A biogeographic comparison of sponge fauna from Gray's Reef National Marine Sanctuary and other hard-bottom reefs of coastal Georgia, U.S.A.

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Abstract: Gray's Reef National Marine Sanctuary and other hard-bottom habitats off the coast of Georgia in the south-eastern USA provide habitat for a diverse assemblage of tropical and temperate benthic organisms. These limestone, sandstone, or relic scallop shell reefs are characterized by hard-bottom ledges and escarpments of moderate relief (1-2 m above the bottom) and raised, sandy plateaus in 13 to 30 m of water. The objectives of this investigation were to 1) provide the first comprehensive list of sponge species found at these north-western Atlantic sites as well as an indication of growth forms and patterns and general habitats and 2) assess whether the sponge fauna of Georgia reefs supports the hypothesis that the Carolinian province represents a transition between temperate and tropical regions. To date, we have found 52 species of sponges, two of which are thought to be undescribed species and 15 of which are new records for the area, from eight reef habitats in this region. Published distributional records indicated that nine of the 48 taxa we could identify to species were previously reported exclusively from tropical habitats, eight only from temperate areas, and 31 from both temperate and tropical locations. This equal mix of temperate and tropical sponge species supports the contention that this area represents a biogeographic transition zone for faunas from disparate oceanic regions. In addition to supporting a biogeographically diverse sponge fauna, the ledge, plateau, and cryptic habitats off Georgia provide the topographic complexity to sustain a variety of growth forms.

Keywords: biogeography, habitat, South Atlantic Bight, sponge morphology, temperate and tropical sponges

Introduction

Sponges are a dominant component of many benthic communities in tropical and temperate regions and are commonly observed on both hard and soft substrata (Reiswig 1973, Sarà and Vacelet 1973, Rützler 1978, Wenner *et al.* 1983, Targett and Schmahl 1984). The abundance, distribution, and diversity of sponges is relatively well documented in tropical Florida, the Caribbean, and Bermuda as well as in some temperate locations off the east coast of the United States from North Carolina to Cape Cod (George and Wilson 1919, Hartman 1964, Sterrer 1986, Alcolado 1990, Schmahl 1990, Diaz 2005, Engel and Pawlik 2005a, 2005b). In contrast, knowledge of sponge communities is more limited for the southern portions of the South Atlantic Bight (SAB), a region of the temperate northwestern Atlantic that includes coastal Georgia (SCWMRD 1982a, 1982b, Wenner *et al.* 1983).

The SAB represents an area extending from Cape Hatteras, NC to Cape Canaveral, FL. These boundaries correspond closely to those of the Carolinian biogeographic province (cf. Gosner 1971). Approximately 30% of the seafloor in this area is composed of hard-bottom areas of lithified limestone or sandstone embedded with fossilized scallop shells or other organisms (Harding and Henry 1994, Erv Garrison pers. comm.). Reefs in the SAB off the coast of Georgia, including those located within Gray's Reef National Marine Sanctuary (GRNMS), are continuous to patchy ledge systems that vary in depth from 13-30 m and are characterized by two distinct habitats: 1) hard-bottom ridges and ledges of moderate relief (1 to 2 m above the seafloor); and 2) sandy plateaus or valleys separating adjacent ledges (Hunt 1974).

Benthic invertebrates inhabiting these ledge systems in the SAB, especially those off Georgia, have received little attention. Most of our knowledge regarding diversity of benthic invertebrates in this area is contained within two large scale investigations carried out more than 25 years ago (SCWMRD 1982a, b). These studies used dredge and trawl collections to provide a description of benthic and nektonic

organisms at a limited number of reef sites througout the SAB, including one site within GRNMS.

Whether the Carolinian province represents a distinct temperate biogeographic province or a transitional region between the temperate Virginian and tropical West Indian provinces has been controversial (Engle and Summers 1999, 2000). Despite a paucity of descriptive information, the reefs of coastal Georgia are ideally situated to study this question. The proximity of these reefs to the warm waters and tropical recruits of the Gulf Stream suggest this area is a likely habitat for a biogeographically diverse mix of benthic organisms, including sponges. Thus, the objectives of this study were to 1) survey the sponges found on SAB reefs of coastal Georgia, including GRNMS, with an emphasis on the growth forms and general habitats occupied by the species present, and 2) evaluate the extent to which the sponges we found are also known from adjacent temperate or tropical regions.

Material and methods

We surveyed sponges at eight sites off Georgia between the summers of 2002 and 2006 (Fig. 1). These sites included hard-bottom ledges within GRNMS (GRNMS Monitoring Site, Station #16, and Patch Reef #1), a neighboring lithified scallop-shell reef outside of the boundaries of the sanctuary (J Reef), three hard-bottom reefs of unknown substrate composition (Anchor Ledge, R2 Live-bottom, and Cabretta Banks), and one artificial substrate (R2 Navy Tower) (Table 1).

We qualitatively estimated sponge species present at these sites by swimming the length of the ledge, across the plateau, or along the substrata looking for both common and rare, as well as cryptic species. We photographed and collected small fragments from sponges for identification in the laboratory. Samples were preserved in 70% ethanol. Skeletal structure was determined from dried thin sections that were cleared and embedded in Permount. Spicule types were determined after dissolving a fragment in bleach (5% sodium hypochlorite). Voucher specimens for each species are kept at the Department of Biology at Georgia Southern University and the Zoological Museum at the University of Amsterdam.

We restricted our biogeographic comparisons to the list of sponge species we collected and identified ourselves. To assess whether the sponges of Georgia reefs represent a temperate, tropical, or transitional fauna, we broadly categorized each species as either tropical or temperate based on zoogeographic provinces that have been observed for the Atlantic coast of the United States (reviewed in Engle and Summers 1999). Specifically, sponge species reported from the Caribbean and southern Florida (south of latitude 26° N) are from the West Indian province and were designated in our study as tropical. Sponges from Bermuda were included in this tropical group based on the close proximity of this island to the Gulf Stream and the documented presence of marine flora and fauna that is characteristically tropical (Sterrer 1986). Sponge species reported from Atlantic coast locations in the United States that are north of the West Indian province up to Cape Cod, MA were designated as temperate. This designation combined records from the Carolinian (Palm Beach, Florida to Cape Hatteras, NC; approximately 26° to 35° N latitude) and Virginian (north of Cape Hatteras, NC to Cape Cod, MA; approximately 35° to 41° N latitude) provinces, but was suitable for our purposes.

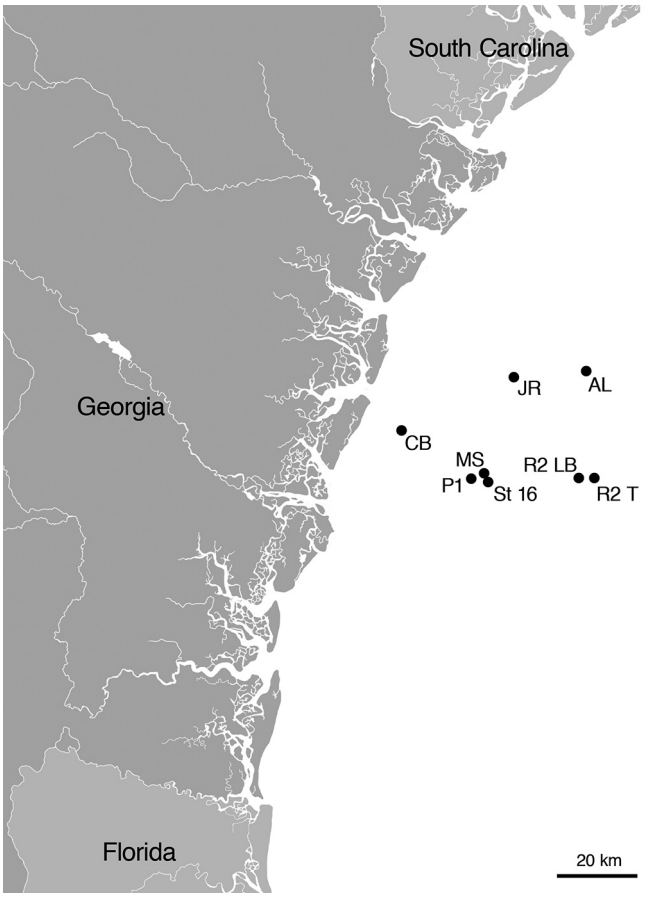

Fig. 1: Map of the 8 sites included in this study. Abbreviations for the sites are as follows: JR= J Reef, AL= Anchor Ledge, CB= Cabretta Banks, MS= GRNMS Monitoring Site, P1= Patch Reef 1, St. 16= Station 16, R2 LB= R2 live-bottom, and R2 T= R2 Tower.

In our description of growth form, we placed the sponges we observed into eight categories (Fig. 2). We classified arborescent species that either grew upright or as repent branches along the substrate as branching sponges (Fig. 2C). Massive sponges were either classified as amorphous (displaying upright growth with no branching or predictable shape; Fig. 2F) or vase (exhibiting a pronounced and deep depression in the center; Fig. 2B). Encrusting sponges displayed little vertical growth and generally took on the shape of the substrata (Fig. 2G), digitate sponges were partially buried under sand with only their small digitate projections visible (Fig. 2D), and globular sponges were more or less spherical (Fig. 2A). Pedunculate sponges were upright fan or beard-shape sponges (Fig. 2E), and the clathrate growth form described sponges with a characteristic flat cushion of small (1 mm diameter) tubes (Fig. 2H).

Table 1: Sites in the coastal Georgia SAB surveyed for sponge fauna between 2002 and 2006 with GPS coordinates, depth ranges (due to tides and depth differences of ledge and plateau), and general topographic characteristics.

Site (abbreviation)	GPS coordinates	Depth range (m)	General characteristics
J Reef (JR)	31° 36.056 N 80º 47.431 W	18-20	Sandstone and lithified scallop shell ledge/plateau
Anchor Ledge (AL)	31° 37.688 N 80º 34.662 W	25-30	Sandstone and limestone ledge/plateau
GRNMS Monitoring Site (MS)	31° 23.815 N 80º 53.461 W	14-22	Sandstone and limestone ledge/plateau
Patch Reef #1 (P1)	31° 24.340 N 80º 51.983 W	14-22	Patchy hard-bottom area without defined ledge or plateau
Cabretta Banks (CB)	31° 22.382 N 81º 04.039 W	13	Thin veneer of sand over limestone substrate
Station 16 (St. 16)	31° 23.791 N 80º 53.419 W	14-22	Sandstone and limestone ledge/plateau
R2 Live-bottom (R2 LB)	31° 24.305 N 80° 35.490 W	25-30	Patchy hard-bottom areas without defined ledge or plateau
R2 Tower (R2 T)	31° 22.300 N 80° 34.010 W	25-30	Artificial substrate provided by pilings of navy tower

Results

We encountered 52 species of sponges from GRNMS and neighboring hard-bottom reefs (Table 2), 48 of which we could identify to species. Two of the four species identified only to genus (*Raspailia* sp. and *Coelosphaera* sp.) are thought to be new to science.

Nine of the 48 species we identified have been reported previously only from tropical regions, eight only from temperate regions, and 31 from both of these regions (Table 2). Of these 48 species, 15 are new records for the Carolinian province, two are endemic to this region, and 31 species have been either previously found in this area or have a distribution beyond this region (Table 2).

Twenty-five of the 52 species from GRNMS and neighboring reefs were found predominantly on the hard-bottom areas provided by the scarp, ledge, and rocky outcroppings around the ledge. Eight of these 25 species were primarily or exclusively cryptic and were located under ledges, between cracks and crevices on the scarp and between or under other sponges, gorgonians, tunicates, and bivalves (Table 3). On the other hand, none of the 12 species found predominantly on the sandy bottom around the ledges or on the plateau were observed in cryptic locations.

Of the rare sponges encountered in our surveys (found only 1-2 times), ten species were observed exclusively in cryptic locations on the reef either under the rocks or ledges (*Tethya* sp., *Callyspongia* (*Callyspongia*) *fallax*, *Chalinula molitba*) or surrounded and partially covered by other organisms (*Coelosphaera* sp. nov., *Mycale* (*Carmia*) *fibrexilis*, *Leucandra* sp., *Geodia gibberosa*, *Spheciospongia vesparium*, *Aulospongus pearsi*, *Clathrina canariensis*). The remaining five species of sponges were found in cryptic locations on the metal substrate of the R2 tower (*Igernella notabilis* and *Phorbas* aff. *amaranthus*), or were common on both the hard bottom, scarp region and the sandy plateau (*Cliona celata*, *Halichondria bowerbanki*, *Smenospongia cerebriformis*).

The two dominant sponge growth forms were encrusting (40% of species) and amorphous/massive (25% of species), followed by branching, pedunculate, and digitate species. The scarp habitat, with its hard substrata, was heavily colonized by encrusting (36% of species) or amorphous/massive (32% of species) sponges. On the other hand, 66% of the species present on the sparsely colonized, sandy plateau were either digitate (*Raspailia* sp. nov., *Ciocalypta gibbsi*, *Aulospongus samariensis*, *Axinyssa ambrosia*) or pedunculate (*Clathria* (*Clathria*) *carteri*, *Axinella waltonsmithi*, *Axinella bookhouti*, *Higginsia strigilata*, and *Clathria* (*Clathria*) *prolifera*) (Table 3).

Discussion

Our results show that reefs in the SAB off coastal Georgia are characterized by three major habitat types, each with a distinctive set of sponge species and sponge growth forms. While a combination of biotic (predation and competition) and abiotic (sedimentation and current regime) factors likely maintain the differences in sponge species that we observed between scarp and plateau habitats, we have yet to conduct extensive investigations to determine which of these factors are most important in structuring this sponge community. However, initial observations indicating higher densities of spongivorous fish predators on scarp habitats (Ruzicka 2005) and greater sediment stress on the plateau (Gleason, pers. obs.) allow generation of hypotheses for future studies. The third major habitat type, the cryptic region, was either the predominant or sole habitat for many of the rare sponges we encountered. Again, we have not determined why these species appear to be relegated to these hidden locations, but

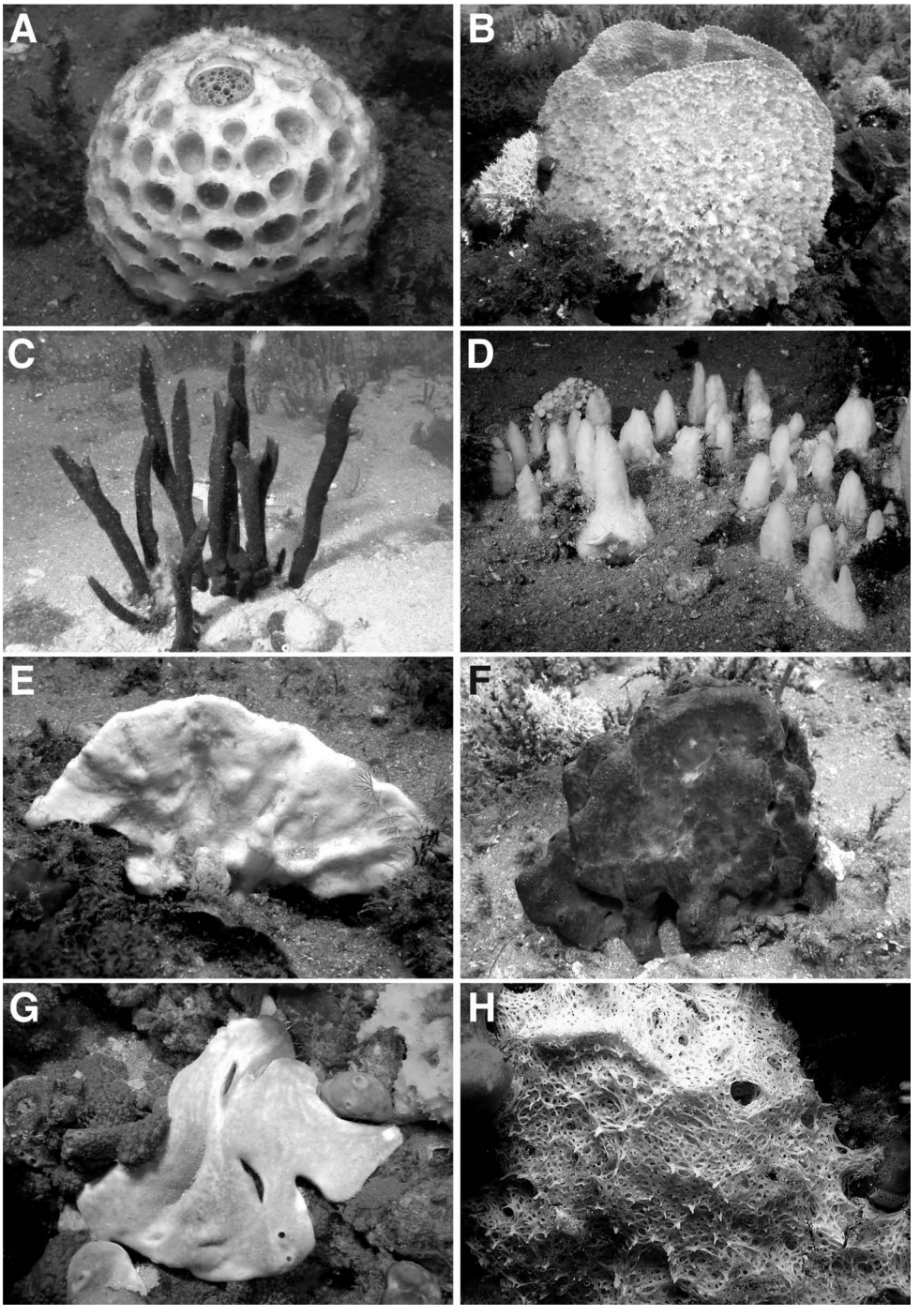

Fig. 2: Examples of sponge growth forms. **A.** Globular (*Cinachyrella alloclada*); **B.** Vase (*Ircinia campana*); **C.** Branching (*Axinella pomponiae*); **D.** Digitate (*Axinyssa ambrosia*); **E.** Pedunculate (*Axinella waltonsmithi*); **F.** Amorphous (*Ircinia felix*); **G.** Encrusting (*Chondrosia collectrix* complex); **H.** Clathrate (*Clathrina coriacea* complex). Photographs by Rob Ruzicka (A, C, D, G), Greg McFall (B, E, F), and Bernard Picton and Christine Morrow (H).

feeding by spongivorous fish and invertebrate predators or competitive exclusion by faster growing, open reef species might play a role (Meesters *et al.* 1991, Wulff 1997).

As might be expected given the scarcity of published literature on sponges in this region, a relatively large number of our records represent major range extensions, particularly for tropical sponges, of which nine species are newly reported in temperate regions. This study also extends the southern range of *Mycale fibrexilis*, which was previously known only from the Cape Cod region (Hartman 1964). In addition, from these Georgia reefs, we have identified fifteen sponge species that represent new records for the Carolinian province and two species that are considered endemic to this area. The diverse and balanced assortment of temperate and tropical sponge species found on Georgia reefs supports the contention that the Carolinian province is a true biogeographic transition zone between temperate and tropical Atlantic waters. This is consistent with recent generic-level analyses of benthic

Table 2: List of sponge species observed in surveys of eight coastal Georgia reefs. For each of the species observed, an * in one of the distribution columns indicates the region or regions where this species has been reported prior to this investigation. ** indicates that this species is a new record for the Carolinian province and *** indicates that this species is endemic to the Carolinian province. The tropical region includes Caribbean locations, Southern Florida, and Bermuda. Temperate refers to locations from Georgia and North Carolina to Cape Cod and both refers to species found in both tropical and temperate localities. The following references (Rf.) were used in compiling these data: **1.** George and Wilson (1919); **2.** de Laubenfels (1953); **3.** Wells *et al.* (1960); **4.** Hartman (1964); **5.** Wiedenmayer (1977); **6.** van Soest (1978); **7.** van Soest (1980); **8.** SCWMRD (1982a, b); **9.** van Soest (1984); **10.** Sterrer (1986); **11.** Bibiloni *et al.* (1989); **12.** Alcolado (1990); **13.** Alvarez *et al.* (1990); **14.** Schmahl (1990); **15.** van Soest *et al.* (1990); **16.** Alvarez *et al.* (1998); **17.** Diaz (2005); **18.** Engel and Pawlik (2005a, b); and **19.** van Soest *et al.* (2005).

Species	References	Distribution		
		Tropical	Temperate	Both
Aiolochroia crassa (Hyatt, 1875)	17, 18a, 5, 10, 6, 14, 12, 13			**
Aplysilla longispina George and Wilson, 1919	10, 1			*
Aplysina fulva (Pallas, 1776)	17, 12, 18a, 6, 5	**		
Aulospongus pearsi (Wells, Wells and Gray, 1960)	3, 8a, 8b		***	
Aulospongus samariensis Hooper, Lehnert and Zea, 1999	19	**		
Axinella bookhouti Wells, Wells and Gray, 1960	3, 8a, 8b, 2		*	
Axinella pomponiae Alvarez, van Soest and Rützler, 1998	16		*	
Axinella waltonsmithi (de Laubenfels, 1953)	16, 8a, 8b, 2		*	
Axinyssa ambrosia (de Laubenfels, 1934)	15	**		
Callyspongia (Callyspongia) fallax (Duchassaing and Michelotti, 1864)	17, 14, 7, 5, 8a, 13			*
*Chalinula molitba (*de Laubenfels, 1949*)*	17, 7, 5, 10, 14			**
Chondrilla nucula complex Schmidt, 1862	17, 14, 12, 18a, 5, 10, 18b, 8a,b			*
Chondrosia collectrix complex Schmidt, 1862	17, 14, 5, 10, 8a			*
Chondrosia reniformis complex Nardo, 1847	5			**
Cinachyrella alloclada (Uliczka, 1929)	17, 14, 5, 10, 8a, 8b, 18a, 13			*
Ciocalypta gibbsi (Wells, Wells and Gray,1960)	3, 15, 8a			*
Clathria (Clathria) carteri Topsent, 1889	3			*
Clathria (Clathria) prolifera (Ellis and Solander, 1786)	9, 4, 1, 8a, 8b, 4			*
Clathria (Thalysias) schoenus (de Laubenfels, 1936)	17, 12, 9	**		
Clathrina canariensis (Miklucho-Maclay, 1868)	3, 18b, 8a			*
Clathrina coriacea complex (Montagu, 1818)	14, 12, 5, 10, 8a, 8b			*
Cliona caribbaea Carter, 1882	17, 14, 3, 10, 8a, 14, 2			*
Cliona celata complex Grant, 1826	3, 1, 4, 8a			*
Coelosphaera sp. nov.				
Coscinoderma lanuga de Laubenfels, 1936	19, 3			*
Desmapsamma anchorata (Carter, 1882)	17, 9	**		
Dragmacidon reticulatum (Ridley and Dendy, 1886)	17			**
Dysidea fragilis complex (Montagu, 1818)	14, 11, 16, 3, 5, 2			*
Geodia gibberosa Lamarck, 1815	12, 3, 5, 10, 8a, 8b, 18b, 2			*
Halichondria bowerbanki Burton, 1930	3, 15, 8a, 4		*	
Higginsia strigilata (Lamarck,1814)	3, 5, 1, 8a, 2			*
Hyrtios violaceus (Duchassaing and Michelotti, 1864)	5	**		
Igernella notabilis (Duchassaing and Michelotti, 1864)	6	**		
Ircinia campana (Lamarck, 1816)	17, 14, 13, 18a, 6, 3, 8a, 8b, 2			*
Ircinia felix (Duchassaing and Michelotti, 1864)	17, 14, 12, 13, 1, 8a, 8b, 18a, 6, 5, 10			*
Leucandra sp.				
Leucetta imberbis (Duchassaing and Michelotti, 1864)	19, 3			*
Lissodendoryx (Anomodoryx) sigmata (de Laubenfels, 1946)	9, 5, 8a			*
Mycale (Carmia) fibrexilis Wilson, 1891	4		**	
Niphates erecta Duchassaing and Michelotti, 1864	17, 14, 12, 13, 18a, 7, 3, 5, 10, 8a			*
Phorbas aff. amaranthus Duchassaing and Michelotti, 1864	18a, 8b, 9, 14			*
Ptilocaulis walpersi (Alvarez *et al.* 1998)	17, 16, 18a, 15	**		
Raspailia sp. nov.				
Scopalina ruetzleri (Wiedenmayer, 1977)	17, 12, 18a, 5, 10, 14, 13			**
Smenospongia cerebriformis (Duchassaing and Michelotti, 1864)	18a, 8a		*	
Spheciospongia vesparium (Lamarck, 1815)	17, 14, 11, 3, 5, 1, 8a, 2			*
Spirastrella coccinea (Duchassaing and Michelotti, 1868)	17, 14, 12, 18a, 3, 5, 8a			*
Spirastrella mollis Verill, 1907	17, 10	**		
Spongia graminea Hyatt, 1877	3, 2			*
*Spongia (Spongia) tubulifera (*Lamarck, 1814*)*	17, 6, 5, 8b			*
Stelletta carolinensis (Wells, Wells and Gray, 1960)	3		***	
Tethya sp.	17, 14, 12, 5, 10, 2, 8b			*

Table 3: List of sponge species observed in surveys of eight coastal Georgia reefs along with their habitat(s) and their dominant growth form(s). The habitat column refers to the general environment where this species was predominantly found: H = hard substrate of the scarp, ledge, or rocky outcroppings, S = sandy substrate around ledges and on top of plateau, Cr = cryptic locations in crevices, under rocks, ledges, and other organisms, As = artificial substrate of R2 tower. Growth forms are characterized in the following categories: A = amorphous, B = branching, C = clathrate, D = digitate, E = encrusting, G = globular, P = pedunculate, and V = vase.

Species	Habitat	Growth form
Aiolochroia crassa	H	E/A
Aplysilla longispina	H	E
Aplysina fulva	H	B
Aulospongus pearsi	Cr	A
Aulospongus samariensis	S	D
Axinella bookhouti	S	P
Axinella pomponiae	S	B
Axinella waltonsmithi	S	P
Axinyssa ambrosia	S	D
Callyspongia (Callyspongia) fallax	Cr	E
Chalinula molitba	Cr	E
Chondrilla nucula complex	H	E
Chondrosia collectrix complex	H	E
Chondrosia reniformis complex	H/Cr	E
Cinachyrella alloclada	S	G
Ciocalypta gibbsi	S	D
Clathria (Clathria) carteri	S	P
Clathria (Clathria) prolifera	H	P
Clathria (Thalysias) schoenus	H/Cr	E
Clathrina canariensis	Cr	C
Clathrina coriacea complex	H/Cr	E/C
Cliona caribbaea	H	E
Cliona celata complex	S/H	E/V
Coelosphaera sp. nov.	Cr	D/E
Coscinoderma lanuga	H	A
Desmapsamma anchorata	H	B
Dragmacidon reticulatum	H/Cr	A
Dysidea fragilis complex	H	A
Geodia gibberosa	Cr	E
Halichondria bowerbanki	S/H	E
Higginsia strigilata	S	P
Hyrtios violaceus	H	A
Igernella notabilis	Cr/As	A
Ircinia campana	H	V
Ircinia felix	H	A
Leucandra sp.	Cr	A
Leucetta imberbis	H/Cr	A
Lissodendoryx (Anomodoryx) sigmata	S	A
Mycale (Carmia) fibrexilis	Cr	E
Niphates erecta	H	B
Phorbas aff. amaranthus	As/Cr	E
Ptilocaulis walpersi	S	B
Raspailia sp. nov.	S	D
Scopalina ruetzleri	H	E
Smenospongia cerebriformis	S/H	A
Spheciospongia vesparium	Cr	E/G
Spirastrella coccinea	H	E
Spirastrella mollis	H	E
Spongia graminea	H/Cr	A
Spongia (Spongia) tubulifera	H/Cr	E/A
Stelletta carolinensis	H/Cr	G
Tethya sp.	Cr	G

estuarine macroinvertebrates (Engle and Summers 1999, 2000).

Curiously, our survey of the sponges of the reefs in and around GRNMS revealed a dramatically different result from that of the last major faunal survey of the area, done a quarter century earlier by the South Carolina Wildlife and Marine Resources Department (1982a). That investigation, surveying GRNMS and neighboring areas, identified 61 and 77 sponges to species when collecting by dredge or trawl, respectively, but only about 20 of these species were also encountered in our surveys. Thus, we failed to find almost two-thirds of the sponges that they reported from the area, and likewise they did not report nearly two-thirds of the species that we found. This discrepancy is as yet unexplained, and may be due to any number of factors. For example, our extensive diver surveys of scarp, plateau, and cryptic sponge populations may have allowed us to find sponges restricted to the plateau and scarp, which are usually not captured in dredge and trawls. Alternatively, the discrepancies may reflect developments in sponge taxonomy and diagnostic tools, or real changes in the composition of the sponge fauna over the last 25 years.

The results of this study, although still preliminary, present the first comprehensive list of the sponge fauna from coastal Georgia waters, thereby providing data on the habitats and dominant growth forms of this biogeographically and taxonomically diverse collection of sponges. Data from this study support the contention that this area represents an important zone of convergence for sponge faunas from disparate oceanic regions. In addition to the species documented above, we anticipate that the number of sponge species reported will continue to increase as we explore other sites in this region and more closely survey existing sites. Finally, this report is part of a larger project creating a field guide and web site designed to document the benthic invertebrate fauna and cryptic fishes in this area (see http://www.bio.georgiasouthern.edu/gr-inverts/index.html). These tools are providing an important database for the scientific community, the marine sanctuaries program, and recreational divers in this region.

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References

Alcolado PM (1990) General features of Cuban sponge communities. *In:* Rützler K (ed.). *New perspectives in sponge biology*. Smithsonian Institution Press, Washington DC. pp. 351-357

Alvarez B, Diaz MC, Laughlin R (1990) The sponge fauna on a fringing coral reef in Venezuela, I: composition, distribution, and abundance. *In:* Rützler K (ed.). *New perspectives in sponge biology*. Smithsonian Institution Press, Washington, DC. pp. 358-366

Alvarez B, van Soest RWM, Rützler K (1998) A revision of Axinellidae (Porifera: Demospongiae) of the central West Atlantic region. *Smith Contrib Zool* 598: 1-45

Bibiloni MA, Uriz MJ, Gili JM (1989) Sponge communities in 3 submarine caves of the Balearic Islands (Western Mediterranean) – adaptations and faunistic composition. *PSZN Mar Ecol* 10(4): 317-334

de Laubenfels MW (1953) Sponges from the Gulf of Mexico. *Bull Mar Sci Gulf Carib* 2(3): 511-557

Diaz MC (2005) Common sponges from shallow marine habitats from Bocas del Toro region, Panama. *Caribb J Sci* 41(3): 465-475

Engel S, Pawlik JR (2005a) Interactions among Florida sponges. I. Reef habitats. *Mar Ecol Progr Ser* 303: 133-144

Engel S, Pawlik JR (2005b) Interactions among Florida sponges. II. Mangrove habitats. *Mar Ecol Progr Ser* 303: 145-152

Engel VD, Summers JK (1999) Latitudinal gradients in benthic community composition in Western Atlantic estuaries. *J Biogeogr* 26: 1007-1023

Engel VD, Summers JK (2000) Biogeography of benthic macroinvertebrates in estuaries along the Gulf of Mexico and western Atlantic coasts. *Hydrobiologia* 436: 17-23

George WC, Wilson HV (1919) Sponges of Beaufort (N.C.) harbor and vicinity. *Bull Bur Fish* 36: 130-179

Gosner KL (1971) *Guide to identification of marine and estuarine invertebrates*. Wiley-Interscience, New York

Harding JL, Henry VJ Jr. (1994) Geological history of Gray's Reef National Marine Sanctuary: a final report to the National Oceanographic Atmospheric Administration, Marine Estuarine Management Division under cooperative agreement NA-87-AA-H-CZ033. pp. 58

Hartman WD (1964) Chapter 1: Phylum Porifera. *In:* Smith RI (ed). *Keys to marine invertebrates of the Woods Hole region: a manual for the identification of the more common invertebrates*. Marine Biological Laboratory, Woods Hole. pp. 1-7

Hunt JL (1974) *The geology and origin of Gray's Reef, Georgia Continental Shelf*. PhD Thesis, University of Georgia, Athens

Meesters E, Knijn R, Willemsen P, Pennartz R, Roebers G, van Soest RWM (1991) Sub-rubble communities of Curacao and Bonaire coral reefs. *Coral Reefs* 10: 189-197

Reiswig HM (1973) Population dynamics of three Jamaican Demospongia. *Bull Mar Sci* 23: 191-226

Rützler K (1978) Sponges in coral reefs. *In:* Stoddart DE, Johannes JE (eds). *Coral reefs: research methods*. *Monographs on oceanographic methodology, vol. 5*. UNESCO, Paris. pp. 299-313

Ruzicka R (2005) *Sponge community structure and anti-predator defenses on temperate reefs of the South Atlantic Bight*. MSc Thesis, Georgia Southern University, Statesboro

Sarà M, Vacelet J (1973) Écologie des Démosponges. *In:* Grassé PP (ed). *Traité de zoologie (anatomie, systématique, biologie)*. Paris, Masson. pp. 462-576

Schmahl GP (1990) Community structure and ecology of sponges associated with four southern Florida coral reefs. *In:* Rützler K (ed). *New perspectives in sponge biology*. Smithsonian Institution Press, Washington DC. pp. 376-383

SCWMRD - South Carolina Wildlife and Marine Resources Department (1982a) *South Atlantic OC area living marine resources study: Year II-Volume I: An Investigation of live-bottom habitats off South Carolina and Georgia*. Washington DC. pp. 1-189

SCWMRD - South Carolina Wildlife and Marine Resources Department (1982b) *South Atlantic OC area living marine resources study: Year II-Volume II: An investigation of live-bottom habitats off North Carolina*. Washington DC. pp. 1-143

Sterrer W (1986) Marine fauna and flora of Bermuda. John Wiley and Sons, New York

Targett NM, Schmahl GP (1984) *Chemical ecology and distribution of sponges in the Salt River Canyon, St. Croix, U.S.V.I.* NOAA Technical Memorandum. pp. 1-29

van Soest RWM (1978) Marine sponges from Curacao and other Caribbean localities. Part I. Keratosa. *Stud Fauna Curacao Caribb Isl* 56(179): 1-94

van Soest RWM (1980) Marine sponges from Curacao and other Caribbean localities. Part II. Haplosclerida. *Stud Fauna Curacao Caribb Isl* 62(191): 1-173

van Soest RWM (1984) Marine sponges from Curacao and other Caribbean localities. Part III. Poecilosclerida. *Stud Fauna Curacao Caribb Isl* 66(199): 1-167

van Soest RWM, Diaz MC, Pomponi SA (1990) Phylogenetic classification of the Halichondrids (Porifera, Demospongiae). *Beaufortia* 40: 15-62

van Soest RWM, Boury-Esnault N, Janussen D, Hooper J (2005) World Porifera Database. http://www.marinespecies.org/porifera. Accessed September 1st to September 20th, 2006

Wells HM, Wells MJ, Gray IE (1960) Marine sponges of North Carolina. *J Elisha Mitchell Sci Soc* 76(2): 200-245

Wenner EL, Knott DM, Dolah RF van, Burrell VG (1983) Invertebrate communities associated with hard bottom habitats in the South Atlantic Bight. *Estuar Coast Mar Sci* 17: 143-158

Wiedenmayer F (1977) Shallow water sponges of the Western Bahamas. *Experientia Suppl* 28: 1-287

Wulff JL (1997) Parrotfish predation on cryptic sponges of Caribbean coral reefs. *Mar Biol* 129: 41-52

Zea S (1993) Cover of sponges and other sessile organisms in rocky and coral reef habitats of Santa Marta, Colombian Caribbean Sea. *Carib J Sci* 29(1-2): 75-88