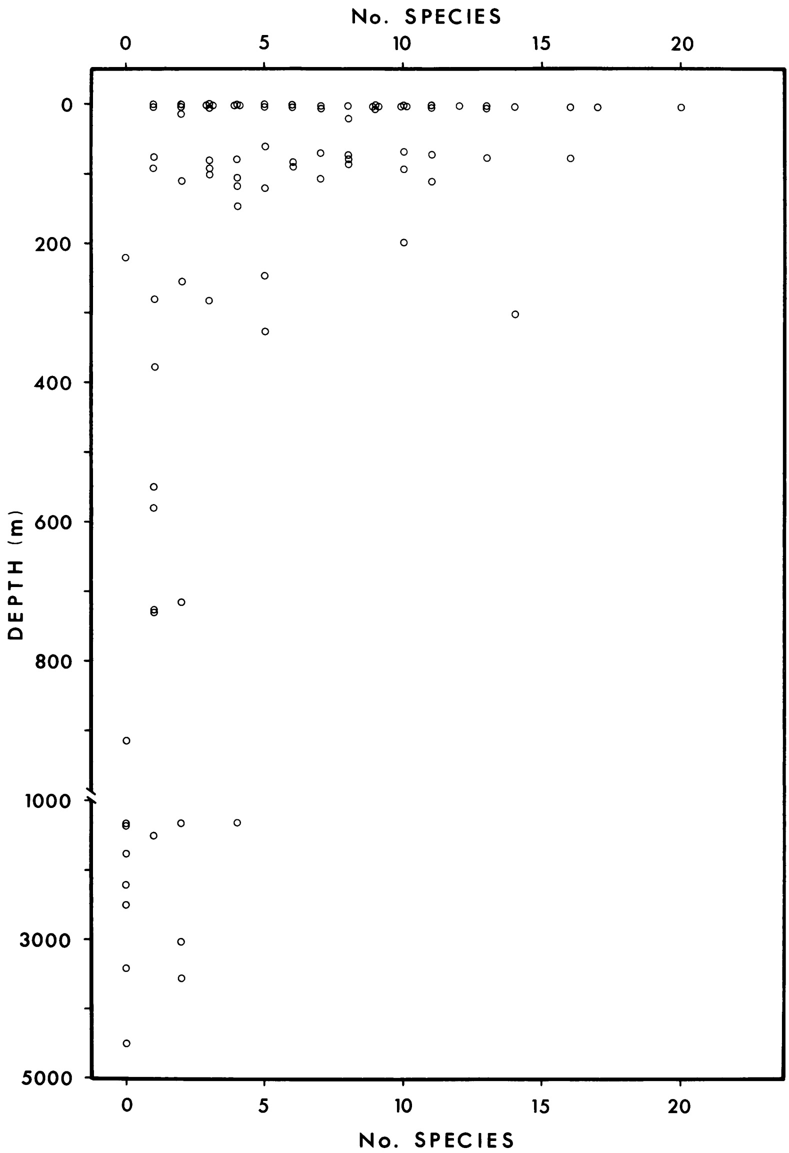

Fig. 2. Numbers of species of hydroids in each of 88 samples taken at various depths between 0 and 4550 m in waters around Bermuda.

depths. The fauna of the upper 100 m has been most extensively sampled and is considered best known. Assemblages from regions below 500 m have been sampled the least and are poorest known. However, data on numbers of hydroid species per sample (Tables 1 and 3; Fig. 2), as well as direct observations by diving and by submersible, indicate that changes in diversity are pronounced along the bathymetric

Table 3
Data on numbers of hydroid species collected from various depth zones in the Bermuda area

Depth (m)	No. samples	Anthoathecates No. species/sample			Leptothecates No. species/sample			Combined No. species/sample		
		Range	Mean	S.E.	Range	Mean	S.E.	Range	Mean	S.E.
0–25	36	0–8	2.2	0.30	0–14	5.3	0.61	1–20	7.5	0.82
26–100	17	0–1	0.3	0.11	1–15	6.6	0.92	1–16	7.0	0.99
101–200	9	0–5	0.9	0.56	2–9	4.7	0.73	2–11	5.5	1.04
201–500	8	0–4	1.8	0.49	0–10	2.1	0.49	0–14	3.9	1.59
501–1000	6	0–2	0.3	0.33	0–1	0.3	0.21	0–2	0.7	0.33
1001–2000	6	0–1	0.3	0.21	0–3	0.8	0.54	0–4	1.2	0.65
2001–3000	2	0–0	0.0	0.00	0–0	0.0	0.00	0–0	0.0	0.00
3001–4000	3	0–0	0.0	0.00	0–2	1.3	0.67	0–2	1.3	0.67
> 4000	1	0–0	0.0	0.00	0.0	0–0	0.00	0–0	0.0	0.00

gradient. The richest assemblage of species was found in shallow waters of the Bermuda Platform, where hydroids were a significant and conspicuous component of the epifauna. The fauna generally appeared to be sparse below 500 m, even on rocks and other substrates commonly occupied by hydroids in nearsurface environments.

The relative scarcity of hydroids in deep waters off Bermuda, noted here, coincides with results from earlier studies in the area. None of these cnidarians was present in benthic samples from four deep stations (depths of 1000, 1500, 2000, 2500 m) on the Bermuda Pedestal collected by Sanders, Hessler, and Hampson (1965). Moreover, Tizard *et al.* (1885, pp. 161, 162) observed that benthic invertebrates in general were sparse in deep dredgings and trawlings off this oceanic island in relation to comparable depths off the coast of the North American continent. Hydroids were reported (Allman, 1883) only from the shallowest (32 fathoms = 59 m) of a total of 10 benthos stations by H.M.S. Challenger (depths of 32, 120, 265, 435, 506, 1075, 1250, 1325, 1575, 2650 fm) around Bermuda.

Evidence for a comparatively depauperate hydroid fauna in deeper waters off Bermuda generally corresponds with existing information on bathymetric distribution of species reported elsewhere from the western and central North Atlantic. In a collection of hydroids from the Mid-Atlantic Ridge, Calder and Vervoort (1998) found nine species in samples from depths of 500–1000 m, eight from 1001–2000 m, three from both 2001–3000 and 3001–4000 m, and one (*Cryptolarella abyssicola*) from below 4000 m. Along the east coasts of North America and northern South America, collecting efforts historically have been far greater in neritic waters than in the adjacent deep-sea. Nevertheless, among 424 species reported overall from the region, only 10 have ever been recorded from depths of 2500 m or greater (Fraser, 1944; Calder, 1996, 1997b). Of these, just four (*Eucuspidella pedunculata*, *Acryptolaria longitheca*, *Cryptolarella abyssicola*, *Halisiphonia megalotheca*) have been reported from depths below 4000 m. That one of these (*Acryptolaria longitheca*) was found at abyssal depths during this study lends support to the assumption of low hydroid

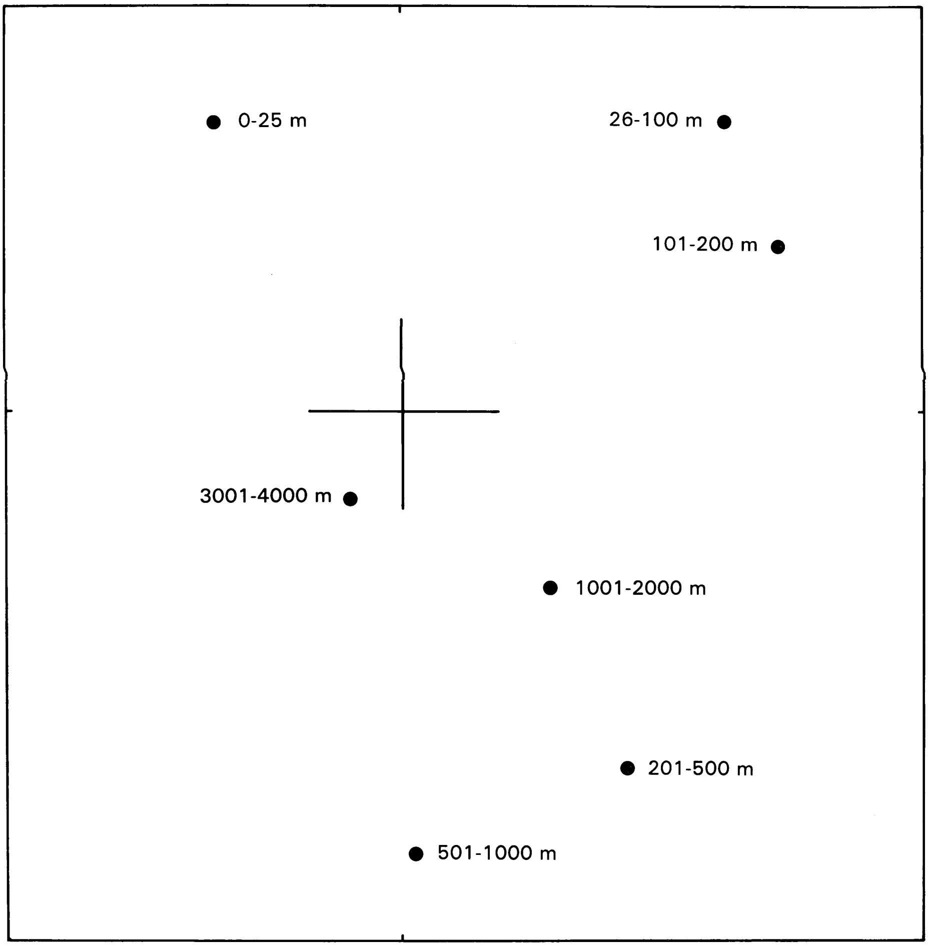

Fig. 3. Principal components analysis of hydroid data from seven bathymetric zones around Bermuda.

diversity in the deep-sea around Bermuda. Identical collections (*Acryptolaria longitheca*, *Opercularella* sp.) from 3011 and 3550 m by submersible here also indicate that diversity of hydroids is low on the largely sediment-covered slope of the Bermuda Pedestal at abyssal depths, even where favorable substrates exist. Elsewhere, Millard (1978) reported only eight species from depths below 1000 m off the comparatively well-studied coast of southern Africa, and Vervoort's (1966) partial list of 41 species of hydroids from bottoms below 2000 m in all oceans implies low diversity of the group at great depths worldwide.

Bathymetric ranges of hydroids appear, at least in some cases, to be greater at higher latitudes than at lower ones (Calder, 1997b). Several species reported by Broch (1918), Kramp (1932, 1951), and Vervoort (1972) from bathyal and abyssal bottoms in Baffin Bay, Davis Strait, the Labrador Sea, and Denmark Strait were found at depths far below their usual lower limits in waters farther south. Among these were five sertulariids (*Diphasia fallax*, *Salacia laxa*, *Sertularia robusta*, *Tamarisca tamarisca*, *Thuiaria thuja*), most commonly found in cold neritic waters of the boreal zone, that were reported from depths exceeding 2000 m. Of the essentially tropical hydroid fauna inhabiting neritic waters around Bermuda (Calder, 1992), only three species (*Egmundella superba*, *Lafoea coalescens*, *Filellum serratum*) were found below 1000 m. Water temperatures, measured during DSV Alvin dives, declined from 16.5 to 6.6°C between 500 and 1000 m and reached 2.2°C at 3550 m. While the importance of temperature in the decline of species numbers with depth along the bathymetric ecocline is unclear, few if any of the tropical hydroids inhabiting the shallow Bermuda Platform would survive in the cold conditions of the mid-bathyal zone and deeper. At the same time, there was no noteworthy increase in numbers of cold water hydroid species with depth on the Bermuda Pedestal to compensate for the decline in numbers of tropical species.

A significant factor in the abundance, species composition, diversity, and distribution of hydroids is the nature of the substrate (Calder, 1991b). Most areas of the Bermuda Pedestal examined between 3550 and 195 m during submersible dives (DSV Alvin, SDL-1) were covered with sediment, an unfavorable bottom type for this largely epifaunal group. Yet diversity and abundance of these cnidarians appeared to be low below 500 m, even where hard substrates were present (Table 2). In particular, hydroids were scarce on rocky outcrops and rubble at these depths, even though space for settlement and growth was available. Moreover, wooden fouling panels immersed at 4550 m on the Bermuda Rise over a six month period during the study had no hydroids or other sessile macrofauna on them when recovered. Most hydroids collected at great depths were present on other invertebrates, including stalks of glass sponges, octocorals, and gastropod shells occupied by hermit crabs. Low hydroid diversity in deep waters of the study area thus appears due to factors other than simply the paucity of suitable substrates.

Reduced hydroid diversity in the deep sea might be predicted from the trophic habits of these animals. According to Menzies *et al.* (1973), most abyssal invertebrates are either detritophages or sestophages, whereas hydroids typically prey on small zooplankton. Nevertheless, factors influencing the occurrence and vertical distribution of organisms generally in deep-sea environments are not well known. Various authors have considered availability of food, as well as bottom type, hydrostatic pressure, bottom water currents, and biological interactions to be important (see Dickinson and Carey, 1978). A belief that water temperature is a major factor in determining bathymetric zonation of deep-sea biota is pervasive, but largely untested (Gage and Tyler, 1991). As noted by Hecker (1990), bathymetric zonation patterns of deep-sea benthos are likely attributable to a combination of factors, both physical and biological.

In spite of the apparent low diversity and abundance of hydroids in lower bathyal and abyssal regions, at least around Bermuda, the deep sea remains a worthwhile area for investigations on hydrozoans. A recent indication of this was the description by Vervoort (1993) of a remarkable fauna from New Caledonia, the Loyalty Islands, and other areas of the western Pacific. Among some 66 species of sertulariids, mostly from depths between 200 and 700 m, 38 were new. Although endemism is especially high in that region, Vervoort's study demonstrates the potential of further work on hydroids from intermediate to great depths of the oceans.

Acknowledgements

I am indebted to J.R.H. Lightbourn for opportunities to collect aboard his vessels NORTH STAR and POLARIS from 1977 to 1992, and for his hospitality during field trips to Bermuda. Collections from Argus Bank were provided by Dr. Wolfgang Sterrer, and those from a North Lagoon tanker mooring by Dr. John Markham. Thanks are due to the personnel of R/V Culver, R/V BBS II, R/V Weatherbird, R/V Weatherbird II, R/V Atlantis II, R/V Edwin Link, and FS Meteor, to the pilots of DSV Alvin and staff of the Alvin group at the Woods Hole Oceanographic Institution, and to the pilots of SDL-1 and officers and crew of HMCS Cormorant of the Canadian Navy, for assistance and support. I am also grateful to E.B. Tucker for collecting trips on his vessel Miss Wendy. Dr. T.D. Dickey and John Kemp permitted the attachment of my hydroid fouling panels to the ALTOMOOR–2 mooring off Bermuda. For logistical support at the Bermuda Aquarium, Museum, and Zoo, I thank Dr. Wolfgang Sterrer (Curator) and Richard Winchell (Director). Funds in support of the fieldwork were provided by the Royal Ontario Museum, the Natural Sciences and Engineering Research Council of Canada, the Bermuda Natural History Museum, Exxon Corporation, and the Canadian Associates of the Bermuda Biological Station. Participation in Cruise 35/2 of FS Meteor, Prof. Dr. Dieter Meischner, Chief Scientist, was made possible with support from the Deutschen Forschungsgemeinschaft (DFG) and the Bundesminister für Bildung und Forschung (BMBF), Germany. The research is also part of a Royal Ontario Museum–Smithsonian Institution joint project *Systematics, Evolution, and Biogeography of Marine Organisms in Tropical Marine Habitats*, funded by an anonymous donor.

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