Distribution of deep-water Alcyonacea off the Northeast Coast of the United States

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Abstract. A database of deep-water alcyonacean records has been assembled using information that reaches back to the work of A.E. Verrill from the 1800s. These database records fall into two time periods, those from 1874 to 1920, and from 1950 to 2001. A total of 25 species in 10 families are so far known from the northeastern U.S. Most of these species are common in deeper waters of the continental shelf, with a few being restricted to the canyons and other slope environments. A comparison of western and eastern North Atlantic records indicates there is little similarity between the regions. In the cold-temperate to boreal part of the region there is about 41 % similarity of the "stoloniferous" and "massive body" soft coral species, but only about 28 % similarity amongst all the "gorgonian" species. In the warm temperate part of the region the similarity for all groups is less than 10 %. Deep-water alcyonaceans are strongly impacted by bottom fishing gear so it is likely that modern distributional records will not be exactly similar to those from deep in the past.

Keywords. Alcyonacea, continental slope, database, distributions, octocorals

Introduction

Deep-water corals have been an increasing focus for marine conservation since about 1998. Attention was brought to bear on deep corals in Europe and Canada, especially in Norway, where large deep reefs, constructed by *Lophelia pertusa* over thousands of years were found to be easily destroyed by mobile fishing gear (Fosså et al. 2000). In Canada, long-line fishermen who had occasionally pulled large corals from the depths were concerned about the possibility that these coral areas would be destroyed in a short time period by the trawl fisheries (Breeze et al. 1997; Gass 2002). Following the First International Symposium on Deep-Sea Corals, held in Halifax in 2000, deep-dwelling corals became the "poster child" of non-governmental organizations, symbolizing all that was wrong with fisheries management, especially in the United States where the record of protection of these

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species has been dismal compared to Europe and Canada, both of the latter having recently established no trawling zones in areas where deep corals are known to be abundant.

A significant part of the problem regarding conservation of deep-water corals in the United States is the lack of a comprehensive knowledge about the distribution of deep-water coral taxa in this region. It should be noted, however, that along the American east coast deep-water corals have been known since at least 1862 when Verrill documented the presence of a *Primnoa* "on Georges Bank" (Verrill 1862). Several other deep-water coral species from depths greater than 200 fathoms (365 m) off the coasts of New England and Nova Scotia were documented by Verrill during the latter part of the 19th century (e.g., Verrill 1878a, 1878b, 1879, 1884). Many specimens were captured during dredging programs instituted by the U.S. Fish Commission (as the National Marine Fisheries Service was known in those days), but an equally large number of specimens were brought to Verrill's attention by schooner captains who had pulled the corals from the bottom while tub trawling. While few "reefs" have been found off northeast North America (there is one news report of a *Lophelia* reef about 1 km long off Nova Scotia), the coral fauna is diverse and includes several octocoral species as well as hard corals (Breeze et al. 1997; Gass 2002). Seventeen species of scleractinian corals (hard corals) are known from Cape Hatteras to the Gulf of Maine (Cairns and Chapman 2001). Only one species (*Astrangia poculata*) occurs in shallow water and 71 % of the 17 species occur deeper than 1000 m. Forty-seven percent of the scleractinian corals from the cold-temperate U.S. coast are widespread species and 28 % occur across the Atlantic, with only a single species, *Vaughanella margaritata*, endemic to the NW Atlantic (Cairns and Chapman 2001). Photographic transects of the slope and canyon faunas south of Georges Bank recorded over 25 species of both hard corals and octocorals with several taxa dominant in the overall megafaunal community (Hecker et al. 1980, 1983; Valentine et al. 1980; Cooper et al. 1987; Hecker 1990). However, seven species (two hard corals and five soft corals, respectively) tend to occur in high densities in different areas of the canyon/slope environment: *Desmosmilia lymani*, *Flabellum alabastrum*, *Acanella arbuscula*, *Anthomastus agassizii*, *Eunepthya* (now *Capnella*) *florida*, *Paramuricea borealis* (now *P. grandis*), and *Primnoa resedaeformis* (Valentine et al. 1980; Hecker 1990).

The benthic fauna of the Northeast Peak of Georges Bank was characterized as having two octocorals, *Primnoa resedaeformis* and *Paragorgia arborea*, as common components based on dredge sampling (Theroux and Grosslein 1987). Wigley (1968) described *Paragorgia* as a common component of the gravel fauna of the Gulf of Maine and stated that representative gravel faunas occurred on "Cashes Ledge, parts of Great South Channel, the northeastern part of Georges Bank, western Browns Bank, Jeffreys Ledge, and numerous other smaller banks in the Gulf of Maine region."

The report by Theroux and Wigley (1998) on the distribution of macrobenthic invertebrates off the northeastern United States, while an excellent summary of the distribution of major taxonomic groups, lacked taxonomic specificity for corals. Stony corals were lumped with all of the Zoantharia (including burrowing anemones, solitary epibenthic anemones, and colonial anemones). However, the distribution of the Alcyonaria (now the Octocorallia), comprising the soft corals (Alcyonacea and Gorgonacea, now combined under the single name Alcyonacea) and sea pens (Pennatulacea), showed patterns useful for predicting the distribution of soft coral taxa (based on 63 samples, 6 % of total). These taxa were patchily distributed primarily along the outer margin of the continental shelf and on the continental slope and rise. They were not collected in samples shallower than 50 m depth (and it is unclear if deeper samples included the shallow soft coral *Gersemia rubiformis,* as there were many samples unidentified to the level of genus in the database). Alcyonaceans and gorgonaceans (soft corals) were collected from gravel and rock outcrop habitats while pennatulids were collected from sand-silt and silt-clay sediments.

As one can see, deep-water corals have been recorded, often sporadically, for the northeastern United States for more than 125 years. Until now, however, these various records have not been pulled together into one database which can be analyzed for distributional patterns. In this paper we present a summary of the known records of deep-water alcyonaceans from the northeastern United States, and compare these records to the alcyonacean fauna of the North Atlantic Ocean as a whole (see Appendix 1).

Methods

We created a GIS database of known occurrences of deep-water corals (soft corals and sea fans of the Order Alcyonacea) off the northeastern United States. The database was first constructed in Microsoft Access, then ported to ArcView for record mapping. The dataset includes records from published accounts of Verrill (as cited above), Deichmann (1936), and the detailed maps of camera tows from Hecker et al. (1980, 1983), as well as the web-accessible records of the Yale Peabody Museum collection, Northeast Fisheries Science Center Benthic Database records (of identified coral taxa), and observations from recent NOAA supported studies in 2001 (NURC, Ocean Exploration projects). This database does not currently include other possible data sources: (1) photographic transect studies in submarine canyons led by Richard Cooper (e.g., Valentine et al. 1980; Cooper et al. 1987), (2) video records from the NURC North Atlantic and Great Lakes (office in Groton, Connecticut) video archive, (3) specimens deposited in museums by the U.S. Northeast Fisheries Science Center and not yet identified, and (4) specimens in museums from this area but whose records are not available electronically.

For the broader geographic comparisons, we used records compiled from the following sources: Madsen (1944), Bayer (1957, 1964a, 1964b, 1979, 2001), Carpine and Grasshoff (1975), Grasshoff (1977, 1981, 1985, 1989), Cairns (2001), and Cairns and Bayer (2002). The classification of alcyonaceans used here is that of Bayer and Grasshoff, as updated and modified by Williams and Cairns and posted on Gary Williams' web site (http://www.calacademy.org/research/izg/OCTOCLASS.htm) where no formal suborder level names are used within the Order Alcyonacea.

Results and discussion

In all, the database currently contains 761 records, from the years 1874 to 2001. Certain locations, such as Oceanographer and Lydonia Canyons, as well as a few other locations examined with a towed camera sled by Hecker et al. (1980, 1983), have a high density of data records, most of which do not show well at the scale of the illustrations used here. That information can be obtained by requesting from the authors a copy of the ArcView database CD (Watling et al. 2003).

The database records fall into two distinct time periods: 1874-1920 (Fig. 1) and 1950-2001 (Fig. 2). The early records come primarily from the expeditions of many U.S. vessels, most of which were involved in mapping of the seabed and various oceanographic features. The corals were obtained incidentally in dredge hauls, and most were identified by Louis de Pourtalès and A.E. Verrill. All of these records are summarized in Deichmann (1936), or are listed on the Yale Peabody Museum web site of specimen records (http://www.peabody.yale.edu/collections/iz/).

The records from 1950 onwards come from a variety of sources, and represent a series of explorations of the continental shelf and slope of the U.S. The earliest represent corals found in sediment samples taken by the U.S. Geological Survey. Many of the canyon and slope records are from early Alvin submersible dives, also made for geological studies as well as baseline studies conducted in anticipation of

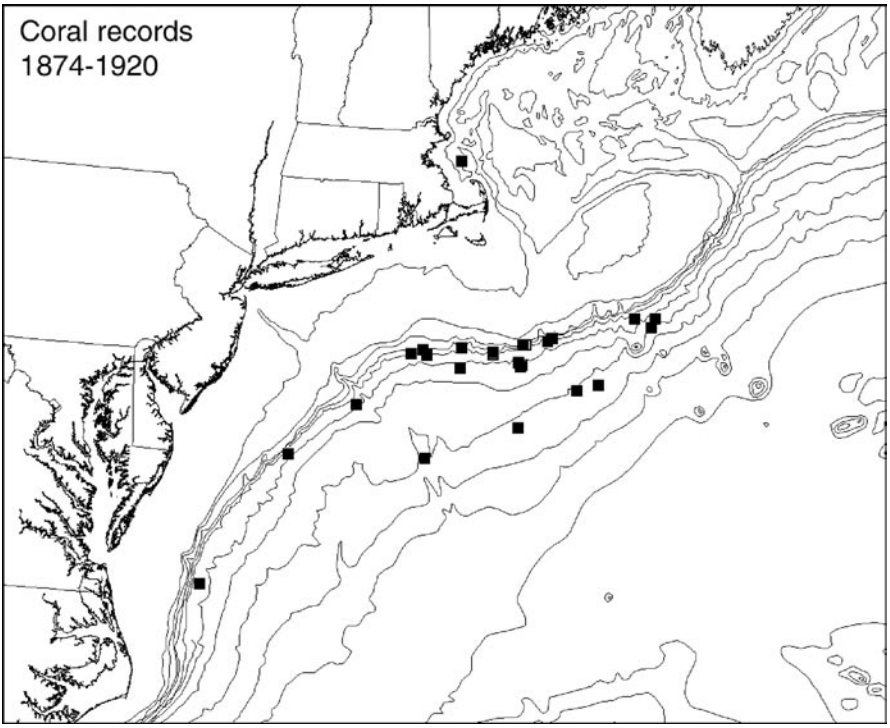

Fig. 1 Coral records for the years 1874-1920. With the exception of the single record off Boston, all are from deep-water along the continental slope and rise

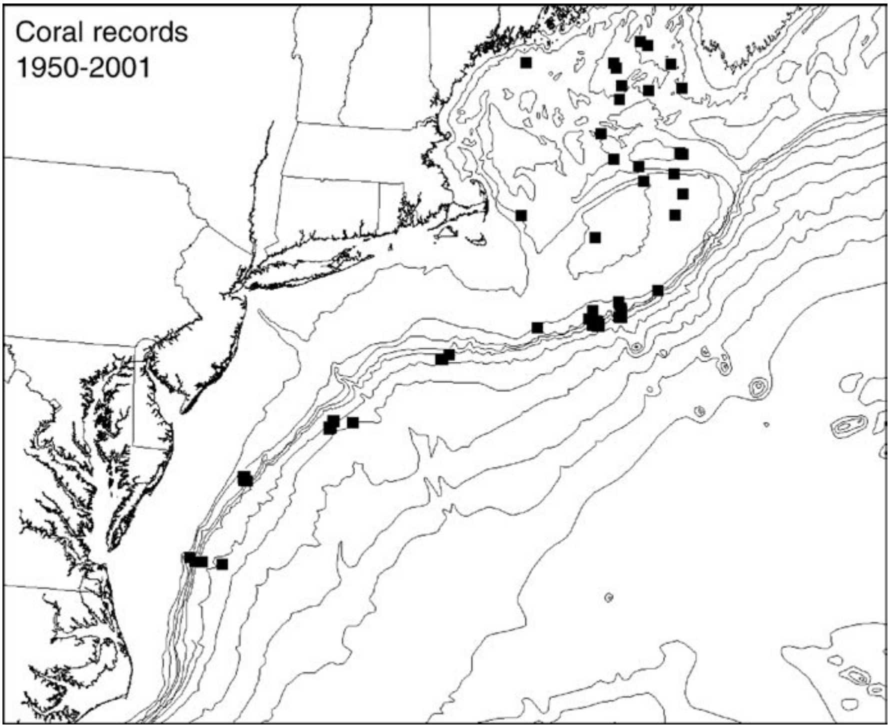

Fig. 2 Coral records for the years 1950-2001. There is a broad distribution of coral records from the Gulf of Maine, reflecting records from the U.S. National Marine Fisheries Service, and clusters of records from various canyons along the continental slope. Most of the latter are attributable to geological surveys of the canyons and baseline environmental surveys preparatory to proposed oil drilling

exploratory oil drilling, with the species identified from 35 mm film images by Dr. Barbara Hecker or her associates and recorded in Hecker et al. (1980, 1983). Other records, especially in Oceanographer, Lydonia, and Baltimore Canyons, as well as sites along the continental slope come from 35 mm film images made by Hecker et al. (1980, 1983) using a towed camera system. As a part of the Hecker et al. (1980) report, Dennis Opresko prepared a guide to the common octocorals, and a limited number of "voucher" specimens were examined to ground truth the identifications made from the film. In fact, Hecker et al. (1980, 1983) acknowledge that it was very difficult to be certain of all identifications in part because "voucher" specimens were often contracted whereas on film a specimen might look quite different, a fact that needs to be kept in mind when examining the distribution patterns in the database. The last of the modern records used here are from trawl samples made for fisheries investigations by the National Marine Fisheries Service. In some cases, these records include a species identification, but many times do not. If species identification was not given, the record was not used when the database was ported over to ArcView. Again there is uncertainty about the accuracy of the identifications.

A total of 25 species in 10 families have been recorded from the northeastern U.S. continental shelf and slope north of Cape Hatteras (Table 1). Species in the "Holaxonia", "Scleraxonia", and "Calcaxonia" are the best documented, primarily because of their larger form, but also because they are most abundant in the deeper waters of the continental slope. The Clavulariidae are most likely under-represented in NW Atlantic waters. Because of their small size they are probably overlooked by biologists unfamiliar with their general morphology.

Records in the database fell into two time periods, 1920 and earlier, and 1950 and later. The early records, beginning with what is now *Clavularia modesta* (Verrill) from Stellwagen Bank in 1874, are all from dredge samples obtained by U.S. Coast Survey vessels. Most of the effort was directed toward sampling in the deep waters off the continental shelf. After a hiatus of three decades or so, exploration of the continental slope began again, this time by geologists and then deep-sea biologists.

Table 1 List of Alcyonacea known to occur on the northeastern U.S. (north of Cape Hatteras) continental shelf and slope

"Stoloniferous forms"

Clavulariidae

Clavularia modesta (Verrill, 1874)
Clavularia rudis (Verrill, 1922)

"massive body forms"

Alcyoniidae

Alcyonium digitatum Linné, 1758
Anthomastus grandiflorus Verrill, 1878
Anthomastus agassizii Verrill 1922

Nephtheidae

Gersemia rubriformis (Ehrenberg, 1834)
Gersemia fructicosa (Sars, 1860)
Capnella florida (Rathke, 1806)
Capnella glomerata (Verrill, 1869)

"Holaxonia"

Acanthogorgiidae

Acanthogorgia armata Verrill, 1878

Plexauridae

Paramuricea grandis Verrill, 1883
Paramuricea placomus (Linné, 1758)
***Paramuricea* n. sp.**
Swiftia casta (Verrill, 1883)

"Scleraxonia"

Anthothelidae

Anthothela grandiflora (Sars, 1856)

Paragorgiidae

Paragorgia arborea (Linné, 1758)

"Calcaxonia"

Chrysogorgiidae

Chrysogorgia agassizii (Verrill, 1883)
Iridogorgia pourtalesii Verrill, 1883
Radicipes gracilis (Verrill, 1884)

Primnoidae

Narella laxa Deichmann, 1936
Primnoa resedaeformis (Gunnerus, 1763)
Thouarella n. sp.

Isididae

Acanella arbuscula (Johnson, 1862)
Keratoisis ornata Verrill, 1878
Keratoisis grayi Wright, 1869
Lepidisis caryophyllia Verrill, 1883

Much of the geological work was directed first to understanding the formation of deep-sea canyons, and then to the search for deep oil deposits. Biologists became a significant part of this work in the 1980s as environmental baseline studies were conducted in case deep-water oil drilling was to commence. Other coral records were produced, especially in the Georges Bank and Gulf of Maine waters, as bycatch from the National Marine Fisheries Service spring and fall groundfish surveys.

For the species in the database, two distinct distributional patterns emerge. Most of the alcyonaceans are species of deep-water, for example, those in the genera *Anthomastus*, *Acanthogorgia*, *Acanella*, *Anthothela*, *Lepidisis*, *Radicipes*, *Clavularia*, and *Swiftia* (Figs. 3 and 4). The records of all these species are for depths greater than 500 m. Other species, such as *Paragorgia arborea*, *Primnoa resedaeformis*, and those in the genus *Paramuricea*, range throughout shelf waters to the upper continental slope (Figs. 3 and 4). *Paragorgia arborea* and *P. resedaeformis* are widespread North Atlantic and North Pacific species (Madsen 1944; Tendal 1992). Not shown in these maps, and not common in the database as it is now constructed, are the numerous nearshore records of *Gersemia rubiformis* and *Alcyonium* species.

Cairns and Chapman (2001) analyzed distributional records of deep-water scleractinian corals. They divided the eastern and western Atlantic into several

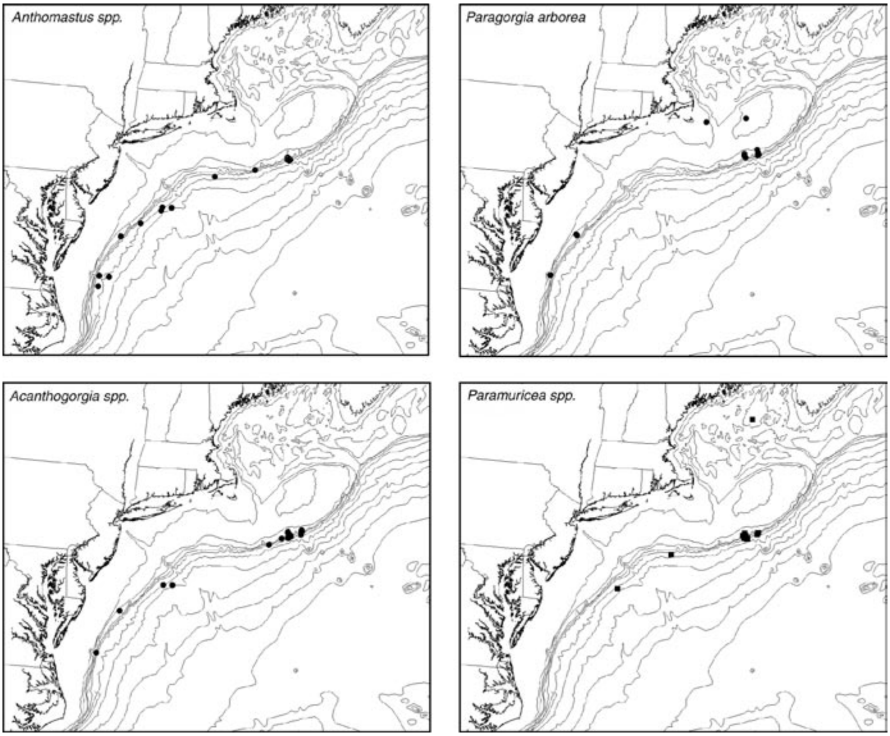

Fig. 3 Distribution of four alcyonacean genera along the east coast of the United States

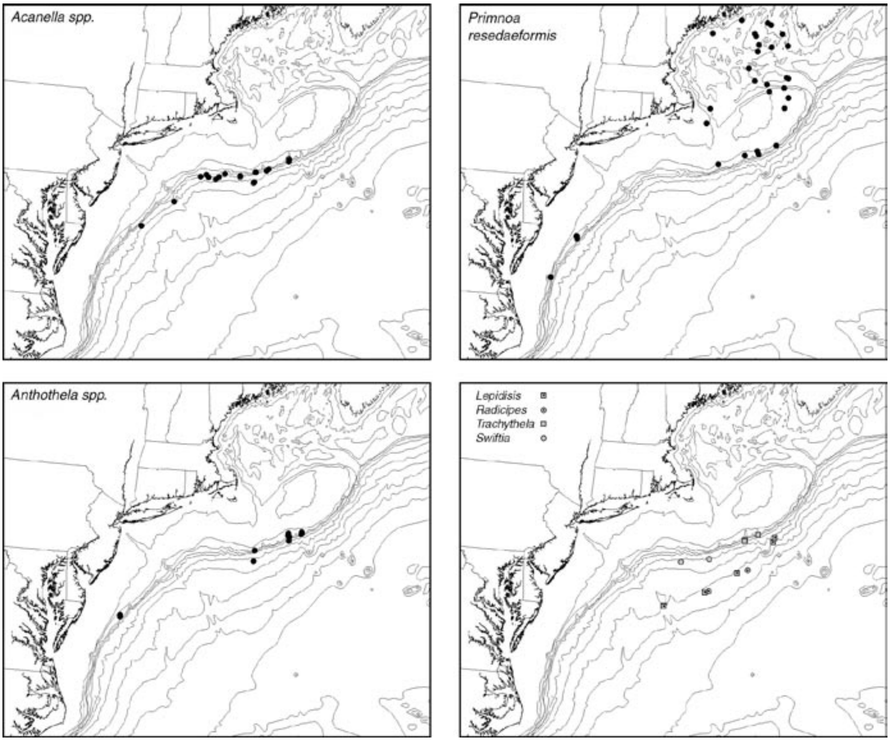

Fig. 4 Distribution of seven genera along the U.S. east coast

regions, four of which are adopted here with slight modifications. The eastern Atlantic includes regions IIB, ranging from the English Channel to northern Scandinavia and Iceland, and IIIA extending from the English Channel south to western Africa, including the Azores and associated seamounts. In the western Atlantic, region IIA extends from the Straits of Belle Isle in northern Newfoundland south to Cape Hatteras, and IA from Cape Hatteras to the Florida Straits (see Appendix 2). In this paper, we extended region IIA northwards to Baffin Island and Davis Straits. Cairns and Chapman had labelled those waters as part of their Arctic region. The extension of region IIA, we believe, is strengthened by an analysis of cumacean distributions, several species of which are seen to track Norwegian-Greenland Sea Overflow Water south of Iceland to the Davis Straits and southward along the northeastern U.S. continental slope in what is usually called the Western Boundary Undercurrent (Watling, unpublished).

A summary of the species distributions for these regions is given in Table 2 and Appendix 1. As a result of extending region IIA into the Davis Straits area, four additional species are included, all in the Family Clavulariidae. The greatest similarity of Regions IIA and IIB is in the "stoloniferous" and "massive body form" soft corals, where 7 of the 17 species (41 %) recorded to date can be found on both sides of the Atlantic. For the remaining alcyonaceans, the "Gorgonacea" of old, only 6 of 21 species (28 %) are common to both regions.

Table 2 Zoogeographic relationships of alcyonaceans of the temperate and cold-water North Atlantic region. Roman numerals and letters in the first line refer to regions as defined by Cairns and Chapman (2001) and used for analysis of deep scleractinian patterns

	IIA *E. Canada to Cape Hatteras*	*IIB* *Boreal Eastern Atlantic*	*IIA : IIB in common*	*IA* *Cape Hatteras to Florida Straits*	*IIIA* *Lusitanian-Mediterranean*	*IA : IIIA in common*
"Stoloniferous forms"						
Clavulariidae	6	7	2	2	8	0
"massive body forms"						
Alcyoniidae	3	2	2	1	6	1
Nephtheidae	3	3	3	0	1	0
"Scleraxonia"						
Anthothelidae	1	1	1	1	1	0
Paragorgiidae	1	1	1	2	2	1
Coralliidae	0	0	0	2	5	1
"Holaxonia"						
Acanthogorgiidae	1	0	0	2	2	0
Plexauridae	4	4	1	4	22	0
Gorgoniidae	0	0	0	4	9	0
"Calcaxonia"						
Chrysogorgiidae	3	0	0	4	8	2
Ellisellidae	0	0	0	1	3	0
Primnoidae	3	1	1	6	10	2
Isididae	4	3	2	4	12	3
Total Species	29	22	13	33	89	10

For the warm-temperate regions IA and IIIA, the picture is vastly different (Table 2). Only 1 of the 17 species (5 %) of soft corals, and 8 of 95 species (8 %) of “gorgonaceans” are common to both regions. This disparity is most likely due to the very different amount of hard substrate area involved. Region IIIA includes the Azores, Madeira, and several seamount groups that increase total habitat area. In Region IA, the deep slope widens along the Blake Plateau, but narrows again quickly off Florida, and seamounts are absent. Our recent work on the New England seamount chain suggests that the diversity of “gorgonaceans” in the western Atlantic might be more similar to that of the eastern Atlantic than we currently have data to support, but this statement will have to await detailed taxonomic work.

Fishing has had significant impacts on deep-water coral populations worldwide. While the effects of fishing on the deep reefs off Norway have been by now well-documented (e.g., Fosså et al. 2000), similar data for alcyonacean communities are sparse. Observations of the impacts of a single trawl tow through *Primnoa* habitat in the Gulf of Alaska, where 1000 kg of coral were landed, showed seven years later that 7 of 31 colonies remaining in the trawl path were missing 80-99 % of their branches and boulders with corals attached were tipped and dragged (Krieger 2001). Damage was restricted to the net path. Approximately 50 colonies were observed within 10 m of the net (where bridles would have swept over the seafloor) and no damaged colonies or disturbed boulders were observed. Long-line gear is also noted to tip and dislodge corals (Krieger 2001). Bycatch data from a long-line survey in the Gulf of Alaska and Aleutian Islands showed *Primnoa* and other coral taxa were caught on 619 of 541,350 hooks fished at 150-900 m depths (Krieger 2001).

Corals are clearly sensitive to fishing gear impacts and recovery rates are extremely slow based on our knowledge of recruitment, growth rates, and age structure. The ability to age deep-water octocorals is relatively new and various methods are used in different studies. For *Primnoa resedaeformis*, a common outer shelf-upper slope species, Risk et al. (2002) estimates linear growth rates at the distal tips of the colonies at 1.5-2.5 mm yr^{-1} based on comparisons of live specimens with growth rates through the base of a sub-fossil specimen collected from the Northeast Channel at 450 m. Growth rates of this species in the Gulf of Alaska are reported as 1.60-2.32 cm yr^{-1}, although these samples were collected at less than 200 m depth (Andrews et al. 2002). Age estimates for only a few specimens demonstrate this species lives for hundreds of years. The colony collected from the Northeast Channel (Risk et al. 2002) has an estimated age of >300 years, which is in accordance with age estimates of the same species collected in Alaska (>100 years; Andrews et al. 2002).

Data on recruitment patterns is even more limited. A single series of observations in the Gulf of Alaska suggest that recruitment of *Primnoa* sp. is patchy and aperiodic (Krieger 2001). No recruitment of new colonies was observed in an area where *Primnoa* was removed by trawling after seven years. However, six new colonies were observed at a second site one year after trawling. Four of these colonies were attached to the bases of colonies removed by trawling. Recruits of *Primnoa* were also observed on two 7 cm diameter cables (>15 colonies each). On the other hand, our limited observations of corals in the Gulf of Maine and in submarine canyons has revealed abundant new recruits of both *Primnoa resedaeformis* and *Paramuricea* spp. (Watling, Auster, and France, unpublished observations). Whether these young colonies were produced by larval recruitment or branch dropping (as in shallow-water gorgonians) is impossible to say at this time.

In conclusion, our knowledge of the biology of deep-water alcyonaceans in the North Atlantic is still very limited. Unfortunately, because of the widespread use of fishing gear in this region, it may be that many records, especially of the gorgonians, may be simply historical. That is, if recruitment rates away from centers of colony abundance are really low, reestablishment of populations in areas where there has been widespread removal, is likely to take a very long time.

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Appendix 1

Complete list of all alcyonacean species included in the biogeographic comparison (see Table 2) of the eastern and western Atlantic regions, as defined in Cairns and Chapman (2001), that are north of the tropics

	IIA W N Atlantic E. Canada to Cape Hatteras	**IIB Boreal Eastern Atlantic**	**IA W N Atlantic Cape Hatteras to Florida Straits**	**IIIA Lusitanian-Mediterranean**
"Stoloniferous forms"				
Clavulariidae				
Anthelia borealis (Koren and Danielssen, 1883)		X		X
Anthelia fallax Broch, 1912		X		X
Clavularia alba (Grieg, 1888)	X	X		
Clavularia arctica (Sars, 1860)		X		X
Clavularia griegii Madsen, 1944		X		
Clavularia levidensis Madsen, 1944	X			
Clavularia marioni (von Koch, 1891)				X
Clavularia modesta (Verrill, 1874)	X			
Clavularia rudis (Verrill, 1922)	X			
Clavularia venustella Madsen, 1944	X			
Sarcodictyon roseum (Philippi, 1842)		X		X
Scleranthelia rugosa (Pourtalès, 1867				X
Scyphopodium ingolfi (Madsen, 1944)			X	X
Telesto fructiculosa Dana, 1846			X	
Telestula septentrionalis Madsen, 1944	X	X		X
	6	7	2	**8**
"massive body forms"				
Paralcyoniidae				
Paralcyonium spinulosum Delle Chiaje, 1822				X
	0	0		**1**
Alcyoniidae				
Alcyonium acaule Marion, 1878				X
Alcyonium coralloides (Pallas, 1766)				X
Alcyonium digitatum Linnaeus, 1758	X	X		X
Alcyonium palmatum Pallas, 1766				X
Anthomastus agassizii Verrill 1922	X			
Anthomastus grandiflorus Verrill, 1878	X	X	X	X
Ceratocaulon wandeli Jungersen, 1892				X
	3	2	1	**6**

Appendix 1 continued

	IIA W N Atlantic E. Canada to Cape Hatteras	IIB Boreal Eastern Atlantic	IA W N Atlantic Cape Hatteras to Florida Straits	IIIA Lusitanian-Mediterranean
Nephtheidae				
Gersemia rubiformis (Ehrenberg, 1834)	X	X		
Capnella florida (Rathke, 1806)	X	X		X
Capnella glomerata (Verrill, 1869)	X	X		
	3	3	0	**1**
"Scleraxonia"				
Anthothelidae				
Anthothela grandiflora (M. Sars, 1856)	X	X		X
Titanidium suberosum (Ellis and Solander, 1786)			X	
	1	1	1	**1**
Paragorgiidae				
Paragorgia boschmai Bayer, 1964			X	
Paragorgia arborea (Linnaeus, 1758)	X	X		X
Paragorgia johnsoni Gray, 1862			X	X
	1	1	2	**2**
Coralliidae				
Corallium maderense (Johnson, 1899)				X
Corallium medea Bayer, 1964			X	
***Corallium* sp.**				
Corallium johnsoni Gray, 1860				X
Corallium niobe Bayer, 1964			X	X
Corallium rubrum (Linnaeus, 1758)				X
Corallium tricolor (Johnson, 1899)				X
	0	0	2	**5**
"Holaxonia"				
Acanthogorgiidae				
Acanthogorgia armata Verrill, 1878	X			X
Acanthogorgia hirsuta Gray, 1857				X
Acanthogorgia schrammi (Duchassaing and Michelotti, 1864)			X	
Acanthogorgia aspera Pourtalès, 1867			X	
	1	0	2	**2**

Appendix 1 continued

	IIA W N Atlantic E. Canada to Cape Hatteras	IIB Boreal Eastern Atlantic	IA W N Atlantic Cape Hatteras to Florida Straits	IIIA Lusitanian-Mediterranean
Plexauridae				
Bebryce mollis Molippi, 1842				X
Dentomuricea meteor Grasshoff, 1977				X
Echinomuricea klavereni Carpine and Grasshoff, 1975				X
Muricea pendula Verrill, 1868			X	
Muriceides kuekenthali (Broch, 1912)		X		
Muriceides lepida Carpine and Grasshoff, 1975				X
Muriceides paucituberculata (Marion, 1882)				X
Paramuricea clavata (Risso, 1826)				X
Paramuricea grandis (Verrill, 1883)	X			
Paramuricea grayi (Johnson, 1861)				X
Paramuricea macrospina (Koch, 1882)				X
***Paramuricea* sp.** GOM	X		X	
Paramuricea biscaya Grasshoff, 1977				X
Paramuricea candida Grasshoff, 1977				X
Paramuricea placomus (Linnaeus, 1758)	X	X		X
Placogorgia massiliensis Carpine and Grasshoff, 1975				X
Placogorgia becena Grasshoff, 1977				X
Placogorgia coronata Carpine and Grasshoff, 1975				X
Placogorgia graciosa (Tixier-Durivault and d'Hond, 1975)				X
Placogorgia intermedia (Thomson, 1927)				X
Placogorgia terceira Grasshoff, 1977				X
Spinimuricea atlantica (Johnson, 1862)				X
Swiftia casta (Verrill, 1883)	X		X	
Swiftia pourtalesii Deichmann, 1936			X	
Swiftia borealis (Kramp, 1930)		X		
Swiftia dubia (Thomson, 1929)				X
Swiftia pallida Madsen, 1970				X
Swiftia rosea (Grieg, 1887)		X		
Thesea talismani Grasshoff, 1986				X
Villogorgia bebrycoides (Koch, 1887)				X
	4	4	4	**22**
Gorgoniidae				
Eunicella filiformis Studer, 1879				X
Eunicella gazella Studer, 1878				X

Appendix 1 continued

	IIA W N Atlantic E. Canada to Cape Hatteras	IIB Boreal Eastern Atlantic	IA W N Atlantic Cape Hatteras to Florida Straits	IIIA Lusitanian-Mediterranean
Eunicella labiata Thomson, 1927				X
(?Eunicella) modesta Verrill, 1883			X	
Eunicella verrucosa (Pallas, 1766)				X
Leptogorgia albipunctata Stiasny, 1936				X
Leptogorgia purpureoviolacea (Stiasny, 1936)				X
Leptogorgia sarmentosa (Esper, 1791)				X
Leptogorgia viminalis (Pallas, 1766)				X
Leptogorgia virgulata (Lamarck, 1815)			X	
Leptogorgia setacea (Pallas, 1766)			X	
Leptogorgia hebes Verrill, 1869			X	
Lophogorgia capeverdiensis Grasshoff, 1986				X
	0	0	4	**9**
"Calcaxonia"				
Chrysogorgiidae				
Chrysogorgia herdendorfi Cairns, 2001			X	
Chrysogorgia agassizii (Verrill, 1883)	X			X
Chrysogorgia campanula Madsen, 1944				X
Chrysogorgia elegans (Verrill, 1883)			X	X
Chrysogorgia quadruplex Thomson, 1927				X
Distichogorgia sconsa Bayer, 1979			X	
Iridogorgia pourtalesii Verrill, 1883	X			X
Metallogorgia melanotrichos (Wright and Studer, 1889)				X
Radicipes challengeri (Wright, 1885)				X
Radicipes gracilis (Verrill, 1884)	X		X	X
	3	0	4	**8**
Ellisellidae				
Ctenocella (Ellisella) paraplexauroides Stiasny, 1936				X
Nicella granifera (Kölliker, 1865)				X
Ctenocella (Viminella) flagellum (Johnson, 1863)				X
Ctenocella (Ellisella) schmitti (Bayer, 1961)			X	
	0	0	1	**3**

Appendix 1 continued

	IIA W N Atlantic E. Canada to Cape Hatteras	IIB Boreal Eastern Atlantic	IA W N Atlantic Cape Hatteras to Florida Straits	IIIA Lusitanian-Mediterranean
Primnoidae				
Callogorgia americana Cairns and Bayer 2002			X	
Callogorgia verticillata (Pallas, 1766)				X
Calyptrophora gerdae Bayer, 2001			X	
Calyptrophora josephinae (Lindstroem, 1877)				X
Calyptrophora trilepis (Pourtalès, 1868)			X	
Candidella (=Stenella) imbricata (Johnson, 1862)			X	X
Narella bellissima (Kükenthal, 1915)				X
Narella laxa Deichmann, 1936	X			X
Narella regularis (Duchassaing and Michelotti, 1860)			X	X
Narella versluysi (Hickson, 1909)				X
Paracalyptrophora josephinae (Lindström, 1877)				X
Plumarella pourtalesii (Verrill, 1883)			X	
Primnoa resedaeformis (Gunnerus, 1763)	X	**X**		X
Primnoella jungerseni Madsen, 1944				X
***Thouarella* n. sp.**	X			
Thouarella hilgendorfi (Studer, 1879)				X
	3	1	6	**11**
Isididae				
Acanella arbuscula (Johnson, 1862)	X	X		X
Chelidonisis aurantiaca Studer, 1891				X
Isidella longiflora (Verrill, 1883)				X
Isidella elongata (Esper, 1788)				X
Isidella lofotensis Sars, 1868		X		X
Keratoisis ornata Verrill, 1878	X		X	
Keratoisis flexibilis (Pourtalès, 1868)			X	X
Keratoisis grayi Wright, 1869	X	X	X	X
Lepidisis caryophyllia Verrill, 1883	X			X
Lepidisis cyanae Grasshoff, 1986				X
Lepidisis longiflora Verrill, 1883			X	X
Lepidisis macrospiculata (Kükenthal, 1915)				X
	4	3	4	**12**
Total Alcyonacea	**29**	**22**	**33**	**91**

Appendix 2

Reprint of Figure 3 from Cairns and Chapman (2001) showing regions used in a biogeographic comparison of scleractinian corals of the North Atlantic Ocean