Proc 8th Int Coral Reef Sym 2:1387–1392. 1997

BIODIVERSITY AND DISTRIBUTION OF DEEP AND SHALLOW WATER SPONGES IN THE BAHAMAS

John K. Reed and Shirley A. Pomponi

Harbor Branch Oceanographic Institution, 5600 U.S. 1 North, Fort Pierce, Florida, U.S.A. 34946

ABSTRACT

Nine expeditions were conducted in the Bahamas from 1987 to 1995 for the purpose of collecting marine organisms for biomedical research. Collections concentrated on sponges from various deep water habitats: the fore reef slope and escarpment (30-60 m), the deep fore reef slope and escarpment (60-150 m), and the deep shelf slope (150-922 m). A total of 417 sites were sampled throughout the archipelago using the *Johnson-Sea-Link* and *Clelia* Research Submersibles, ROV, and scuba. For each sample, a taxonomic voucher specimen was prepared, and each was documented with in situ and laboratory photographs and videotapes. Collection site and sample descriptions were transcribed into a database. A total of 3058 sponges were collected from all depth zones: 922-300 m, 19.2%; 300-60 m, 39.6%; and <60 m, 41.2%. Nearly 300 species were enumerated, representing 20 orders, 61 families, and 137 genera. Distributional patterns of the taxa were analyzed with depth and latitude.

INTRODUCTION

Biological surveys of our aquatic and terrestrial resources have had a renewed emphasis during the last decade. The urgency for documentation of biodiversity throughout various biotopes is increasing as habitats and species are impacted by human and natural events. In the marine environment, shallow water coastal habitats are best known due to ease of access. These habitats are also the first to be observed if degrading and thus the need for surveys of their biodiverstiy is immediate.

Our knowledge of deep water habitats and biodiversity, however, is woefully inadequate and certainly less comprehensive than that of shallow marine environments. In part, this is due to the difficulty and cost involved with sampling or surveying deep habitats. This is especially true of irregular, hard bottom rocky habitats where conventional methods of trawling or dredging are not feasible for thorough sampling. These methods are also destructive and non-selective. While less intrusive methods, such as scuba collections or camera sleds, have been used in shallow water, these are not suitable for the deep rocky habitats of the continental shelf and slope.

With the advent of modern research submersibles these deep water habitats are slowly being surveyed. Submersibles have led to the discovery and study of numerous deep water biotopes including coral banks, continental shelves and slopes, and mid-oceanic vents. Far from being impoverished in terms of species richness and habitat diversity, some deep water habitats have proved to be equally diverse as shallow tropical reefs. Deep water coral banks, typically comprised of monospecific, azooxanthellate corals such as *Oculina* and *Lophelia* which occur at depths of 70-100 m and 130->1000 m, respectively, are extremely species-rich (Mullins et al. 1981; Reed 1980, 1992). Other very diverse deep reef environments which are extensions of shallow tropical reefs have been studied by submersible in the Bahamas (Porter 1973; Colin 1976; Reed 1985), Florida (Pomponi 1981), Jamaica (Lang 1974; Land and Moore 1977), Belize (James and Ginsburg 1979; Colin 1974), and Enewetak Atoll in the Pacific (Colin et al. 1986).

The majority of taxonomic literature on deep water sponges in the western Atlantic and Caribbean has origins from dredge and trawl records from well-known expeditions (*Challenger* 1873-1876, *Blake* 1879-1880, *Fish Hawk* 1899, and *Galathea* 1950-1952). Recent taxonomic studies of sponges collected by research submersibles are providing a better understanding of their phylogeny and diversity (Reed and Pomponi 1991; Pomponi et al. 1991; Diaz et al. 1993; Kelly-Borges and Pomponi, 1994; Kelly-Borges et al. 1994; Maldonado and Young, 1996). The taxonomy of deep water sponge fauna in the West Indies on the lower shelf down to 500 m is poorly known and few studies document their abundance and diversity (Schmidt, 1879, 1880; de Laubenfels 1934; Van Soest 1978, 1980, 1984; Van Soest and Stentoft 1988; Van Soest et al. 1990; Maldonado and Young, 1996).

This study is the result of a compilation of data from nine expeditions conducted throughout the Bahama Islands (Fig. 1) from 1987 to 1995. Collections and observations of benthic invertebrates utilizing manned submersibles, scuba, and remotely-operated-vehicles (ROV) provided detailed data on the depth, geographical and taxonomic distribution of shallow and deep water Porifera to depths of 922 m.

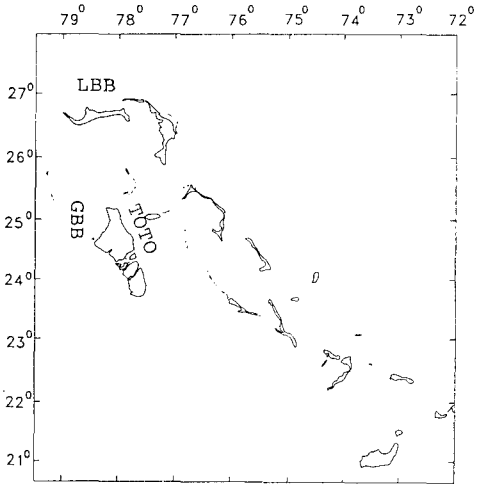

Fig. 1: Bahama Islands. LBB: Little Bahama Bank, GBB: Great Bahama Bank, TOTO: Tongue of the Ocean.

METHODS AND MATERIALS

All collections and observations were made by the Division of Biomedical Marine Research (DBMR) at Harbor Branch Oceanographic Institution (HBOI). The specific objectives of the expeditions were: 1) to observe, photograph and collect selected marine invertebrates and algae in deep and shallow water, 2) to prepare samples for subsequent isolation and characterization of novel compounds with therapeutic potential, and 3) to document the biodiversity of deep water benthic communities with videotapes, 35-mm photographs, and taxonomic reference specimens.

Samples were collected in shallow water (0-45 m) by wading, snorkeling, and scuba diving; and in deep water (45-922 m) with HBOI's *Johnson-Sea-Link I* and *II* (*JSL*) Research Submersibles, the *Clelia* Research Submersible, and the *Hysub* remotely-operated-vehicle (ROV). The submersibles are equipped with a manipulator arm which includes clam-shell grab, jaws, and suction hose; 12-bin rotating basket; color video camera; 35-mm camera; and a data recorder (Seabird) to log temperature, conductivity, salinity, and depth. The support vessels are HBOI's R/V *Seward Johnson* (62 m), R/V *Edwin Link* (51 m), and R/V *Sea Diver* (34 m).

Collection site coordinates were determined with Loran or Global Positioning System (GPS) navigation and coordinates were plotted using "The Bahamas Chart Kit" (1984 edition). Collection site descriptions, including latitude, longitude, habitat, depth, temperature, current, and weather conditions; along with sample descriptions, including morphology, color, abundance, taxonomy, and photographic reference for each sample were recorded at the time of collection. All data were transcribed into a DBMR database (Microsoft ACCESS).

Samples were photographed and videotaped in situ. Some shallow water samples were photographed in situ with a Nikonos V camera. Each sample was also photographed on deck. Original 35-mm slide photographs and videotapes are stored in DBMR's Photographic Library at HBOI.

Taxonomic reference specimens were subsampled from most specimens and stored in 20 dram scintillation vials and/or in 2 to 16 oz glass jars. All specimens are preserved in 70% ethanol. Some duplicate specimens were not vouchered. Taxonomic specimens are stored in DBMR's Reference Museum at HBOI.

Subsamples of sponges were extracted in ethanol for subsequent biological and chemical evaluation. Additional subsamples were used for isolation and culture of associated microorganisms, and for invertebrate cell culture. After taxonomic reference specimens were prepared, the remainder of each sample was stored at -20°C in a portable freezer on board the ship and transferred to DBMR's freezers at HBOI.

RESULTS

Collection sites

During nine expeditions throughout the Bahama Islands, 417 collection sites were sampled, of which 212 were deep water (184 submersible and 28 ROV) and 205 were shallow water (scuba and snorkel). The Bahamas consist of nearly 400 islands and islets which stretch over 540 nm from 27°N and 79°W to 21°N and 73°W (Fig. 1). Most of the larger islands are situated on two large sand banks, Little Bahama Bank to the north and Great Bahama Bank in the central region. To the southeast a series of outer islands are isolated from the banks and are separated from each other by channels from 1500 to 4700 m deep.

All major habitats were sampled, from the surface to 922 m. In deep water (>50 m) the following habitats occur: mud, sand and rubble slopes, low relief (<1 m) rock pavement, medium-high relief rock outcrops, rock boulders (1-10 m), pinnacles, reef crest and wall, fore reef slope, crevices/caves, and seamounts. At scuba depths (10-50 m) primary habitats are the deep fore reef slope and wall, patch reefs, spur and groove, sand chutes, caves, and *Thalassia* grassbeds. Shallower than 10 m, the habitats consist of *Thalassia* grassbeds, *Halimeda* and *Neogoniolithon* algal reefs, mud and sand flats, hard bottom flats and channels, red and black mangroves, patch reefs, brackish lagoons, inland salt lakes, caves, and shipwrecks.

The general geomorphology of the shelf edge throughout the Bahamas can be characterized into the following zones (modified from Reed, 1985):

Shallow reef zone (0-30 m)- Patch and fringing reefs are most common at 10,20, and 30 m depths. The reefs at 20-30 m typically occur at the top edge of the shelf break and are transected by sand chutes which cut through the reef crest allowing sediment to move from the shelf to the deep slopes.

Fore reef escarpment and slope (30-60 m)- The seaward facies of the shelf edge reefs often form overhanging rock buttresses or near-vertical rock walls to depths of 35-45 m. Below this a steep sand/rubble or rocky fore reef slope (45-70°) often occurs down to the next deep escarpment.

Deep fore reef escarpment and slope (60-150 m)- A vertical wall occurs at most sites, the top of which is approximately 60-70 m deep but may be as shallow as 45 m at some sites. These escarpments, which may extend to depths of 120-150 m (or as shallow as 90 m at a few sites), have highly convoluted facies consisting of overhanging buttresses, ledges, crevices, and caves. The top edge is also incised with sand chutes.

Island slope (150-300 m)- This zone often consists of steep (50-70°) rocky slopes which may be covered with sediment or rubble. Boulders (1-5 m high) are present at some sites between 200 and 300 m.

Deep island slope (300->1000 m)- This is highly variable amoung the sites, ranging from fine mud and sand slopes (5-50°) to rock pinnacles and boulders (up to 10 m high) and vertical walls.

Physical parameters

Collections were made during every month except February. Surface water temperatures were as low as 18°C on the shallow tidal channels during winter cold fronts and as high as 30+°C in protected areas in the summer. Shallow water temperatures on the shelf edge reefs averaged between 20 and 30°C during all collection periods. A thermocline of 1-3°C was common between 50 and 100 m and was most obvious in August and November-December. It was very slight or non-existent during collections in May-June. Below the thermocline, temperatures gradually declined with increasing depth throughout the year and at all sites down to a low of 6.0°C recorded at 908 m. Average temperature ranges were: 25.0-22.0°C at 60-150 m, 23.0-16.8°C at 150-300 m, 16.1-9.1°C at 300-600 m, 12.0-6.0°C at 600-900 m, and 6.0-7.0°C at 900 m.

Salinities were commonly ~36.5 ppt near the surface and gradually increased to a maximum level between 100 and 200 m. The highest salinity recorded was 36.7 ppt near 200 m. At all sites, salinities then decreased with depth to a low of 35.08 ppt at 914 m.

Bottom currents between 100 and 900 m often ranged from 0 to 0.5 knots (kn) and averaged ~0.1-0.2 kn. Only on a few occasions were stronger currents encountered, except for sites off Bimini and western Little Bahama Bank which impinge upon the Florida Current (Gulf Stream). Visibility at the deep sites was usually 15-30 m but occasionally as low as 5-10 m. Visibility at the shallow shelf-edge reefs ranged from 100+ m to 5 m.

Samples and taxonomy

A total of 3059 Porifera were collected during the nine expeditions. Of these, 41.6% (1273) were identified to species level, 70.0% to genus, 80.7% to family, 92.0% to order, and 96.8% to class (Fig. 2).

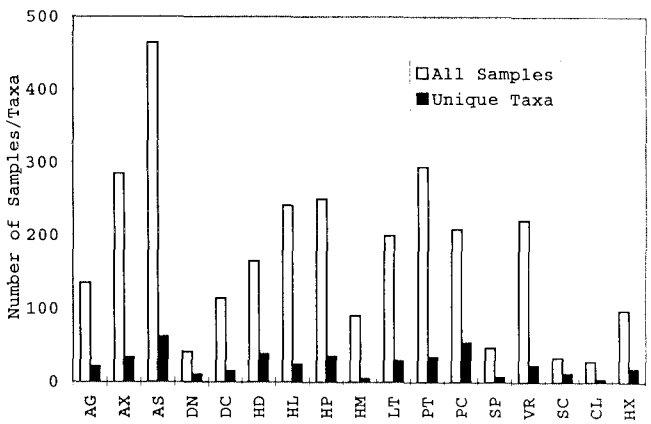

Fig. 2: Number of specimens and taxa by order or class. AG: Agelasida, AX: Axinellida, AS: Astrophorida, DN: Dendroceratida, DC: Dictyoceratida, HD: Hadromerida, HL: Halichondrida, HP: Haplosclerida, HM: Homosclerophorida, LT: Lithistida, PT: Petrosida, PC: Poecilosclerida, SP: Spirophorida, VR: Verongida, SC: sclerosponges, CL: Calcarea, HX: Hexactinellida.

All classes of Porifera were represented: Demospongiae (2803 specimens), Hexactinellida (98), Calcarea (28), and the sclerosponges (33). Although the latter group is no longer recognized as a valid class, we have kept the "sclerosponges" grouped as such for these analyses. Figure 2 shows the distribution of samples among the 20 represented orders. These were dominated by the Astrophorida (=Choristida, 465 specimens), Petrosida (294), Axinellida (285), Haplosclerida (250), Halichondrida (242), Verongida (222), Poecilosclerida (209), Lithistida (200), Hadromerida (164), and Agelasida (135). Rare orders consisting of 20 or fewer specimens each were the Leucettida (Class Calcarea); the Amphidiscosa, Dictyonina, and Lyssacina (Class Hexactinellida); and Calcifibrospongida and Ceratoporellida (sclerosponges).

A total of 61 families were represented and were dominated by Petrosiidae (218), Halichondriidae (204), Geodiidae (179), Niphatidae (143), Aplysinidae (141), Agelasidae (135), Pachastrellidae (110), and Thorectidae (101). Rare families represented by five or fewer specimens per family were the Leucettidae (Calcarea);

Desmoxyidae, Hemiastrellidae, Calthropellidae, Theneidae, Thrombidae, Dictyodendrillidae, Dysideidae, Halisarcidae, Spongiidae, Clionidae, Placospongiidae, Stylocordylidae, Tethyidae, Timeidae, Adociidae, Scleritodermidae, Vetulinidae, Desmacellidae, Hymedesmiidae, Phorbasidae, Tedaniidae, Ianthellidae (Demospongiae); Hyalonematidae, Caulophacidae, and Euplectellidae (Hexactinellida); and Calcifibrospongidae (sclerosponge).

A total of 429 unique taxa were identified, some of which were only identified to the level of order, family, or genus. Of these, 298 species-level taxa were identified. Some of these are new species which are currently under study and some were only identified as Genus sp.1, sp.2, etc. Of the 2143 specimens that were identified at least to the generic level, there were 137 distinct genera. Figure 2 shows the number of unique taxa that were identified for each order (i.e., the lowest taxon to which each sample was identified). In general, the Astrophorida were the most diverse order (62), followed by Poecilosclerida (54), Hadromerida (38), Haplosclerida (35), Petrosida (34), Axinellida (33), Lithistida (29), Halichondrida (24), and Verongida (23). The most diverse families were the Axinellidae (31 taxa), Halichondriidae (24), Geodiidae (24), Petrosiidae (23), Niphatidae (22), and Agelasidae (21).

Depth distribution

The depth distribution of the samples was categorized into six depth zones (30 m zone: 0-30 m depth range; 60 m: 31-60 m; 150 m: 61-150 m; 300 m: 151-300 m; 600 m: 301-600 m; and 922 m: 601-922 m) which reflect the general geomorphological zones described above. Figure 3 shows the number of orders, genera, species, and unique taxa that were found within each depth zone.

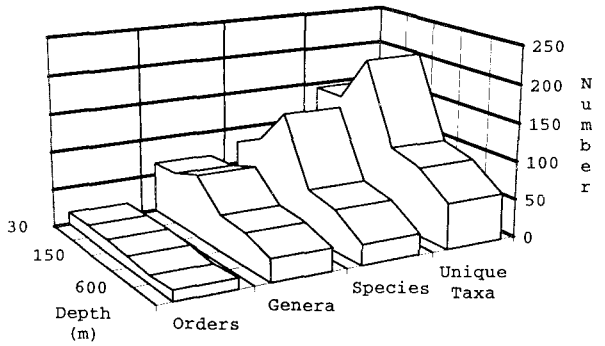

Fig. 3: Number of orders, genera, species, and unique taxa for each depth zone (30, 60, 150, 300, 600, 922 m).

Since the emphasis of the collections was deep water Porifera, the 30 m zone was not sampled as extensively and may not reflect the true diversity of the shallow habitats. Similarly, thinly encrusting samples (particularly in the Poecilosclerida and Dendroceratida) and stony hard samples (e.g., the sclerosponges) are more difficult to collect, and the numbers reported here may not reflect their true abundance and diversity. The number of orders per depth zone was relatively consistent (~17 orders each) throughout the shallower zones (30, 60 and 150 m). The 600 m zone had the least number of orders (11). The number of taxa was greatest at the 150 m zone (206 taxa) and abruptly decreased to 101 taxa within the 300 m zone to a low of 60 taxa at the 922 m zone. Within the latter zone and at depths over 800 m, only 31 taxa were identified.

The samples were further analyzed to determine which taxa were stenobenthic, or unique to a particular depth zone. There was a distinct shift in the distribution of orders with depth (Fig. 4). For example, the Hadromerida, Haplosclerida, and Poecilosclerida had their peak number of taxa within the 30 m zone. On the deep fore reef escarpment and slope (150 m zone), the Agelasida, Axinellida, Astrophorida, Dendroceratida, Dictyoceratida, Verongida, and the sclerosponges showed distinct peaks in number of taxa. Certain orders and classes were found within the 150 m zone but not on the deeper slope (Verongida, Dendroceratida, Agelasida, and Calcarea). On the island slope (300-922 m zones), the dominant taxa

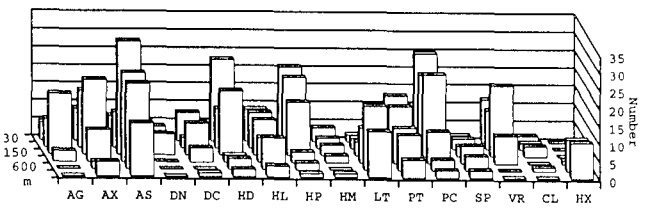

Fig. 4: Number of sponge taxa for each order and at each depth zone. See Fig. 2, 3 for depth zones and legends.

consisted of the Lithistida, Petrosida, Astrophorida, Halichondrida, and Hexactinellida.

Within the 30 and 60 m shallow water zones (depth range 0-60 m), 104 taxa were found to be unique and restricted to that depth range. The following common species occurred exclusively on the reefs of both the 30 m and 60 m zones: *Agelas dispar, Teichaxinella ?burtoni, Chondrilla nucula, Chondrosia collectrix, Anthosigmella varians, Spheciospongia cuspidifera, Topsentia ophiraphidites, T. bahamensis, Cribrochalina dura, Niphates digitalis, Siphonodictyon siphonum, Petrosia weinbergi, Ectyoplasia ferox,* and *Aplysina fulva*.

The dominant groups that were restricted exclusively to the deep wall and slope (150 m zone) consisted of 77 taxa, including *Agelas* (11 species), *Stelletta* (2 spp.), *Caminus* (1 sp.), *Erylus* (2 spp.), *Geodia* (3 spp.), *Phakellia* (2 spp.), *Teichaxinella* (3 spp.), *Smenospongia* (4 spp.), *Aaptos aaptos, Terpios* (2 spp.), *Forcepia ?trilabis, Aplysina* (3 spp.), *Goreauiella* sp., and *Calcifibrospongia actinostromarioides*.

On the island slope, 25 unique taxa were found exclusively within the 300 m zone, including several species of *Discodermia* (5 species), *Xestospongia* (3 spp.), *Axinella ?strongyloxea, Spongosorites siliquaria, Stromatospongia ?norae,* and *Halichondria magniconulosa*. Within the 600 m zone, 35 taxa were unique, including *Pachastrella* (3 spp.), *Poecillastra* (2 spp.), *Topsentia pseudoporrecta, Epipolasis profunda, Margaritella coeloptychioides,* and 4 species of Euretidae (Hexactinellida). Twenty-two taxa were found retricted to the 922 m zone and included *Geodia* cf. *megastrella, Pachastrella abyssi, Phakellia ventilabrum, Racodiscula asteroides, Vetulina stalactites,* and the hexactinellids *Hyalonema* sp. and *Heterotella* (3 spp.).

Within the deepest zone, a unique group of deep water sponges occurred only at depths >800 m. Only 31 taxa were collected here, of which five were identified to species: *Euplectella* (2 new species), *Strongylophora hartmani, Poecillastra ?sollasi,* and *Vetulina stalactites*.

Seven genera (representing seven orders) were ubiquitous and found over the entire range of depth zones: *Geodia* (Astrophorida), *Bubaris* (Axinellida), *Siphonodictyon* (Haplosclerida), *Discodermia* (Lithistida), *Ircinia* (Dictyoceratida), *Topsentia* (Halichondrida), and *Corticium* (Homosclerophorida). No single species occurred over the entire depth range; however, nine species were distributed over four depth zones (30-300 m zones): *Agelas conifera, Erylus transiens, Ptilocaulis spiculifer, Mycale laxissima, Iotrochota birotulata, Cinachyrella kuekenthali, Pseudoceratina crassa, Aplysina lacunosa,* and *Verongula gigantea*.

Geographical distribution

To analyze the geographical distribution of Porifera within the Bahamas, seven zones or regions were delimited by specific latitude and longitude coordinates. Each sample (3049 total) was codified in the database to indicate the region in which it was collected. Region 1 (north of 26°N) consisted of Little Bahama Bank sites and the northern-most sector. Region 2 (west of 79°W) was the western sector, primarily west of Bimini and Little Bahama Bank which is influenced by the Florida Current (Gulf Stream). Region 3 (east of 76°W) was the eastern sector and consisted of the outer islands, such as Cat, San Salvador, Long, Acklins, and Inagua Islands. These

islands are surrounded by deep water and are not influenced by either of the two sand banks (Little Bahama and Great Bahama Banks). Region 4 (south of 24°30'N) was the southern sector, Region 5 (south of 24°30'N and east of 76°W) the southeastern sector, and Region 6 (north of 24°30'N) the northern sector. Region 7 was the central sector and the sites were within or adjacent to the Tongue of the Ocean.

In general, few differences were apparent between species distributions of Regions 1 and 6 (both in the north); therefore, Region 1 was combined with Region 6 as the North Region. Similarly Regions 3,4 and 5 overlapped, and the majority of sites of the Southeast Region (5) were inclusive within the East (3) and South (4) Regions; therefore, these regions were combined as the South Region.

Figure 5 compares the number of taxa for each order of Porifera between the North and South Regions. For most orders, the North Region was more diverse than the South Region. This was especially true for the Astrophorida, Axinellida, and Dendroceratida. Only the Lithistida, Dictyoceratida, Verongida, and Hexactinellida were more taxa-rich at the southern Bahamian sites.

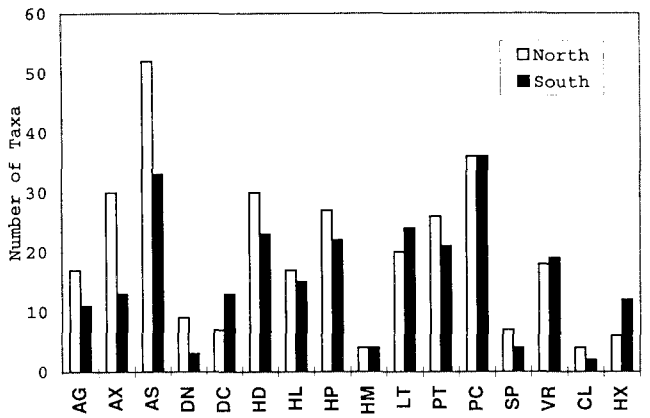

Fig. 5: Number of sponge taxa by order at North and South Regions. See text for region descriptions and Fig. 2 for legend.

A comparison of the West, Central, and East Regions revealed a general trend of increasing diversity from west to east in the Bahamas (Fig. 6). The Astrophorida, Dictyoceratida, Hadromerida, Halichondrida, Haplosclerida, Lithistida, Petrosida, Poecilosclerida, Verongida, and Hexactinellida had the greatest number of taxa at the eastern sites. Three groups had greatest diversity in the Central Region (Agelasida, Axinellida, and Calcarea). In the West Region, only the Halichondrida and Hexactinellida were more diverse than in the Central Region and no order had more taxa in the western than in the eastern Bahamas.

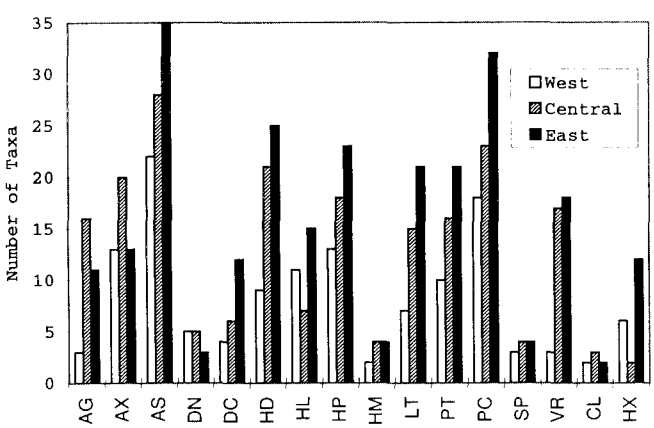

Fig. 6: Number of sponge taxa for each order at West, Central, and East collection sites. See text for region descriptions and Fig. 2 for legend.

Overall, the Northern Region had the most taxa (321) and identified species (235) of all regions. This was followed by the Southern Region (265 taxa, 162 species) and Eastern Region (261 taxa, 162 species). The Central Region was intermediate in diversity (211 taxa, 147 species) and the Western Region was lowest (134 taxa, 85 species).

Although the Northern Region appeared to be the most diverse, the southeastern sector (overlap of Regions 3, 4 and 5) had the highest number of endemic taxa (97) and identified species (61) that were exclusively found there and not elsewhere in the Bahamas. Species that were unique to the southeastern sites included *Agelas* spp. (4 sp.), *Erylus goffrilleri*, *Geodia* new sp., *Poecillastra sollasi*, *Teichaxinella ?burtoni*, *Smenospongia* (4 species), *Topsentia bahamensis*, *T. ophiraphidites*, *Cribrochalina dura*, *C. ?spiculosa*, *Petrosia pellasarca*, *Margaritella coeloptychioides*, and *Ceratoporella nicholsoni*.

In the northwest sector (overlap of Regions 1,2 and 6), 54 taxa and 44 species were endemic. These consisted in part of *Geodia* cf. *megastrella*, *Pachastrella* (4 species), *Phakellia ventilabrum*, *Teichaxinella ?corrugata*, *Aaptos* (2 spp.), *Epipolasis profunda*, *Spongosorites arenatus*, *Topsentia pseudoporrecta*, *Discodermia polydiscus*, *Theonella* new sp., and 4 species of Hexactinellida.

In the Tongue of the Ocean (Central Region), 48 taxa and 44 species were endemic and did not occur elsewhere in the Bahamas. These species included *Agelas* (8 species), *Stelletta* (2 spp.), *Geodia* (2 spp.), *Oceanapia* (2 spp.), *Xestospongia* (2 spp.), *Axinyssa ambrosia*, *Haliclona* new sp., *Discodermia* (2 spp.), *Aplysina* (2 spp.), *Goreauiella* sp., and *Stromatospongia ?norae*.

A total of 47 taxa were ubiquitous and were present in all regions regardless of the depth. These included the following common species: *Agelas clathrodes*, *A. flabelliformis*, *Erylus formosus*, *Geodia neptuni*, *Phakellia folium*, *Pseudaxinella lunaecharta*, *Ptilocaulis gracilis*, *Teichaxinella morchella*, *Ircinia felix*, *Spirastrella cunctatrix*, *Myrmekioderma styx*, *Callyspongia plicifera*, *Amphimedon compressa*, *Niphates erecta*, *Siphonodictyon coralliphagum*, *Corallistes typus*, *Mycale laxissima*, *Ectyoplasia ferox*, and *Aplysina fulva*.

DISCUSSION

The structure and diversity of the deep water benthic communities in the Bahamas is very dependent upon the geomorphology of the shelf edge slope. Major faunal breaks in the distribution of sponges are apparent from our submersible observations and collections. These faunal breaks or zones are consistent within specific habitats that are commonly found within the various geomorphological depth zones.

Sponges of the shallow Bahamian reefs (<30 m) are well known from previous studies (de Laubenfels 1949; Wiedenmayer 1977; Bunt et al. 1981). The next deeper reef zone is the fore reef escarpment and slope (60 m zone) which generally extends from 30 to 60 m. This zone consists of many subhabitats, each of which may support a unique sponge association. In general, many of the species common to the 60 m zone also occur at depths of <30 m. Pomponi (1981) found most sponges on the deep reefs (to 50 m) off the Florida Keys to also occur on the shallow reef. In the Bahamas, Bunt et al. (1981) also reported little species differentiation between depths of 13 and 38 m.

Species characteristic of the 60 m zone are the large and common *Agelas dispar*, *A. conifera*, *Teichaxinella morchella*, *Pseudoceratina crassa*, *Ptilocaulis gracilis*, *Xestospongia muta*, *Iotrochota birotulata*, *Myrmekioderma styx*, *Geodia neptuni*, *Aplysina lacunosa*, and *A. archeri*. Species which characterize this zone and also occur exclusively here are *"Thorecta horridus"*, *Stelletta ?kallitetilla*, *Strongylacidon viridis*, and *Discodermia dissoluta*.

The main geomorphological feature of the 150 m zone (60-150 m depth range) is the deep fore reef escarpment. This deep wall which is present at many of the sites is also common to the deep fore reefs at Jamaica (Goreau and

Land 1974; Lang 1974; Land and Moore 1977) and Belize (James and Ginsburg 1979). The 150 m zone is the most species rich of all the zones, with 206 taxa of which 147 were identified to species. Similarly, Maldonado and Young (1996) found the greatest abundance and diversity of megabenthic sponges at 100 m off New Providence Island in the central Bahamas. Van Soest and Stentoft (1988) found in Barbados that a zone from 137 to 177 m was the richest in sponge species and population densities, and Lewis (1965) reported for this same area that the sponge/coral community was dominant at depths of 50 to 150 m. Although we did not calculate percent cover or densities in this study, observations at most dive sites revealed dense populations of sponges, coral, gorgonians, and algae on the deep fore reef wall.

The 150 m zone is characterized by massive species, such as *Agelas flabelliformis, Oceanapia bartschi, Erylus geodiformis, Xestospongia portoricensis, Phakellia folium, Calcifibrospongia actinostromarioides* and *?Goreauiella* sp. 46% of the sponge species in this zone are stenotopic, occurring exclusively within this zone, compared to 33% species within the 60 m zone and 28% in the 30 m zone. The sclerosponges of the 150 m zone are an important component of the community, consisting of six genera and at least nine species. They contribute to the framework of the deep reef where they are very common in caves and deep crevices, as well as on vertical facies of the deep wall. Sclerosponges were common from 90 to 180 m, and one species was found as deep as 335 m. Lang et al. (1975) found sclerosponges to be a primary substrate builder at depths of 70-100 m in Jamaica, but reported that they were scarce at the same depths in Belize. In contrast, sclerosponges do not make a major contribution to the deep reef framework at Enewetok Atoll in the Pacific (Colin et al. 1986).

Below the deep fore reef escarpment, the 300 m depth zone extends from 150 to 300 m. The primary hard bottom habitat of this zone at many sites consists of a steeply sloped rock pavement, low ledges, and talus debris sliding down from above. On the smooth sloped surfaces, which commonly have a veneer of calcareous sediment, a rock outcrop or ledge often provides habitat for sponges, crinoids, anenomes, gorgonians, and ahermatypic corals. At some sites, 1-5 m boulders also provide habitat at the lower regions of this zone. In Jamaica, at depths of 200-300m, Land and Moore (1977) found large limestone blocks which supported demosponges, ahermatypic corals and echinoderms on their vertical surfaces. At this depth in Barbados, Lewis (1965) described a cnidaria/mollusc/echinoderm dominated community and listed 7 sponge species. At Enewetak Atoll, Colin et al. (1986) found boulders at depths of 160-300 m which supported some tunicates and anemones; however, the smooth sloped rock with sediment veneer were poor sites for sessile invertebrates.

Overall, the 300 m zone is species-poor compared to the zones immediately above and below. Maldonado and Young (1996) suggest that this zone is depauperate because the deep reef species do not extend to this depth, and the species which they consider to be true deep water taxa (including lithistids) do not yet occur. Their detailed analyses of a single transect off New Providence Island also showed a significant correlation of abundance with vertical surfaces, and their depauperate zone at 200 m consisted of relatively shallow sloping surfaces. In contrast, we found that in general, the 300 m zone consisted of steep (50-70°) rocky slopes which may be covered with sediment or rubble. Our data also indicate that species characteristic of this zone include lithistids, such as *Theonella* sp. and *Discodermia* spp., as well as *Dercitus* sp., *Axinyssa ambrosia, Halichondria magniconulosa, Stromatospongia ?norae, Axinella ?strongyloxea, Asteropus simplex, Spongosorites ruetzleri, Stelletta* spp., and *Spongosorites siliquaria*.

The deep island slope which extends from 300 to >1000 m has a unique and distinct sponge association and offers several habitats. Many sites have fine white calcareous mud and sand which support various echinoids, asteroids, molluscs, and crustacea, but no sponge fauna or other sessile species. However, any small rock outcrop or boulder is like an oasis, providing habitat for sponges, corals and gorgonians. Some sites have 10 m boulders or vertical walled cliffs within this zone. Although these vertical facies provide excellent habitat, the sponge diversities and densities on these were quite variable among sites for unknown reasons. Sponge densities at many sites are very high with numerous sponges occurring per m^2.

Very few other studies with submersibles have ventured beyond 300 m (the depth limit for the *Pisces* class of submersible) on the deep fore reef, including those cited previously for Jamaica, Belize, and Enewetak. Reed and Pomponi (1991) described the deep slope sponge fauna to depths of 914 m in the eastern Atlantic. Maldonado and Young (1996) reported a bimodal distribution of sponge abundance with peaks at 100 m and between 400-500 m, based on a single transect between 91 and 531 m off New Providence Island in the central Bahamas. While we found the greatest abundance of sponges in the 150 m depth zone (Fig. 3), more detailed analyses by order showed no general trend. Studies of deep water bioherms (Mullins et al. 1981; Reed 1992) describe habitats totally different from those found in this study at similar depths. Only the lithoherm sites (600-700 m) off western Little Bahama Bank are somewhat similar to the *Lophelia* coral banks (500 m) found off southeastern United States (Neumann et al. 1977; Reed 1992). Both sites are influenced by the Florida Current (Gulf Stream), and large (50 cm tall) current-oriented fan sponges (*Phakellia ventilabrum*) are common as well as *Pachastrella* sp., *Euplectella* sp., and *Farrea* sp.

The deep slope sponges are dominated by the lithistids, petrosids, halichondrids, and hexactinellids. Within the 600 m zone, 49% of the identified species are stenobenthic. The highest degree of unique species occuring within a restricted depth zone occurs at 922 m, at which 55% of the taxa are stenobenthic. Dominant species characteristic of these two zones include *Poecillastra sollasi, Corallistes* new sp., *Leiodermatium* sp., *Racodiscula ?asteroides, Pachastrella abyssi, Epipolasis profunda, Phakellia ventilabrum, ?Stylocordyla* sp., and *Strongylacidon hartmani*. The most characteristic species are the stony hard Lithistida, in particular, the cup-shaped *Corallistes* sp. and half-meter diameter folded colonies of *Vetulina stalactites*, along with hexactinellid sponges. The Hexactinellida, which occur exclusively at these lower depth zones, consist of six genera (*Hyalonema, Farrea, Margaritella, Heterotella*, and two unidentified genera of Euretidae) comprising at least 13 species.

Overall, the diversity of Porifera on the deep reefs and upper continental slope to 922 m in the Bahamas is very diverse and abundant, but also highly variable among sites. Although the environmental variables are relatively similar over the latitudinal range of the Bahamas (21-27°N), there are some geographical variations. In shallower water (13-38 m), Bunt at al. (1981) found little evidence of geographical zonation throughout the Bahamas, but he did report on a Florida reef richer in sessile species than the Bahamas. Neumann and Ball (1970), in a comparison of submersible sites off Bimini in the western Bahamas and southeastern Florida, reported greater diversity and density of benthic communities off south Florida. Within the Bahamas, Wiedenmayer (1977) considered the Bimini region higher in sponge diversity than the windward side of Great Bahama Bank. He also found greater species numbers and endemism on the outer platform and reefs (45 species, 79% endemic) than the inshore lagoon (16 species, 43% endemic). Colin (1976) considered the sponges at Berry Islands in the Bahamas less rich than Jamaica or Belize.

This is the first survey by submersible to extensively evaluate deep water sponge communities in the Bahamas. Previous studies by the authors using submersibles to 914 m in the eastern Atlantic (Reed and Pomponi 1991) reported 58 sponge species at Cape Verde, 39 in the Canary Islands, 33 in the Azores, 29 at Senegal, 24 at Sierra Leone, and 21 at Madeira. Recent but unpublished studies using the *Johnson-Sea-Link* submersibles throughout the Caribbean from the Antilles to Jamaica, Turks and Caicos and Belize indicate that the Bahamas are at least as rich as or richer than elsewhere in the Caribbean, western or eastern Atlantic Ocean. The collections and data compiled by this study represent a wealth of information on habitats, physical parameters,and taxonomic diversity, most of which remains to be analyzed. Yet to be studied are in-depth analyses of taxonomy, including descriptions of new species and

new geographic and depth records for the sponges of the Bahama Islands.

ACKNOWLEDGMENTS

Numerous individuals contributed to this research over the past ten years. A collective force of taxonomists, chemists, microbiologists, ecologists, scientific divers, ship and submersible crews made this project possible. Although too numerous to list individually, we thank each of them. We acknowledge the Division of Biomedical Marine Research, Harbor Branch Oceanographic Institution for providing financial support for the majority of this research. We also gratefully acknowledge the various sponge taxonomists and technicians who assisted with the numerous identifications, especially M. Kelly-Borges, M. C. Diaz, R. W. M. Van Soest, W. de Weerdt, B. Alvarez-Glasby, E. V. Robinson, M. Maldonado, and C. A. Adams. We are indebted to the government of the Bahama Islands for extending the privilege of conducting this research in their territorial waters. This is contribution number 1143 of the Harbor Branch Oceanographic Institution.

REFERENCES

Bunt JS, Williams WT, Chalker BE (1981) Coral associations at depths of 45 to 125 feet in the Bahamian region. Proc. Fourth Int. Coral Reef Symp. 1:707-714

Colin PL (1974) Observation and collection of deep reef fishes off of the coasts of Jamaica and British Honduras (Belize). Mar Biol 24:29-38

Colin PL (1976) Observations of deep-reef fishes in the Tongue-of-the-Ocean, Bahamas. Bull Mar Sci 26:603-605

Colin PL, Devaney DM, Hillis-Colinvaux L, Suchanek TH, Harrison JT (1986) Geology and biological zonation of the reef slope, 50-360 m depth at Enewetak Atoll, Marshall Islands. Bull Mar Sci 38-111-128

Diaz MC, Pomponi SA, Van Soest RWM (1993) A systematic revision of the central West Atlantic Halichondrida (Demospongiae, Porifera). Part III: Description of valid species. Sci Mar 57:283-306

Goreau TF, Land LS (1974) Fore-reef morphology and despositional processes, North Jamaica. Bull Mar Sci 23:77-85

James NP, Ginsburg RN (1979) The seaward margin of Belize barrier reef and atoll reefs. Blackwell Scientific Publications, Oxford

Kelly-Borges M, Pomponi SA (1994) Phylogeny and classification of lithistid sponges: a preliminary assessment using ribosomal DNA sequence comparisons. Mar Molec Biol Biotech 3:87-103

Kelly-Borges M, Robinson EV, Gunasekera SP, Gunasekera M, Gulavita NK, Pomponi SA (1994) Species differentiation in the marine sponge genus *Discodermia* (Demospongiae Lithistida): the utililty of ethanol extract profiles as species-specific chemotaxonomic markers. Biochem Syst Ecol 22:353-365

Land LS, Moore Jr. CH (1977) Deep forereef and upper island slope, North Jamaica. In: Frost SH, Weiss MP, and Saunders JB (ed) Reefs and related carbonates-Ecology and sedimentology. Am Assoc Petrol Geol Stud Geol 4:53-65

Lang JC (1974) Biological zonation at the base of a reef. Amer Scient 62:272-281

Lang JC, Hartman WD, Land LS (1975) Sclerosponges: Primary framework constructors on the Jamaican deep fore-reef. J Mar Res 33:223-231

Laubenfels MW de (1934) New sponges from the Puerto Rican deep. Smithson Misc Coll 91:1-28

Laubenfels MW de (1949) Sponges of the western Bahamas. Am Mus Novit 1431:1-25

Lewis JB (1965) A preliminary description of some marine benthic communities from Barbados, West Indies. Can J Zool 43:1049-1063

Maldonado M, Young CM (1996) Bathymetric patterns of sponge distribution on the Bahamian slope. Deep-sea Research (in press)

Mullins HT, Newton CR, Heath KC, VanBuren HM (1981) Modern deep-water coral mounds north of Little Bahama Bank: criteria for the recognition of deep-water coral bioherms in the rock record. J Sed Petrol 51:999-1013

Neumann AC, Ball MM (1970) Submersible observations in the Straits of Florida: Geology and bottom currents. Geol Soc Am Bull 81:2861-2874

Neumann AC, Kofoed JW, Keller GH (1977) Lithoherms in the Straits of Florida. Geology 5:4-10

Pomponi SA (1981) Sponges. In: Jameson SC (ed) Key Largo Coral Reef National Marine Sanctuary deep water resource survey. NOAA Technical Report CZ/SP-1, U.S. Dept of Commerce, Washington, D.C., pp 55-58

Pomponi SA, Wright AE, Diaz MC, Van Soest RWM (1991) A systematic revision of central Atlantic Halichondrida (Demospongiae, Porifera). Part II: Patterns of distribution of secondary metabolites. In: Keupp H and Reitner J (ed) Fossil and Recent Sponges. Springer-Verlag, Berlin, pp 150-158

Porter JW (1973) Ecology and composition of deep reef communities off the Tongue of the Ocean, Bahama Islands. Discovery 9:3-12

Reed, JK (1980) Distribution and structure of deep-water Oculina varicosa coral reefs off central eastern Florida. Bull Mar Sci 30:667-677

Reed, JK (1985) Deepest distribution of Atlantic hermatypic corals discovered in the Bahamas. Proc. Fifth Int. Coral Reef Symp. 6:249-254

Reed, JK (1992) Submersible studies of deep-water *Oculina* and *Lophelia* coral banks off southeastern U.S.A. Proc. Am. Acad. Underwater Sciences 12th Ann. Scient. Diving Symp., pp 143-151

Reed JK, Pomponi SA (1991) Eastern Atlantic expedition: Submersible and scuba collections for bioactive organisms from the Azores to western Africa. Proc. Am. Acad. Underwater Sciences 11th Ann. Scient. Diving Symp., pp 65-74

Schmidt O (1879) Die spongien des Meerbusen von Mexico, I. Abt. Lithistiden. I. Heft. G. Fischer, Jena. 32 pp

Schmidt O (1880) Die spongien des Meerbushen von Mexico (und des Caribischen Meeres), II. Abt. Hexactinellida, III. Abt. Tetractinelliden, Monactinelliden und Anhang. II. Heft. G. Fisher, Jena, pp 35-90

Soest RWM van (1978) Marine sponges from Curacao and other Caribbean localities. Part I. Keratosa. Stud Fauna Curacao Caribb Isl 56:1-94

Soest RWM van (1980) Marine sponges from Curacao and other Caribbean localities. Part II. Haplosclerida. Stud Fauna Curacao Caribb Isl 62:1-174

Soest RWM van (1984) Marine sponges from Curacao and other Caribbean localities. Part III. Poecilosclerida. Stud Fauna Curacao Caribb Isl 66:1-167

Soest RWM van, Stentoft N (1988) Barbados deep-water sponges. Stud Faun Curacao Caribb Isl 70:1-175

Soest RWM van, Diaz MC, Pomponi SA (1990) Phylogenetic classification of the Halichondrids (Porifera, Demospongiae). Institute of Taxonomic Zoology (Zoological Museum), Univ Amsterdam, 40:27-59

Wiedenmayer F (1977) Shallow-water sponges of the western Bahamas. Birkhauser Verkag-Basel, Switzerland