

**Mollusks taken by Beam Trawl in the vicinity
of Gray's Reef National Marine Sanctuary on the
Continental Shelf off Georgia, Southeastern U.S.**



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Abstract

Mollusks were sorted from samples of shell hash (obtained as bycatch during NOAA-sponsored studies of larval and juvenile fish distribution), and analyzed to gain qualitative insights on species composition, distribution and habitat affinities of the molluscan fauna on the continental shelf off Georgia. Samples came from beam trawls at 37 stations located in the immediate vicinity and offshore of the Gray's Reef National Marine Sanctuary (GRNMS) at depths of 4.9 to 103 m. Two hundred sixty-three (263) taxa of mollusks (~58% as dead shells only) were collected, and nearly all (~99%) were identified to the species level. Ninety-seven of these taxa appeared in samples from one or more of the four stations established near the corners of the GRNMS. Samples were highly variable in terms of appearance, volume and species composition of mollusks, reflecting the extreme patchiness of benthic habitats within this region of the continental shelf. With very few exceptions, the mollusks were generally characteristic of either the Carolinian or Caribbean faunal provinces. The Georgia continental shelf, however, was outside the previously reported ranges for at least 16 of the species reported here. Most of these extralimital species were known previously from the East Coast of Florida, and represented northerly range extensions of 1-5° Latitude (110-560 km). One species represented a more significant range extension from the Bahamas and the southern Caribbean, and two represented southerly range extensions, known previously from only as close as off North Carolina. The high incidence of range extensions found in this study and the potential for discovery of additional species are discussed in the context of the diversity and patchiness of benthic habitats on the continental shelf of the region, and the sensitivity of species recruitment to variability in Gulf Stream patterns and global climate change.

Introduction

The Continental Shelf off the coast of Georgia and South Carolina supports a diverse assortment of demersal and benthic habitats. These range from flat bottoms of quartz and carbonate sands to high-relief, live-bottom rocky ledges that are densely colonized by invertebrates and fish communities (Parker *et al.*, 1983; Nelson *et al.*, 1999; Kendall *et al.*, 2006). Similar “patch reefs” occur along the continental shelf at least as far north as Cape Lookout, North Carolina (Menziés *et al.*, 1966; Shoemaker, 1972; Van Dolah *et al.*, 1994). With the establishment of the Gray’s Reef National Marine Sanctuary (GRNMS) in 1981, a 17.5 square nautical mile (61 km²) portion of live-bottom patch reef habitat was set aside for research, protection, and management. Gray’s Reef contains extensive but discontinuous outcrops of limestone up to ten feet in height separated by flat-bottomed troughs with unconsolidated sediments, mainly sand. Parker *et al.* (1983, 1994) estimated that rocky reefs cover up to 30% of the Georgia shelf area in the vicinity of the GRNMS.

While it is known that live-bottom reef habitats support rich assemblages of invertebrates, the molluscan fauna of the continental shelf off Georgia has received little attention compared to similar areas both to the north and the south. The molluscan assemblages associated with patch reef habitats off North and South Carolina have been described in some detail (eg. Pearse and Williams, 1951, Wells *et al.*, 1961; Menziés *et al.*, 1966; Shoemaker, 1972; Wenner *et al.*, 1983), as have the mollusks associated with the calico scallop fishery off North Carolina (Wells *et al.*, 1964; Porter and Wolfe, 1972). Ward and Blackwelder (1987) have suggested that these communities may have persisted relatively unchanged since the late Pliocene period (2.4 MYA). Wenner *et al.*, (1983) examined diversity and biomass relationships among the epifauna (including mollusks) in the immediate region of the present study, but did not report details of species composition or occurrence. Lee (2006, pers. comm.) has compiled an extensive list of mollusks found off Northeast Florida. While the coastal and inshore molluscan fauna of Georgia has recently been described (Prezant *et al.*, 2002), and the GRNMS has recently sponsored studies of the soft-bottom benthos (Vittor and Associates, Inc., 2004; Hyland *et al.*, 2006) and demersal fish (Cooksey *et al.*, 2004; Kendall *et al.*, 2006; Walsh *et al.*, 2006), the occurrence and distribution of mollusks on the continental shelf of Georgia remain largely undescribed.

The samples analyzed in this study were collected during February and April 2002 as bycatch on two NOAA cruises conducted in support of studies of the distribution and movements of larval and juvenile fish on the continental shelf off the coast of Georgia in the immediate vicinity of the GRNMS (Marancik *et al.*, 2005; Walsh *et al.*, 2006). These samples provided an opportunity for qualitative examination of the molluscan assemblages that occur on the patch reefs and associated habitats in this transitional subtropical shelf region.

Methods

February samples were obtained on the NOAA Ship Oregon II; April samples on the NOAA Ship Ferrel. Sampling stations are mapped in Fig. 1; station coordinates and depths are shown in Appendix I.

Targeted juvenile fish were collected at each station using a standard 2-m beam trawl (Kuipers, 1975) with a 6-mm mesh body and a 3-mm mesh tail bag. The beam trawl had a tickler chain ahead of the trawl and a chain on the foot rope at the front of the trawl. Two-kilogram weights were added to each skid of the trawl to ensure that it stayed on the bottom. Three 5-min bottom tows were made at each station. The catch was sorted on deck to remove larger fish and extraneous material, and the remaining fish, shell hash, and associated invertebrates were preserved in 95% ethanol for later separation of all fish. After removal of the fish, the residual materials (consisting mainly of shell hash) were further examined for mollusks. Procedures for sorting the samples were not rigorously consistent throughout the study, and varied with the volume and character of the sample (Table 1). No record was maintained of the details of sorting throughout the study. Initially (i.e., for most of the Oregon II samples), mollusks were sorted by visual examination— frequently with the naked eye and sometimes (if the proportion of fine-grained materials seemed to warrant it) at low magnification under a dissecting microscope. Sorting of large-volume samples of very coarse shell hash was facilitated by washing the material first through a 12.5-mm mesh hardware cloth to separate large shells and fragments, prior to examination of the finer hash retained on 3-mm mesh hardware cloth or (again, if the proportion of fine-grained materials seemed to warrant it) on fiberglass screen with a mesh size of approximately 1.1 mm. Toward the end of the study, use of the 1.1-mm mesh became more standard. Consequently, small taxa were more likely to have been lost or overlooked in earlier samples.

Materials retained on the screens were sorted under a dissecting microscope. All live-collected mollusks (gastropods with opercula or visible animal material and paired bivalves) along with freshly dead specimens were sorted from the samples. Unusual or rare species were retained regardless of condition, including fresh fragments and representative single valves for bivalves not found paired. For the samples recovered from the Oregon II cruise 8-13 February 2002, species occurrence (but not number of specimens) by station and total number of specimens for all stations were recorded. Except for the species recovered from only one or two stations, the number of specimens per station is not available from that cruise. By contrast, specimens were sorted and enumerated for the individual replicate tow samples at each station from the Ferrel cruise 13-16 April 2002.

Mollusk specimens were identified to the lowest practical taxonomic level (LPTL) using published (e.g. Abbott, 1974; Abbott and Morris, 1995; Redfern, 2001; Williams, 2006; Mikkelsen and Bieler, 2008) and on-line sources for reference, and comparison with previously identified material in the author's personal collection (e.g. Wolfe, 1968; Porter and Wolfe, 1972). Selected specimens were also sent to Harry G. Lee (Jacksonville, Florida), William G. Lyons (St. Petersburg, Florida), or Donn Tippett (U.S. National Museum, Washington, D.C.) for examination and further identification.

Nomenclature generally follows Turgeon *et al.* (1998), with some exceptions based on Rosenberg (2005), or (for bivalves) Mikkelsen and Bieler (2008). All specimens are archived in the author's collection.

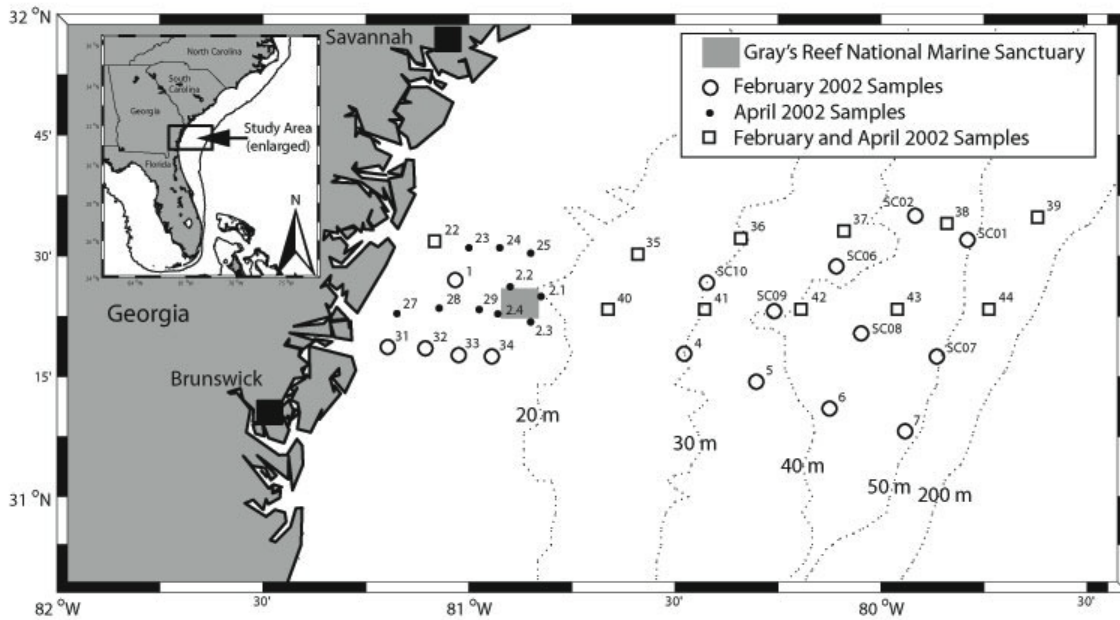


Figure 1. Station locations sampled during February 2002 from the Oregon II and during April 2002 from the Ferrel. Detailed station data are given in Appendix I.

Results

Sample Characteristics

Table 1 describes general characteristics of the samples obtained from the April cruise of the Ferrel (analogous records were not kept for the Oregon II samples). Volume of individual replicate samples ranged from only 7 ml to about 8 liters. Although samples consisted primarily of shell hash, they varied considerably both among stations and among replicates within station, in terms of their overall volumes, and their composition— especially with regard to the mix of large bivalve shells (most commonly including *Argopecten gibbus*, *Anadara lienosa floridana*, *Glycymeris americana*, *Laevicardium serratum*, *Arcinella cornuta*, and others) and the proportion of smaller-grained material. For example, the two smaller replicates from station 22 consisted largely of fragments of sanddollars (*Mellita*), seastars (*Astropecten*) and cordgrass (*Spartina*), while the third replicate was typical shell hash. Replicate #1 from station 25 consisted almost exclusively of shrimp and squid (*Illex illecebrosus*, five individuals); replicate #2 contained several shrimp along with seastar parts; and replicate #3 (1000 ml) was shell-hash; but all three replicates had a paucity of mollusk species. Samples from stations 38, 42 and 43 (and SC02 from the Oregon II cruise) contained high proportions of broken pen shells (mostly *Atrina rigida*). Replicates from stations 27 and 28 consistently had relatively small volumes and contained a glutinous mass of filamentous mucoid material of unknown origin (possibly bryozoans, coelenterate tentacles, or egg mass).

Samples from three replicate tows of the beam trawl were sorted and tallied separately for stations from the April cruise of the Ferrel. Initial sample volumes varied widely among replicates at any given station (Table 1); leading to highly variable species numbers among replicates within a station, with each replicate exhibiting a highly skewed distribution of species with many “rare” taxa unique to that replicate. Coefficients of variation (standard deviation as percent of mean) for the mean number of species per tow at any station ranged from 16.5% to 110%, with an average of 59%. The ratio of total number of species recovered in all tows at a station to the mean number recovered per tow at that station ranged from 1.9 to 3.0 (average: 2.53). The variability was so great among replicates within station that the data from individual replicates could not be used meaningfully, and the data were therefore lumped by station. This also facilitated comparison with the data from the Oregon II cruise in February, where the data from different replicates had been lumped during initial sorting. Similar action was taken with data from those ten stations that were sampled on both cruises: data were combined by station.

Table 1. Characteristics of Beam Trawl Samples from Ferrel cruise April 2002.

STA.	SAMPLE DESCRIPTION	SAMPLE VOLUME (ml)			NOTES
		TOW1	TOW2	TOW3	
02.1	CSH-vCSH	1500	500	1000	<i>Argopecten</i> / <i>Cardiidae</i> / <i>Glycymeris</i>
02.2	FSH-CSH	400	350	600	<i>Argopecten</i> / <i>Cardiidae</i> / <i>Glycymeris</i>
02.3	CSH	250	500	800	<i>Argopecten</i> / <i>Arcinella</i> / <i>Veneridae</i>
02.4	CSH	500	1000	500	<i>Argopecten</i> / <i>Cardiidae</i> / <i>Glycymeris</i>
022	BioD-CSH	350	30	30	<i>Mellita</i> /seastar parts/ <i>Spartina</i>
023	FSH-CSH	1000	1500	200	<i>Anadara</i> / <i>Atrina</i> / <i>Neverita</i> eggcases
024	FSH-CSH	1700	100	200	<i>Argopecten</i> / <i>Cardiidae</i> / <i>Glycymeris</i>
025	BioD-FSH-CSH	200	80	1000	starfish parts/shrimp/squid
027	BioD	100	300	350	filamentous mucous/bryozoa/wormtubes/ <i>Neverita</i> eggcases
028	BioD	120	120	200	filamentous mucous, bryozoa/eggmass?
029	BioD-CSH	400	400	250	tunicata,echinoid,holothuroid.
035	BioD-FSH	30	400	60	<i>Neverita</i> eggcase& urchin fragments
036	FSH-CSH	100	2000	1300	<i>Argopecten</i> / <i>Cardiidae</i> /coral
037	CSH	1000	1500	1200	<i>Argopecten</i> / <i>Glycymeris</i> / <i>Arcinella</i> / <i>Chione</i>
038	CSH	400	600	1800	<i>Atrina rigida</i> hash/bryozoa debris
039	BioD-FSH	125	200	30	<i>Spartina</i> /plant detritus/urchin spines & tests,
040	vCSH	4500	4500	8000	<i>Argopecten</i> / <i>Euvola</i> / <i>Anadara</i> / <i>Chione</i>
041	CSH-vCSH	6000	1500	5000	<i>Argopecten</i> / <i>Anadara</i> / <i>Glycymeris</i>
042	BioD-CSH	800	1500	100	<i>Atrina</i> , <i>Argopecten</i> , bryozoa
043	CSH	1200	1000	1000	<i>Atrina rigida</i> hash/bryozoa/anemones;
044	FSH-CSH	20	7	30	flat circular (1 cm) concretions of 1mm black rocks

BioD = biodebris: plant and invertebrate parts

FSH = fine broken shell hash: nearly all passes through 12.5mm screen

CSH = coarse shell hash: about half retained on 12.5 mm screen

vCSH = very coarse shell hash: nearly all retained on 12.5 mm screen

Total Numbers of Taxa

Examples of two hundred sixty-three (263) molluscan taxa were recovered from the beam trawl samples from all 37 stations (Appendix II). Of these, 120 were noted to be in live or very freshly dead condition from at least one of the stations. As “freshly dead” is a judgment call, many specimens/species may have been overlooked in making this assessment. All but two (*Melanella* sp. and *Olivella* sp.) of the taxa have been identified to species level.

Figure 2 illustrates the highly skewed distribution of the taxa within and among stations. One hundred five (105) of the taxa made “single station” appearances (each was recovered from only one of the 37 stations), and nearly all of these were represented by only one (89) or two (14) specimens. Seventy-seven (77) taxa were recovered from five or more stations, while only eleven (11) were found at fifteen or more; *Olivella mutica* was the most widespread- found at twenty-seven stations.

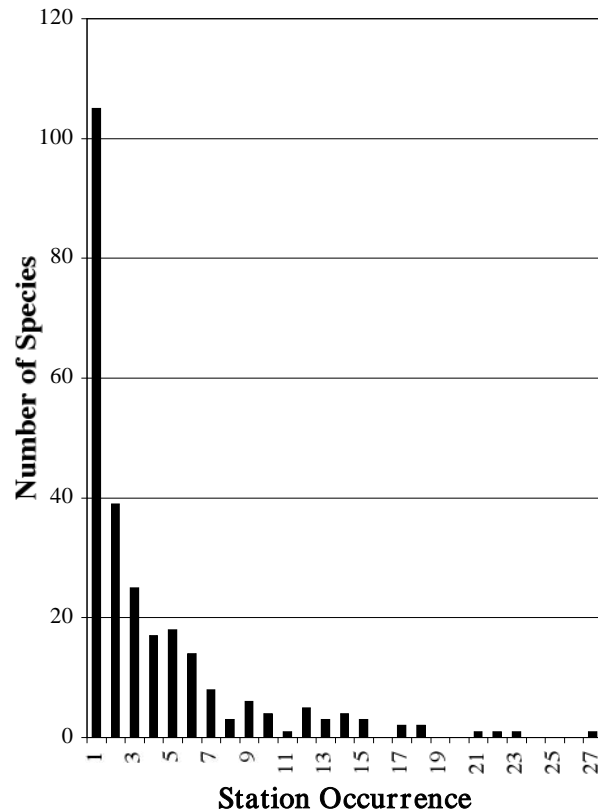


Figure 2. Species Occurrence among Sampling Stations.

Numbers of taxa per station ranged from six (stations 22 & 35) to seventy-two (station 38); the mean was 28.4 ± 17.7 (SD) with a mode of 25. For those ten stations that were sampled on both cruises (Appendix I), the number of taxa ranged from 23 to 56 per station (37.0 ± 10.7 with a mode of 35.5). Diversity of recovered taxa was greatest, however, at four stations that were sampled only once: station 38 with 72 species, 42 (65), 37 (64), and 41 (59),

Species Associations and Community Composition

The data set from this study is suitable only for qualitative examination of community composition due to: (a) the highly skewed distribution in the numbers (and composition) of taxa at all stations, (b) inconsistencies of sample treatment and data recording, and (c) the inconsistency of sampling frequency among stations (ten stations were sampled twice as intensively as the other twenty-seven). Nonetheless, several features stood out and these are discussed in the following sections.

Effect of Depth

To determine whether depth was a factor affecting species occurrence among stations, species distributions were compared qualitatively between two station clusters stratified by depth range. The “shallow” stratum (depth range 8.5 to 22 m) included all ten of the stations sampled twice, along with eight of the remaining twenty-seven, while the remaining nineteen stations were 30 to 103 m deep (Appendix I). Rare species (those found at only one or two stations) were excluded for this comparison. However, the rare species were fairly evenly distributed between the two station strata: 55/105 (52%) of the single-station species came from the deep stations; while the two-station species were divided: 18/39 (46%) from deep stations, 7/39 (18%) from shallow, with the balance split between the two station clusters. Of the 120 taxa that occurred at three or more stations, 26 species were recovered nearly exclusively (>80%) from the “shallow” stratum (Table 2a), while 23 species were recovered nearly exclusively (>80%) from “deep” stations (Table 2b). The remaining 71 species were distributed more evenly and broadly across the range of station depth. Because of small samples and high sample/station variability, the depth affinities indicated for the species in Tables 2a and 2b cannot be viewed as limiting.

With very few exceptions, the “shallow” species listed in Table 2a are well known species components of nearshore (intertidal to 10 m) habitats of the southeastern U.S. Possible exceptions may include *Strombus alatus*, *Cancellaria reticulata*, *Epitonium championi*, and *Spondylus americanus*, which typically occur farther offshore; but most of the species in Table 3a (except *Spondylus americanus*, *Pythinella cuneata*, and *Nemocardium peramabile*) are found regularly on beaches south and west of Cape Lookout, North Carolina.

Table 2a. Species Found Mainly in “Shallow” (4.9-22m) Stations.

SPECIES	FAMILY	OCCURRENCE		
		TOTAL # OF STA'S	FRACTION @ 4.9-22m	#RETRIEVED ALL STA'S
SPECIES RECOVERED NEARLY EXCLUSIVELY FROM SHALLOW (≤ 22 m) STATIONS				
<i>Angulus sybariticus</i> (Dall, 1881)	Tellinidae	15	0.80	39
<i>Terebra dislocata</i> (Say, 1822)	Terebridae	10	0.80	18
<i>Neverita duplicata</i> (Say, 1822)	Naticidae	7	1.00	7
<i>Cerithium atratum</i> (Born, 1778)	Cerithiidae	7	0.86	9
<i>Nassarius acutus</i> (Say, 1822)	Nassariidae	6	0.83	125
<i>Terebra protexta</i> (Conrad, 1846)	Terebridae	6	0.83	9
<i>Strombus alatus</i> Gmelin, 1791	Strombidae	5	1.00	10
<i>Cancellaria reticulata</i> (Linnaeus, 1767)	Cancellariidae	5	1.00	8
<i>Eupleura caudata</i> (Say, 1822)	Muricidae	5	1.00	7
<i>Epitonium championi</i> Clench & Turner, 1952	Epitoniidae	5	1.00	6
<i>Oliva sayana</i> Ravenel, 1834	Olividae	5	1.00	6
<i>Kurtziella atrostyla</i> (Tryon, 1884)	Turridae	5	0.80	15
<i>Pandora trilineata</i> Say, 1822	Pandoridae	5	0.80	10.5
<i>Spondylus americanus</i> (Hermann, 1781)	Spondylidae	5	0.80	3.5
<i>Strigilla mirabilis</i> (Philippi, 1841)	Tellinidae	4	1.00	8
<i>Pyramidella suturalis</i> H.C. Lea, 1843	Pyramidellidae	4	1.00	6
<i>Spisula raveneli</i> (Conrad, 1831)	Mactridae	4	1.00	3.5
<i>Pythinella cuneata</i> (Verrill & Bush, 1898)	Leptonidae	3	1.00	106
<i>Kurtziella limonitella</i> (Dall, 1884)	Turridae	3	1.00	19
<i>Ilyanassa obsoleta</i> (Say, 1822)	Nassariidae	3	1.00	7
<i>Turbo castanea</i> Gmelin, 1791	Turbinidae	3	1.00	7
<i>Graptacme eborea</i> (Conrad, 1846)	Dentaliidae	3	1.00	4
<i>Epitonium rupicola</i> (Kurtz, 1860)	Epitoniidae	3	1.00	4
<i>Nemocardium peramabile</i> (Dall, 1881)	Cardiidae	3	1.00	3
<i>Dinocardium robustum</i> (Lightfoot, 1786)	Cardiidae	3	1.00	2
<i>Trachycardium muricatum</i> (Linnaeus, 1758)	Cardiidae	3	1.00	1.5

Table 2b. Species Found Mainly in “Deep” (~30-103m) Stations.

SPECIES	FAMILY	OCCURRENCE		
		TOTAL # OF STA'S	FRACTION @ 4.9-22m	#RETRIEVED ALL STA'S
SPECIES RECOVERED NEARLY EXCLUSIVELY FROM DEEP (≥30m) STATIONS				
<i>Polinices porcellanus</i> (d'Orbigny, 1839)	Naticidae	14	0.14	59
<i>Naticarius canrena</i> (Linnaeus, 1758)	Naticidae	12	0.08	23
<i>Nassarius albus</i> (Say, 1826)	Nassariidae	10	0.00	21
<i>Caryocorbula contracta</i> (Say, 1822)	Corbulidae	8	0.13	13
<i>Atrina rigida</i> (Lightfoot, 1786)	Pinnidae	7	0.14	100
<i>Prunum hartleyanum</i> (Schwengel, 1941)	Marginellidae	7	0.14	21
<i>Cerodrillia bealiana</i> Schwengel & McGinty, 1942	Turridae	7	0.14	8
<i>Nassarius consensus</i> (Ravenel, 1861)	Nassariidae	7	0.00	21
<i>Euvola raveneli</i> (Dall, 1898)	Pectinidae	6	0.17	8.5
<i>Xenophora conchyliphora</i> (Born, 1780)	Xenophoridae	6	0.00	11
<i>Semicassis granulata</i> (Born, 1778)	Cassidae	6	0.00	6
<i>Merisca aequistriata</i> (Say, 1824)	Tellinidae	5	0.20	3.5
<i>Cirsotrema dalli</i> Rehder, 1945	Epitoniidae	5	0.00	6
<i>Aequipecten muscosus</i> (W. Wood, 1828)	Pectinidae	5	0.00	4.5
<i>Cymatium cingulatum</i> (Lamarck, 1822)	Cymatiidae	4	0.00	38
<i>Epitonium angulatum</i> (Say, 1831)	Epitoniidae	4	0.00	5
<i>Busycon sinistrum</i> Hollister, 1954	Melongenidae	4	0.00	3
<i>Similipecten nanus</i> (Verrill & Bush, 1897)	Propeamussidae	3	0.00	12.5
<i>Transenella stimpsoni</i> Dall, 1902	Veneridae	3	0.00	5.5
<i>Graptacme calamus</i> Dall, 1889	Dentaliidae	3	0.00	4
<i>Dentimargo aureocinctus</i> (Stearns, 1872)	Marginellidae	3	0.00	4
<i>Astarte smithi</i> Dall, 1886	Astartidae	3	0.00	3.5
<i>Varicorbula limatula</i> (Conrad, 1846)	Corbulidae	3	0.00	2

Many of the “deep” species (Table 2b) are components of the calico scallop community off North Carolina (Porter and Wolfe, 1972), which occur there in depths of 20-40 m. Three of the species in Table 2b (*Atrina rigida*, *Epitonium angulatum*, and *Busycon sinistrum*) are known to occur intertidally or in the shallow subtidal throughout the southeastern U.S., so their appearance in this table is clearly an aberrant result.

Stations 44 and 39, were substantially deeper than any others (at 103 and 90 m, respectively), and might have been expected to yield species more characteristic of deep habitats. These stations, however, had only three species in common, and all three were found commonly in the shallow stations as well. Replicate tows from both of these deep stations yielded very small sample volumes (Table 1), and relatively few taxa per station (12 and 16, respectively). While station 39 yielded an unusually high proportion of single-station (7/16) or two-station (2/16) species, these categories accounted for only one species each of the 12 recovered from station 44. Seven of the twelve species recovered from station 44 and six of the sixteen from station 39 occurred at six or more stations, encompassing a broad range of depths as shallow as 8.5 m. Only two species recovered from these two stations were clearly recognizable as “deep-water species”: *Cochlespira radiata* (a freshly dead specimen), and *Thracia conradi* (two single valves). Samples from station 39 contained very little shell hash and notable amounts of biodebris, including urchin parts and *Spartina* and seagrass fragments, suggesting that the station was in a depositional area that received material transported across the continental shelf from the coast.

The “*Atrina-Cymatium*” Community

Stations 38 and 43 from the Ferrel cruise were characterized by large sample volumes with an unusual preponderance of broken pen shell (*Atrina rigida*) hash— mostly from shells 100-125 mm long (Table 1). To a lesser degree, two stations from the Oregon II cruise (SC01 and SC02) shared this same trait.

Three species of *Cymatium* (see cover photograph) appeared in samples from one or more of these four stations and at no other stations. *Cymatium cingulatum* occurred in replicate tow #3 from station 38 (two specimens, recently dead); in all three replicate tows from station 43 (1, 28, and 5 specimens, respectively- all either live or recently dead); and recently dead specimens were also obtained from stations SC01 and SC02. *Cymatium parthenopeum* also occurred in all three replicate tows from station 43 (2, 8, and 6 specimens, respectively- all either live or recently dead); and a live specimen was obtained from station SC01. One recently dead specimen of *Cymatium krebsii* also appeared in tow #2 from station 43. Associated with and attached to fragments of the shell hash of *Atrina rigida* was an unidentified light brown organism with branched filamentous strands up to ~2-3 cm long (referred to as “Bryozoa” in Table 1) that bore a striking resemblance to the periostracum of the Cymatiidae, and especially to that of *C. parthenopeum*.

While most of the pen shell hash consisted of broken dead shells, many of the fragments had intact hinge ligaments, delicate unbroken spines, and interior surfaces free of fouling organisms; suggesting that the species is living at or very near the locations where the material was found. One recent and intact specimen of *Atrina seminuda* was picked out from among the abundant *A. rigida*. Rosenberg (2005) cites records of live occurrences for these two species at very shallow depth ranges (0.3-2 m and 1.5-2.4 m, respectively), while Mikkelsen and Bieler (2008) indicate that both species usually occur at depths less than 30 m. Stations 38, 43, SC01, and SC02 are clustered fairly closely together at depths of 43-47 m (Fig. 1, Appendix I), so these records may represent unusually deep occurrences for both species.

Typically, each of these *Atrina-Cymatium* stations had its own complement of other species unique to that station. The calico scallop *Argopecten gibbus* was the only other species recorded at all four of these stations. Twenty-five other species occurred at either two or three of these stations, but only one of these (*Eulithidium thalassicola*) was found at no other station. The remaining species, were all found in addition at several other stations. Based on their relative occurrence at other stations and at similar depths, the following species were judged to be most closely associated with the *Atrina-Cymatium* community: *Similipecten nanus*, *Depressiscala nautlae*, *Busycon sinistrum*, *Cirsotrema dalli*, *Aequipecten muscosus*, *Xenophora conchyliophora*, *Semicassis granulata*, *Arcinella cornuta*, *Calliostoma yucatecanum*, *Arene tricarinata*, *Naticarius canrena*, *Conus anabathrum*, *Polinices porcellanus*, and *Chama macerophylla*. It is no surprise that several of these associated species appeared also in the cluster of “deep” species (Table 2b).

The *Nassarius acutus*—*Phascolion*—*Pythinella* Connection

Samples from stations 27 and 28 afforded a unique opportunity to examine and analyze the commensal relationship between a bivalve and a sipunculid worm that occupies vacant shells of small gastropods (Hampson, 1964; Gage 1966). The three tows from station 27 yielded 86 specimens (29, 17, and 40, respectively) of *Nassarius acutus*. Only nine other specimens were recovered from four tows at three other stations (#’s 22, 23, and 42) from the Ferrel cruise. A total of thirty specimens were retrieved from the Oregon II cruise— at stations 28, 23 and 24; and “live?” specimens were noted at station 28. About 75% of these *N. acuta* shells were occupied by hermit crabs; a few appeared quite freshly dead. At least twenty-two of these shells were occupied, however, by a sipunculid worm—presumed to be *Phascolion strombus* (Montagu, 1804)— and it was one or more of these specimens that I had erroneously judged to be “live”, mistaking the anterior end of the sipunculid (preserved with tentacles retracted) for a gastropod with an operculum.

Of those shells containing sipunculids, nineteen (86%) had commensal bivalves [Galeommatoidea: Leptonidae: *Pythinella cuneata* (Verrill and Bush, 1898)] attached— usually clustered around the tentacular ring of the sipunculid and half-buried in the mucoid mass filling the aperture of the gastropod shell (Fig. 3a-c). These bivalves probably graze- at least in part- on materials caught in the mucous secreted by the sipunculid. Specimens ranged in size from juveniles < 1 mm to adults just over 3 mm. The fifteen adult specimens were on 13 different shells (maximum of two). The 39 mid-size (1-2.5 mm) specimens were attached on 15 shells, usually (on all but four shells) in conjunction with a full-sized individual. There were 75 small (< 1 mm) specimens on eight different *Nassarius* shells, accompanied in seven cases by at least one full-size and in six cases also by at least one mid-size specimen. The mean number of bivalves per sipunculid (including the three with no clam attached) was 5.5 ± 6.8 (sd); without those three zeros the mean rose to 6.6 ± 7.0 . While *Nassarius acutus* was found at four other stations, *Pythinella cuneata* made only one other appearance (at station 31) where it was associated with a sipunculid in the aperture of *Epitonium championi* (Fig. 3d).

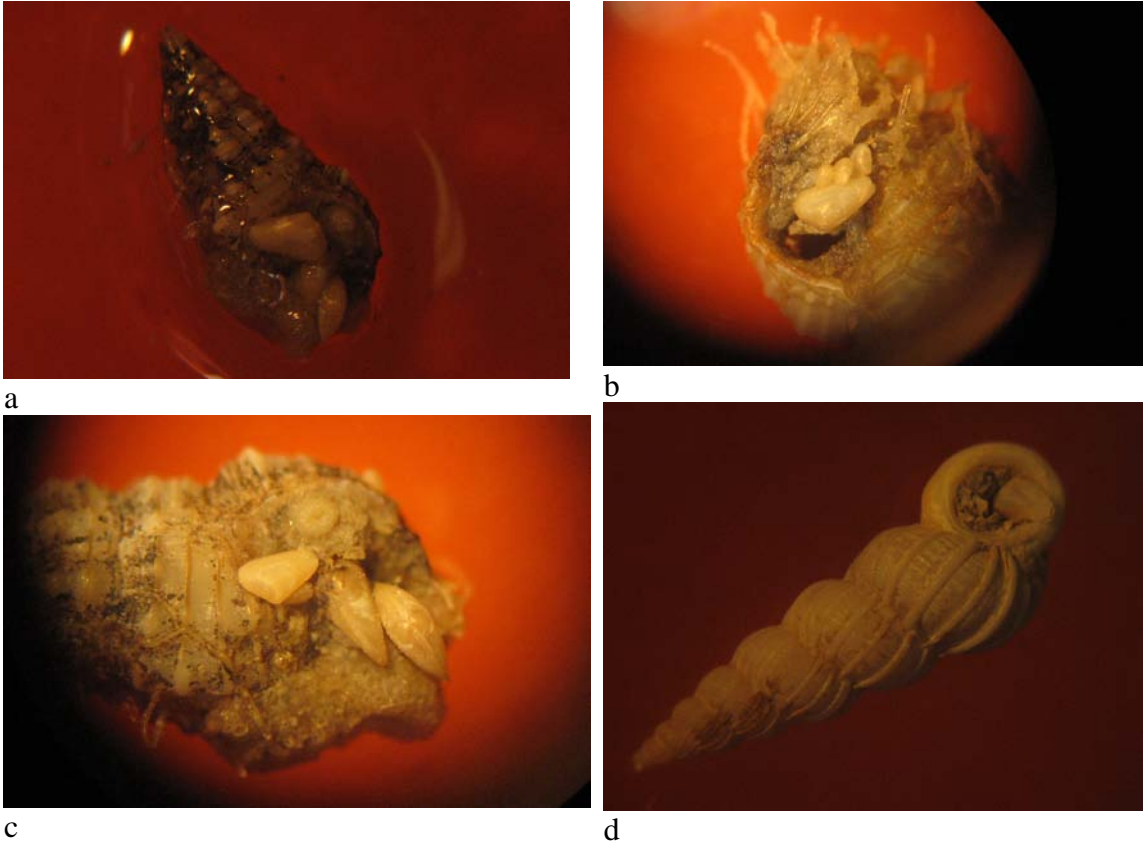


Figure 3. The bivalve *Pythinella cuneata* (Verrill & Bush, 1898) has a commensal relationship with sipunculids that occupy gastropod shells: a. here in *Nassarius acutus*. b. large *Pythinella* ~ 3mm; sipunculid retracted. c. five *Pythinella*; sipunculid oral ring in view. d. *Pythinella* & sipunculid on *Epitonium championi*.

The samples containing *Pythinella cuneata* also exhibited other distinctive characteristics. As mentioned previously, the Ferrel samples from stations 27 and 28 exhibited the very unique character of small sample volumes consisting largely of a sticky mass of mucoid material (Table 1). Unusually large numbers of *Neverita* eggcases (sand collars) also were noted in these samples. The three tows from station 27 contained 12 ± 2.6 (sd) species each with a total of 23 species combined. The three tows from station 28 contained 1.3 ± 0.6 species each with a total of only four species. The species totals from the three replicate tows for these same two stations in the Oregon II samples were essentially reversed— with only two species from station 27 and 22 from station 28. So— while there is considerable evidence that the two stations are very similar, the data also demonstrate the extreme variability and patchiness of species distributions on the continental shelf. When the two cruises are taken together the cumulative species totals and composition show high concordance: 25 and 24 total species for stations 27 and 28, respectively, with 15 species in common. Most notable among these (in terms of their scarcity at other stations) were two turrid species (*Kurtziella limonitella* and *K. atrostyla*), *Pyramidella suturalis*, *Neverita duplicata*, and *Mitrella lunata* (abundant in tow 3 from Ferrel station 27). Several gastropod species that were relatively rare in the overall dataset made appearances at either station 27 or 28, including *Rictaxis punctostriatus*, *Sinum perspectivus*, *Cerodrillia simpsoni*, *Rubellatoma rubella*, *Sigatica carolinensis*, *Acteon candens*, *Epitonium candeanum*, *E. championi*, *E. krebsii*, and *E. rupicola*. Epitoniids are well-known predators upon anemones and corals, and the turrids are also predators, feeding largely upon worms and other small benthic meiofauna. While the specific nature of the mucoid material in these samples remains a mystery, it bore some resemblance to the bryozoan *Zoobotryon verticillatum*, commonly known as animal grass. The absence of more typical shell hash and the presence of the diverse collection of gastropods, however, might reflect a habitat of relatively fine-grained sediment, populated by anemones and polychaetes, and loaded with organic detritus (and associated detritivores) at these stations.

Rock-dwelling Species

Two species of rock-boring bivalves were represented by single valves in the beam trawl samples from two stations: *Coralliophaga coralliophaga* at 2.4 and *Jouannetia quillingi* at 33. Both species have been collected by the author from burrows in the limestone marl rock that forms the rocky ledges and reefs at 10-15 fms off Beaufort, North Carolina (Wolfe, 1968). I have also collected *C. coralliophaga* live from burrows in soft sandstone just below the intertidal zone at Myrtle Beach, South Carolina. Species found in the present study that were associated with *J. quillingi* on limestone boulders in North Carolina are: *Lithophaga bisulcata*, *Diplodonta punctata* (wedged into crevices and burrow-holes), *Chama congregata*, *Chama macerophylla*, *Chama radians*, and *Vermicularia knorri*, (Wolfe, 1968). Other species that are likely associated with the rock outcrops include: *Spondylus americanus*, *Diodora cayenensis*, *Calliostoma pulchra*, *C. yucatecanum*, the muricids *Calotrophon ostrearum*, *Haustellum rubidum*, *Murexiella leviculus*, and *Stramonita haemastoma floridana*, *Erosaria acicularis*, and *Simnia lena uniplicata* (on gorgonian coral). Station numbers where these species were best represented in the samples were: 42, 40, 2.1, 2.4, 43, 41, 36, and 33. The occurrence of many of these species at low numbers in many different samples; however, suggests that suitable rock habitat is exposed in small patches over extensive areas of the shelf.

Range Extensions

Prior records of distribution and occurrence were examined for each species on the list of taxa (Appendix II) in order to identify unusual records and possible range extensions. I started with Rosenberg's (2005) online Malacolog database, which reports northern and southern range limits of records for most species known to occur in the Western Atlantic. Other authorities, including previous studies of molluscan fauna of similar continental shelf habitats off the coast of the southeastern United States (Wells *et al.*, 1964; Porter and Wolfe, 1972; Shoemaker, 1972; Porter, 1974; Wenner *et al.*, 1983) were also consulted to verify published distributions. Table 3 lists twenty-one (21) taxa found in this study that were flagged as possible range extensions, based strictly on their ranges of latitude as recorded by Rosenberg (2005). The species list (Appendix II) may contain numerous other additions to the molluscan fauna previously recorded on the Continental Shelf of Georgia, but that is not addressed here. As many of the species in Table 3 are represented only by dead specimens, the possibility clearly exists that they were physically transported to this location by oceanographic processes; but their presence here nonetheless indicates that they are living nearby.

Exceptions to the ranges reported in Malacolog are noted here for five of the taxa listed in Table 3 (*Lioberus castaneus*, *Orobitella floridana*, *Varicorbula philippii*, *Epitonium foliaceicosta*, *Oliva reticularis*). All five of these species have been previously reported to occur well to the north of Georgia. Mikkelson and Bieler (2008) described the range of *L. castaneus* as a typical extended Caribbean distribution from North Carolina to Florida, West Indies and Caribbean Central America to Brazil. Porter (1974) cited Coues (1871) for a North Carolina record of this species and a live specimen (DAW1667) was retrieved by the author in 1967 from a settling tank for a laboratory seawater system at Pivers Island, Beaufort, North Carolina. Mikkelson and Bieler (2008) described the range of *Orobitella floridana*, as a more nearly Carolinian distribution from North Carolina to Florida (and Bahamas), and Gulf of Mexico to Caribbean Central America to Brazil; Abbott (1974) noted it only from East and West Florida. Porter (1974) cited Jacot (1921) for a North Carolina record (Cape Lookout) of this species (as *Montacuta floridana*), but had not collected the species in North Carolina. In their review of *Varicorbula*, Mikkelson and Bieler (2001) provisionally recognized *V. philippii* as distinct from *V. limatula* [synonyms: *operculata* (Philippi, 1848) and *disparilis* d'Orbigny 1853], and gave its range (Mikkelson and Bieler, 2008) as North Carolina to Florida, Bermuda, Gulf of Mexico, West Indies, Caribbean Central America, and Brazil. Although not reported off North Carolina by Porter and Wolfe (1972) or Porter (1974), the species was included (with *V. operculata*) in material from the gut contents of starfish (*Astropecten*) on the calico scallop beds there (Mikkelson and Bieler, 2001). Porter (1974) cited Dall (1903) for a North Carolina record (Cape Hatteras) of *Epitonium foliaceicosta* (as *Scala novemcostata*), and a specimen (DAW925) was retrieved in 1966 west of Cape Lookout, at a depth of 12-15 fathoms on calico scallop beds off Beaufort. Merrill and Petit (1969) reported *Oliva reticularis* living off McClellanville, South Carolina at 46m.

Table 3. Possible Range Extensions for Mollusks Found in this Study, Based Primarily on Ranges Reported by Rosenberg (2005).

SPECIES	STA #'s	DEPTH (M)	#RETRVD ALL STA'S	PREVIOUSLY RECORDED RANGE (MALACOLOG)		
				LATITUDE	DEPTH	REGIONS**
<i>Ischnochiton hartmeyeri</i> (Thiele, 1910)	2.4*	18	1	NR	NR	# EFL, FLK, WFL, BAH, YUC, BRZ
<i>Lioberus castaneus</i> (Say, 1822)	42*	40	1	28°N to 24°S	2-42 m	EFL, WFL, YUC
<i>Limatula hendersoni</i> Olsson & McGinty, 1958	38*	43	1	26°N to 9°N	NR	EFL, BAH, PAN
<i>Diplodonta notata</i> Dall & Simpson, 1901	38,42	40-43	1.5	28°N to 18.2°N	4-7	EFL, WFL, FLK; PR
<i>Orobitella floridana</i> (Dall, 1899)	29,34	15-15	2	28°N to 9°N	0-0.5	EFL,WFL,FLK
<i>Ensis megistus</i> Pilsbry & McGinty, 1943	40,42	22-40	1.5	30°N to 26.5°N	0-37	EFL, WFL
<i>Pitar simpsonii</i> Dall, 1889	40	22	0.5	27.7°N to 18°N	0-48	EFL, WFL
<i>Cooperella atlantica</i> Rehder, 1943	2.2*,34*	15-19	2	26°N to 34°S	3-3	EFL, FLK
<i>Varicorbula philippii</i> (E.A. Smith, 1885)	38	43	0.5	32.3°N ; 64.8°W	NR	BER
<i>Caryocorbula</i> cf. <i>cymella</i> (Dall, 1881)	6*	43	1	25°N to 6°S	36-125	FLK
<i>Thracia</i> cf. <i>phaseolina</i> Lamarck, 1822	33	13.4	0.5	25°N to 20°N	1170	FLK; YUC
<i>Thracia conradi</i> Couthouy, 1838	39	90	2x 0.5	45.7°N to 41.2°N	274	NS; ME to NY
<i>Periploma leanum</i> (Conrad, 1831)	24	14	1	47°N to 35°N	0-45	QUE, NS; NY to NC
<i>Barleeia</i> cf. <i>tincta</i> Guppy, 1895	42	40	1	27°N to 10.5°N	0-8	EFL; TRD
<i>Caecum imbricatum</i> Carpenter, 1858	37, SC06*	33-36	2	30°N to 24°S	0-183	EFL, WFL to YUC & BRZ
<i>Epitonium foliaceicosta</i> (d'Orbigny, 1842)	37	33	1	30°N to 21°S	0-219	EFL,WFL,FLK,BAH, CUB, PR, USVI, YUC, BRZ
<i>Calotrophon ostrearum</i> (Conrad, 1846)	2.1,24	14-20	3	30.3°N to 20°N	0-64	EFL WFL, FLK; YUC
<i>Oliva reticularis</i> Lamarck, 1811	39	90	1	32.3°N to 9.4°N	0-200	EFL; BER, BAH, CUB, PR, YUC to VEN
<i>Inodrillia</i> cf. <i>avira</i> Bartsch, 1943	^a [8 sta's]	11-45	13	26°N ; 80°W	183-382	EFL
<i>Kurtziella dorvilliae</i> (Reeve, 1845)	2.4	18	1	28°N to 21°S	0-50	EFL, WFL, USVI to COL, VEN & BRZ
<i>Turbonilla krebsii</i> (Mörch, 1875)	38	43	1	26.67°N to 12°S	0-0	BAH; CUB; USVI; BRZ

**To conserve space, some regions reported in Malacolog have been omitted. REGION CODES: QUE: Québec; NS: Nova Scotia; EFL: East Florida; WFL: West Florida; FLK: Florida Keys; BAH: Bahamas; BER: Bermuda; CUB: Cuba; PR: Puerto Rico; USVI: US Virgin Islands; DR: Dominican Republic; JAM; Jamaica; YUC: Yucatan; BRZ: Brasil; PAN: Panama; COL: Colombia; VEN: Venezuela; TRD: Trinidad

• live-taken specimen

NR = not reported in Malacolog (Rosenberg, 2005)

(Lyons 1980 & pers. comm..)

^a[1,4*,6,32,36,37,42,43]

Three of the taxa noted in Table 3 (*Ensis megistus*, *Caecum imbricatum*, *Calotrophon ostrearum*) had previously been reported to occur off the coast of Florida north of Cape Canaveral (~28.4°N), and so their occurrence on the continental shelf off Georgia represents only a minor extension of reported range. Mikkelson and Bieler (2008) do not recognize *Ensis megister* as a distinct species, showing *E. minor* to occur from New Jersey to Florida and the Gulf of Mexico, and to reach a length of 146 mm. The Georgia specimens were broken single valves that appeared to have been at least 125 mm in length. Porter (1974) reported *C. imbricatum* from North Carolina (erroneously synonymizing the species with *C. cooperi*); Abbott (1974) gave its range as Florida and Bahamas to Texas and West Indies; and Redfern (2001) describes it as “fairly common” in Abaco. Abbott (1974) gave the range of *C. ostrearum* as the “west coast of Florida to the Florida Keys.” H. Lee (pers. comm.) describes it as rare off Jacksonville, Florida. None of these three taxa were found live.

Eight additional species (*Ischnochiton hartmeyeri*, *Limatula hendersoni*, *Diplodonta notata*, *Pitar simpsoni*, *Cooperella atlantica*, *Barleeia* cf. *tincta*, *Inodrillia* cf. *avira*, and *Kurtziella dorvilliae*) have the distinction of prior records on the East Coast of Florida south of Cape Canaveral. For most of these species the Georgia records represent range extensions greater than 325 km. The chiton (*I. hartmeyeri*), a single live specimen from station 2.4, had been previously recorded from Hutchinson Island, southeast Florida, Dry Tortugas and the Florida west coast (Lyons, 1980), although the species has subsequently been reported from additional east Florida locations (W. Lyons, pers. comm.).

Two of the bivalves (*L. hendersoni* and *C. atlantica*) were also found alive. The *Limatula* was identified by H. Lee, and has also been found by him east of St. Augustine, Florida (pers. comm.). *Cooperella atlantica* was previously reported from SE Florida to the Greater Antilles and Brazil (Abbott, 1974; Mikkelson and Bieler, 2008), but has not been found in Jacksonville (H. Lee, pers. comm.). *Pitar simpsoni* (a somewhat worn single valve identified by H. Lee) has been previously recorded from S Florida and the Bahamas to the West Indies and the Gulf of Mexico (Abbott, 1974; Mikkelson and Bieler, 2008). The *Diplodonta notata* is a tenuous distinction of three single valves, based on the pattern of microscopic surface pustules, from other more common Ungulinids (Appendix 2). The species has been reported previously from the Florida Keys and Bahamas through the Gulf of Mexico and Caribbean to Colombia (Mikkelson and Bieler, 2008). A single specimen, dead and worn, resembling *Barleeia tincta*, was retrieved from station 42 at 40 m. *B. tincta* has been reported from Hutchinson Island, Florida (Lyons, 1989); and similar specimens have also been obtained off Jacksonville and other E Florida locations (H. Lee, pers. comm.). Taxonomic confusion surrounding *Kurtziella dorvilliae* is discussed by Rosenberg (2005) and Lee (pers. comm.). The species, previously reported off SE Florida (Abbott, 1974), has also been found off St. Augustine and at Jacksonville Beach (H. Lee, pers. comm.).

Inodrillia cf. avira is only tentatively identified, based on its very close resemblance to the illustration of that species by Abbott (1974: p. 274, species 3095) and Bartsch's (1943) very detailed original description. This species, previously recorded only in deep water off SE Florida (Bartsch, 1943; Abbott, 1974); was retrieved (thirteen specimens) from eight stations ranging from 11-45 m in depth; and at least one specimen was in very fresh condition (station 4*). These specimens were examined by H. Lee and by Donn Tippett, who concurred that they should be properly assigned to *Viridrillia*. Lee has found the same taxon among calico scallops trawled from at least two locations off E. Florida (specimens seen by author). Tippett (pers. comm.) indicated that Bartsch's (1943) *Inodrillia/Viridrillia* material in the U.S. National Museum is in need of serious review, and that the Georgia specimens might even represent a new species.

United States records in Malacolog (Rosenberg, 2005) for two of the Georgia species (*Caryocorbula cf. cymella*, *Thracia cf. phaseolina*) were restricted to the Florida Keys. A single live specimen of *Caryocorbula cf. cymella* was retrieved from station 6 at 43 m. The shell is distinguished from *Caryocorbula contracta* by a thinner, more translucent shell with opaque white mottlings scattered over the surface, and lacking commarginal ridges near the umbones (Mikkelson and Bieler, 2008). These same authors give its range as Florida Keys and West Indies to Brazil. According to Mikkelson and Bieler (2008), *Thracia phaseolina* is a European species, and the W Atlantic species is as yet undescribed. A single valve was found at station 33.

Two taxa in Table 3 (*Thracia conradi*, and *Periploma leanum*) are northern species with reported ranges south only to Long Island Sound, New York and off North Carolina, respectively (Abbott, 1974). Although *Thracia conradi* is typically found in waters deeper than the stations sampled here, two (broken) left valves, the larger 70 mm long and retaining its color and gloss internally, were recovered from station 39 (90 m). It seems improbable that these specimens would have been transported upslope to this location; the species likely occurs live near here. The *P. leanum* (single valve only) appeared at a shallow (14 m) station (#24). Porter (1974) reported *P. leanum* from off Cape Fear (Southport), North Carolina.

The one remaining taxon in Table 3, *Turbonilla krebsii*, was previously known only from the Bahamas (Redfern, 2001) and the Netherlands Antilles (De Jong and Coomans, 1988). While this genus contains a bewildering array of species, the single specimen (~6.5 mm) found in excellent condition at station 38 (43 m) on the Georgia shelf is a dead ringer for those found in Abaco and illustrated by Redfern (2001: Pl. 67, species 626)—down to the orange-brown color and the incised spiral lines and faint cancellate sculpture on the body whorl behind the outer lip. The species occurs also in Bermuda (H. Lee, pers. comm.).

Notes on Other Taxa

Five species listed in Appendix 2 (but not in Table 3) deserve special note here because of residual identification issues, and possible implications for further extensions of range. These taxa are discussed below:

Melanella sp., found at stations 2.2 and 38, strongly resembles *Eulimostraca* sp. B from Abaco (species 340: Redfern, 2001). Lee (pers. comm.) suggests that the species is one he has not seen before, and moreover, that the aperture is “that of a *Melanella*, not *Eulimostraca*”. He further likened the specimen to *Polygireulima amblytera* (A.E. Verrill and Bush, 1900) and to *Polygireulima* sp. A (Pl. 6, fig. 6, in Lyons, 1989)—both recorded previously in southern Florida.

Dentimargo aureocincta, represented by four specimens (dead, but in good condition) from three stations (33-103 m depth), correspond well to the illustration in Redfern (2001: Pl. 47, species 437A) found in Abaco and identified as *Dentimargo* cf. *macnairi* (Bavay, 1922). Malacolog data (Rosenberg, 2005) report the range of *Dentimargo macnairi* as Martinique and Panama (14.5°N). Dall (1927) named several other species of *Dentimargo* from off Georgia for which I could locate no illustrations, but none of Dall’s written descriptions seemed to match these specimens exactly. These four specimens were examined by H. Lee and described by him as a “depauperate morph” of *D. aureocincta*; they are so identified in Appendix 2.

Olivella sp. is represented by two freshly dead, shiny creamy white specimens, 11.5 and 12.9 mm in length, from stations 5 and SC10 at 33-37 m. The shells have 5.5-6 opaque whorls with a very deeply channeled suture; with heavy callus on the parietal area and lacking plicae on the columella and pillar structure; and the aperture is about 1/2 the total length. Based on Dall’s (1889) description and distribution data given by Abbott (1974) and Rosenberg (2005), I speculated that these might be *Belloлива tubulata* (Dall, 1889). Lee (pers. comm.), however, relates they are not that species and that they correspond very closely to an un-named species illustrated by Kaicher (1987: card no. 5019) that he treats as *Olivella* sp. aff. *tunquina* (Duclos, 1835), in his list of NE Florida Marine Mollusks (Lee, 2006). I have not yet seen an illustration that corresponds to this species.

The taxonomy of *Platycythara elata* is somewhat confusing in the literature: the species has variously been assigned to the genera *Daphnella*, *Rubellatoma*, *Vitricythara*, and *Platycythara* (Fargo, 1953; Lyons, 1989; Turgeon *et al.*, 1998), and the discussion continues (Lee, pers. comm.). The single specimen (fresh but with a gaping hole in the body whorl) from the Georgia shelf corresponds extremely well to specimens illustrated by Fargo (1953) and Lyons (1989), and to a specimen recovered from a batfish taken off St. Johns County, Florida and illustrated (scanning electron micrograph, as *Vitricythara auberiana*) by Lee (2006). It is creamy white, however, with a light brown band emanating from the top of the aperture and encircling the body whorl around to the dorsum of the siphonal canal. Similar banding has not been reported on other specimens. The range of *P. elata* is reported (Rosenberg, 2005) as: 34.53°N to 18.2°N; 82°W to 67.2°W, at depths of 11-73m. The type locality is 12

miles east of Frying Pan Shoals, off North Carolina, at 12 fathoms. The species was found off North Carolina also by Wells *et al.*, (1961), but was not found by Porter (1974).

The turrid *Cryoturris fargoii* also deserves special mention. It is a single specimen, collected dead but in good condition, whose identification was confirmed by Harry Lee. This specimen is represented quite well by an illustration in Lyons (1989: Plate XI, fig. 1), and described by him as having a range of “both coasts of Florida.” Three other specimens of *Cryoturris fargoii*, obtained from W of Cape Lookout, North Carolina (at 65 ft in seastar *Astropecten* stomach), Puerto Rico and W Florida, respectively, and verified by D. Tippett (USNM), reside in the author’s collection. Comparing the Georgia specimen with these, I suspect that two species may be involved here. The present specimen, about 5.2 mm long, is tan in color; its spire angle (corresponding with Lyon’s illustration) is greater; and it has more axial riblets than any of the other three specimens, all of which are white. All four of the specimens, however, possess fine spiral lines with microscopic beads, giving the shells a characteristic frosted appearance. Similar specimens have been obtained by Lee (pers. comm.) from scallop beds off eastern Florida, and he also noted variability of spire angle among specimens from different locations. Examination of more specimens may be required to ascertain the identification of this taxon, and the implications for range extension.

Gray’s Reef National Marine Sanctuary [Stations 2.1-2.4] Taxa

Of the 263 taxa recovered in this study (Appendix II), ninety-seven (97) were retrieved from at least one of the four stations (2.1-2.4) bordering the GRNMS. These taxa are identified in Appendix II by an entry in the “STA 2?” column, indicating the actual number of stations (that is, of the four stations 2.x) where the species was found. These four stations all had heavily skewed distributions of species numbers similar to those found throughout the overall set of stations, and exhibited little similarity of species composition. The number of taxa occurring at stations 2.x (2.1 through 2.4) were 51, 32, 35, and 56, respectively, while the numbers of single-station (of the four 2.x stations) species were 19, 12, 6, and 20, respectively. Only eleven taxa occurred at all four of the stations 2.x; fifteen at three, fourteen at two, and 57 occurred at only one. Of the 57 taxa occurring at only one of the stations 2.x, sixteen (16) occurred at only one of the thirty-seven total stations, eight (8) were at 2; seven (7) were at 3; six (6) were at 4; eight (8) were at 5; three (3) were at each of 6 and 7; two (2) at 9; and one each was at 10, 12, 13, and 14.

Since none of the stations 2.x actually lay within the GRNMS, and the species composition exhibited similar degrees of skewness and low concordance among these four stations as among the 37 stations at large (Fig. 2), I conclude that the station 2.x dataset is only slightly more likely to be representative of the GRNMS than the dataset from the overall set of 37 stations. One may treat the station 2.x dataset as reasonably positive evidence of a species’ occurrence within the GRNMS. Given the extreme patchiness of species occurrence noted among trawl replicates and among

stations in this study, and the great diversity of habitats previously documented within the GRNMS, most of the species found in this study are nonetheless quite likely to occur also within the boundaries of the Sanctuary. This is particularly likely since the patch reef habitats characteristic of the GRNMS have been documented as widespread across the Georgia shelf, and extending to depths greater than within the GRNMS itself (Van Dolah *et al.*, 1994). The absence of marked differences in species composition and occurrence with station depth, coupled with the fact that the GRNMS is located near the mid-range depths for this study, further supports this conclusion.

The list of taxa from the present study (Appendix II) was also compared with a list of benthos previously reported to occur within the Gray's Reef National Marine Sanctuary (GRNMS, 2004), which was based on a benthic survey (Vittor and Associates, Inc., 2004). That survey used a Young dredge (sampling area of 0.04 m²) and diver cores (area = 0.0071 m²), both of which are designed for quantitatively sampling benthic infauna. Either three or five replicate samples were taken at each of seven stations within the GRNMS. The beam trawl is more effective at collecting epifauna, and the 5-minute tows covered a much larger area, so the studies are complementary and one should not expect great similarity between the two lists. Benthic collections have also been made within the GRNMS by Hyland *et al.*, (2006), and a few species are mentioned in that work that are not included on the GRNMS (2004) list.

The GRNMS benthos list includes 107 species of mollusks identified to the species level, 34 to genus, 37 only to family, and six only to a taxonomic level higher than family, for a total of 184 taxa. At least twenty-six species (including LPTL's) of bivalves and twenty-eight species of gastropods on the GRNMS list were not found in the present study. The present study identifies one species of chiton, 81 species of bivalves, four species of scaphopods, 108 species of gastropods and one cephalopod not named explicitly on the GRNMS list. Some of these taxa may occur on the GRNMS list as indeterminate LPTL taxa, however, so the apparent discrepancy between study results is probably exaggerated to some extent.

Potential Species Richness

To assist the estimation of the potential total number of molluscan species that might ultimately be found in this region, I generated a "species discovery curve" (Keating *et al.*, 1998; Solow and Smith, 2005) based on presence-absence data for the 263 taxa from the 37 stations in this study (Fig. 4). Total species were cumulated over the 37 sampling stations twelve times, in randomized station order, and least-square regressions were performed on the resultant dataset, using logarithmic and negative exponential functions. In order to improve the fit of the regression curves to the upper portion of the dataset, the first five cumulative values were omitted from both regressions. This had the dual effects of: (a) forcing the curves through 263 species at, or very near, 37 stations, and (b) increasing the projected number of species that would be discovered by additional sampling.

The negative exponential regression approaches an asymptotic maximum of 311 species (compared to a value of 287 for the same regression on the complete dataset). The logarithmic function projects that 311 species would be discovered by sampling a total of 67 stations, and that further sampling would continue to reveal additional species (Fig. 4).

Several more sophisticated extrapolative techniques have been developed and tested for estimating species richness (Chao, 1984; Foggo *et al.*, 2003; Colwell *et al.*, 2004), and Colwell (2006) provides downloadable software (EstimateS©: v. 8.0) enabling ready computation of additional estimates (Table 4). To generate a more robust database than the presence-absence data used for Fig. 4, I employed numbers of individuals for each species at each station, by spreading the species numbers collected during the Oregon II cruise, evenly among their stations of origin, back into the dataset. While this approach no doubt reduced the skewness of species numbers inherent among stations, it nonetheless provided a first order approximation of species distribution and relative abundance. Table 4 presents the estimates of species richness generated by EstimateS© (Colwell, 2006) for eight different extrapolative techniques applied to this reconstructed dataset, using 100 randomized cumulations without replacement.

Estimates of S_{\max} ranged from 308 species (Bootstrap– similar to negative exponential regression of presence-absence data, Fig. 4) to 429 species (Jack2), with a median value in the range of 368-374 species (ACE/Chao 1). Given the limitations of this database, it is impossible to assess the relative merits of these estimates in quantitative terms, but there is a strong consensus among approaches that many species remain to be discovered.

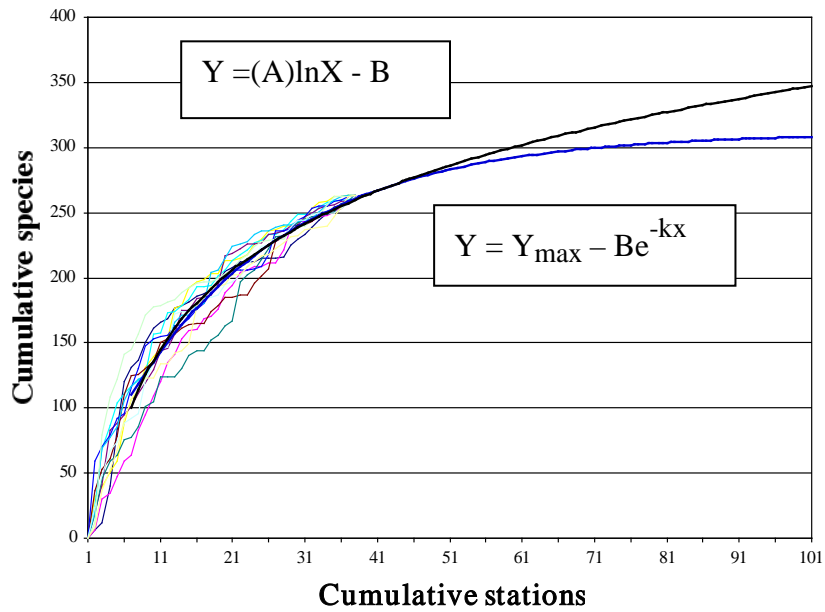


Figure 4. Species discovery curves based on 263 species at 37 Georgia Continental Shelf stations near Gray’s Reef National Marine Sanctuary, illustrating extrapolations based on logarithmic and negative exponential regression of twelve random cumulation curves.

Table 4. Estimates of Mollusk Species Richness (S_{\max}) on the Georgia Continental Shelf, using EstimateS©. See Colwell (2006) for additional references on estimators.

Estimator	S_{\max}
ACE (Abundance-base coverage)	368
ICE (Incidence-base coverage)	383
Chao 1 (Chao, 1984)	374
Chao 2 (Chao, 1987)	404
Jack1 (first-order jackknife)	365
Jack 2 (second-order jackknife)	429
Bootstrap	308
Michaelis-Menton	343

Discussion

Most of the species retrieved in this study were recognized members of either the Caribbean or Carolinian provinces. The Carolinian province is the coastal and near-shore area that extends from Cape Hatteras (some species range north to New Jersey) to Cape Canaveral and on the West Coast of Florida from about Charlotte Harbor or Sarasota northward and around the Gulf of Mexico to the Yucatan Peninsula. The Caribbean province, centered in the West Indies, includes Southern Florida and the Bahamas, with extensions to Bermuda and (along the shelf break and Gulf Stream edge) to off Cape Hatteras. It includes the deeper portions of the Gulf of Mexico, the Greater and Lesser Antilles, Windward and Leeward West Indies, Caribbean Central America (eastern Yucatan to Panama), and coastal South America to about Sao Paulo, Brazil. The Carolinian and Caribbean faunas meet and mix on the Georgia continental shelf where this study was conducted. Provincial affinities of species have been discussed in some detail for the Florida Mixing Grounds (Hopkins *et al.*, 1977) in the northeastern Gulf of Mexico where the Caribbean and Carolinian provinces also meet. Most of the northerly range extensions noted here involved Caribbean species, perhaps suggesting that the fauna of the nearshore region (i.e. the Carolinian Province) had received more thorough study.

A number of species found at the shallower stations sampled here are well-known components of inshore coastal and estuarine communities (Prezant *et al.*, 2002), and dead shells are probably transported onto the shelf by local circulation, including estuarine outwelling (Hanson *et al.*, 1981), and by hermit crabs. The presence of dead specimens of common shallow species at the two deep stations (39 and 44) also suggests that materials are transported across the continental shelf and onto the slope.

Although this study was necessarily qualitative in nature, some associations among taxa were still evident in the data. The over-riding conclusion that can be drawn from these samples, however, relates to the extreme patchiness of the various types of habitats and their associated fauna on the Continental Shelf of Georgia. This was reflected in the great variability of sample volume and sample character— even for replicate tows of the beam trawl at the same station, and in the high proportion of “rare” species within samples (one individual per tow), within stations (one individual per station), or within the entire data set from all stations. Taxa that would be expected to associate with a particular habitat type were frequently intermixed in the same tow with taxa expected from different habitats, demonstrating that the beam trawl was collecting from multiple habitat types during the tow. Each sample came from a 5-minute tow of the beam trawl, so the scale on which this habitat diversity occurs is small. The average bottom area that was swept by the beam trawl was 370 m² (based on ship speed of 1.5 knots (0.77 m/sec) and a fishing width of 1.6 m for the 2-m beam trawl). While the ship usually conducted the tows into the current and wind, the direction of the tows was haphazard (H. Walsh, pers. comm.). As a result some tows were parallel to the coast and shelf break (and to the general pattern of reef outcrops and troughs offshore), while others could have been more nearly

perpendicular to these features. Part of the variability among replicate tows at individual stations probably arose from this variability of towing direction relative to the bathymetric contours and bottom features of the shelf. The effectiveness of the beam trawl no doubt varies considerably depending on the physical character of the bottom.

Since the mesh size of the beam trawl was 3-6 mm, fine material including small mollusks would likely have been excluded unless larger material was first entrained. Thus, the samples were biased against such small species. Nonetheless, many small species (1-5mm) did appear and they were probably entrained along with the large volumes of shell hash seen in some samples. Most of the species found in the soft-bottom infaunal studies (Vittor and Associates, 2004; Hyland *et al.*, 2006) and not reported here were small species, and were probably missed because of the trawl design.

Using dredges, trawls, grabs and suction devices, Wenner *et al.*, (1983) collected epifauna from eight hard-bottom habitats on the shelf off the coast between Jacksonville, Florida and Savannah, Georgia, and one southeast of Charleston, South Carolina (30°25' to 32°29' N). Their stations included three each on the inner shelf (17-22 m depth), the middle shelf (23-38 m) and the outer shelf (47-67 m), so their study area encompassed the area sampled in the present study except for the two deep stations. The focus of their study, however, was on biomass and diversity of numbers, not on details of species occurrence. Although they reported having collected 203 species of mollusks in all, mollusks comprised only about 6% of the total numbers of taxa collected by dredge and trawl in the study (slightly greater in the winter than in the summer). Only four species of mollusk occurred in their samples with sufficient frequency or density to warrant mention of species names. These were *Pteria colymbus*, which occurred in 35% of the 82 trawl samples; *Crassinella lunulata*, which was their 9th most abundant species (16/m²) on the outer shelf in winter; and *Elliptotellina americana* and *Nassarius albus*, which ranked 6th (30/m²) and 9th (23/m²), respectively, in middle shelf samples in summer. Note that neither *Pteria colymbus* nor *Elliptotellina americana* was found in the present study. Their overall species list would no doubt be quite interesting to compare with that in Appendix II.

All of the estimates of potential mollusk species richness are predicated only on beam trawl samples, which are known to be biased against infaunal and small species, as well as species from high profile rocky areas or other habitats that may be poorly compatible with trawling. Because these samples included dead specimens gleaned from shell hash, the habitat bias is reduced, but the number of molluscan species occurring on the Georgia Continental Shelf most likely exceeds that estimated by any of the species discovery techniques (Fig. 4, Table 4).

Many of the species awaiting discovery on the Georgia Continental Shelf may be long-time resident species that have merely been missed or overlooked by the sampling effort to date because of their size, rarity or cryptic habits. Most certainly,

however, new species have been, and will be, introduced to this region also as a result of changing environmental conditions or even human intervention. Seemingly small and subtle changes in either the circulation patterns or the temperature regimes of surface and bottom waters over the shelf could readily modify the recruitment success of planktonic molluscan larvae transported over great distances from upstream reproducing populations (Scheltema, 1989). The seasonal structure of water temperatures over the continental shelf of the South Atlantic Bight is strongly influenced by riverine flow from the landmass, onwelling of cool deep water onto the shelf edge, intrusions of the gulf stream and its eddies, and regional circulation patterns, which are largely wind-driven (Blanton *et al.*, 2003). Tester and Steidinger (1997) described the circuitous paths taken by Gulf Stream eddies over this shelf region, in connection with transport of red tide organisms. Such complexity renders the detection of long-term sea-surface temperature trends very tenuous and uncertain, whether on a regional (Friedland and Hare, 2007) or global (Cane *et al.*, 1997) scale. Nonetheless, the variations in sea-surface temperature and associated circulation patterns have strong implications for transport of eggs and larvae of offshore spawning fish (Stegmann and Yoder, 1996), planktonic veliger larvae of mollusks (Scheltema, 1989), and other organisms (Tester and Steidinger, 1997).

Examples of invasive “alien” marine species recently brought into the South Atlantic Bight by Gulf Stream circulation include: (1) the lionfish (*Pterois volitans*), presently distributed from Cuba to Cape Hatteras, and throughout the Bahamas to Bermuda (Whitfield *et al.*, 2002; Schofield *et al.*, 2008); (2) the green porcelain crab (*Petrolisthes armatus*), distributed northward as far as South Carolina (Hollebone and Hay, 2007) and Bermuda (Simmons, 2007); and (3) the Asian green mussel (*Perna viridis*), so far known only as far north as Georgia (Power *et al.*, 2004; DeVicor and Knott, 2007). While these three examples represent truly “alien” species with historic distributions in the Pacific (lionfish and green mussel) and Brazil (porcelain crab), their rapid spread into the South Atlantic Bight region has been documented only within the past eight years from earlier locations on the west coast (lionfish and green mussel) or southeastern tip (porcelain crab) of Florida.

Another recent molluscan range extension, reported here for the first time, is the zebra periwinkle [*Echinolittorina ziczac* (Gmelin, 1791)], which has been found by the author in colonies at two locations in North Carolina: in June 2005 on a concrete seawall near the Coast Guard Station at Fort Macon, inside Beaufort Inlet, and in August 2007 on the shore end of the rock jetty at Cape Lookout. That species was recently reported (Prezant *et al.*, 2002) to occur in Georgia, but prior to that, was known only well south of Cape Canaveral, Florida (Rosenberg, 2005: Malacolog).

The foregoing examples further reinforce the present finding that of the 263 taxa identified here, at least 16 (6.1%) were species not previously known to occur on the Georgia shelf. Moreover, numerous species associated with the calico scallop community off Beaufort, North Carolina (Wells *et al.*, 1964; Porter and Wolfe, 1972) were not found in the present study. Taken together, the incidence of range extensions reported here, the documented patchiness and diversity of habitat in the

region, the knowledge that additional molluscan members of the Caribbean province have been previously reported in more northerly waters (to Cape Hatteras), and the implications of global climate change, all serve to emphasize that the benthic and epibenthic molluscan fauna of the Georgia Continental Shelf remain only partially described and warrant continued study.

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APPENDIX I. STATION LOCATIONS AND DEPTHS FOR BEAM TRAWLS

Station No.	Sample Date	Sample Date	LATITUDE	LONGITUDE	DEPTH (M)
1	2/9/02	—	31°27.00'N	80°01.60'W	11
2.1	2/10/02	4/16/02	31°24.57'N	80°49.30'W	20
2.2	2/9/02	4/17/02	31°26.10'N	80°54.00'W	19
2.3	2/9/02	4/16/02	31°21.47'N	80°51.00'W	19
2.4	2/9/02	4/17/02	31°22.48'N	80°55.48'W	18
4	2/10/02	—	31°17.50'N	80°28.40'W	33
5	2/10/02	—	31°14.20'N	80°17.70'W	37
6	2/10/02	—	31°11.95'N	80°06.90'W	43
7	2/11/02	—	31°08.10'N	79°56.30'W	47
22	—	4/17/02	31°31.5 'N	80°04.6 'W	4.9
23	2/11/02	4/12/02	31°31.0 'N	81°00.0 'W	12.5
24	2/11/02	4/12/02	31°30.6 'N	80°55.3 'W	14
25	2/11/02	4/12/02	31°30.2 'N	80°50.6 'W	17.5
27	2/12/02	4/16/02	31°22.5 'N	81°09.9 'W	8.5
28	2/12/02	4/17/02	31°22.9 'N	81°03.8 'W	11.2
29	2/11/02	4/17/02	31°23.2 'N	80°58.3 'W	15
31	2/12/02	—	31°18.4 'N	81°11.5 'W	10
32	2/12/02	—	31°17.9 'N	81°06.2 'W	11.2
33	2/12/02	—	31°17.4 'N	81°01.3 'W	13.4
34	2/12/02	—	31°16.9 'N	80°56.4 'W	15
35	—	4/12/02	31°30.21'N	80°35.4 'W	22
36	—	4/12/02	31°32.18'N	80°20.4 'W	31
37	—	4/12/02	31°33.12'N	80°05.4 'W	33
38	—	4/13/02	31°34.03'N	79°50.4 'W	43
39	—	4/13/02	31°34.80'N	79°37.2 'W	90
40	—	4/16/02	31°23.36'N	80°39.74'W	22
41	—	4/14/02	31°23.36'N	80°25.67'W	30
42	—	4/14/02	31°23.36'N	80°11.65'W	40
43	—	4/13/02	31°23.36'N	79°57.60'W	45
44	—	4/13/02	31°23.36'N	79°44.28'W	103
SC01	2/8/02	—	31°32.00'N	79°47.40'W	47
SC02	2/8/02	—	31°35.00'N	79°55.00'W	44
SC06	2/9/02	—	31°28.70'N	80°06.50'W	36
SC07	2/13/02	—	31°17.48'N	79°51.85'W	47
SC08	2/12/02	—	31°20.37'N	80°02.89'W	43
SC09	2/12/02	—	31°23.12'N	80°15.56'W	37
SC10	2/12/02	—	31°26.67'N	80°25.35'W	33

APPENDIX II. MOLLUSCAN TAXA RECOVERED

Taxa are presented in the phylogenetic sequence used by Turgeon *et al.*, (1998). Data for each taxon includes: Station 2 occurrence (# of stations 2.1 to 2.4 represented), the total number of stations where it was collected (#), the depth range of those stations (meters), and the total number of specimens recovered (#). An asterisk (*) before the number of stations indicates that the taxon was collected live from at least one of those stations.

FAMILY	GENUS & SPECIES	STA 2?	STA'S (#)	DEPTH (m)	No. Rcvrd
Amphineura	<i>Ischnochiton hartmeyeri</i> (Thiele, 1910)	*1	*1	18	1
Bivalvia					
Nuculidae	<i>Nucula proxima</i> Say, 1822)		1	30	1
Mytilidae	<i>Lioberus castaneus</i> (Say, 1822)		*1	40	1
Mytilidae	<i>Lithophaga bisulcata</i> (d'Orbigny, 1842)	*1	*1	20	1
Mytilidae	<i>Modiolus squamosus</i> Beuperthuy, 1967		*1	12.5	1
Mytilidae	<i>Musculus lateralis</i> (Say, 1822)	1	*2	12.5-19	2
Arcidae	<i>Anadara floridana</i> (Conrad, 1869)		4	12.5-33	1.5
Arcidae	<i>Anadara notabilis</i> (Röding, 1798)		*2	40-45	1.5
Arcidae	<i>Anadara transversa</i> (Say, 1822)		*6	12.5-43	14.5
Arcidae	<i>Arca zebra</i> (Swainson, 1833)		1	40	0.5
Noetiidae	<i>Arcopsis adamsi</i> (Dall, 1886)	1	1	19	0.5
Glycymerididae	<i>Glycymeris americana</i> (DeFrance, 1829)	3	*9	4.9-40	4
Glycymerididae	<i>Glycymeris spectralis</i> Nicol, 1952		1	45	0.5
Glycymerididae	<i>Glycymeris undata</i> (Linné, 1758)	*2	*9	18-47	13
Glycymerididae	<i>Tucetona pectinata</i> (Gmelin, 1791)	*1	*6	12.5-30	10
Pinnidae	<i>Atrina rigida</i> (Lightfoot, 1786)		*7	12.5-47	100
Pinnidae	<i>Atrina seminuda</i> (Lamarck, 1819)		*1	12.5	1
Limidae	<i>Limaria pellucida</i> (C.B.Adams, 1846)		1	13.4	1
Limidae	<i>Limatula hendersoni</i> Olsson & McGinty, 1958		*1	43	1
Pectinidae	<i>Aequipecten muscosus</i> (W. Wood, 1828)		*5	30-45	4.5
Pectinidae	<i>Argopecten gibbus</i> (Linné, 1758)	*3	*18	12.5-103	20
Pectinidae	<i>Euvola raveneli</i> (Dall, 1898)		*6	22-43	8.5
Pectinidae	<i>Spathochlamys benedicti</i> (Verrill & Bush, 1897)		*1	30	2
Propeamussidae	<i>Similipecten nanus</i> Verrill & Bush, 1897		3	30-45	12.5
Plicatulidae	<i>Plicatula gibbosa</i> Lamarck, 1801	*4	*11	14-43	23
Spondylidae	<i>Spondylus americanus</i> (Hermann, 1781)	*3	*5	15-30	3.5
Anomiidae	<i>Anomia simplex</i> d'Orbigny, 1842	1	*6	13.4-45	12
Ostreidae	<i>Ostrea equestris</i> Say, 1834	*1	*4	8.5-43	6
Lucinidae	<i>Callucina keenae</i> Chavan, 1971		2	33-40	4
Lucinidae	<i>Cavilinga blanda</i> (Dall, 1901)	*3	*14	11-47	46
Lucinidae	<i>Ctena orbiculata</i> (Montagu, 1808)		1	90	0.5
Lucinidae	<i>Divalinga quadrisulcata</i> (d'Orbigny, 1842)	1	3	15-30	6.5
Lucinidae	<i>Luciniscia nassula</i> (Conrad, 1846)		1	12.5	1
Lucinidae	<i>Parvilucina costata</i> (d'Orbigny, 1845)		2	40-43	1
Lucinidae	<i>Parvilucina crenella</i> (Dall, 1901)		1	15	0.5
Lucinidae	<i>Phacoides pectinatus</i> (Gmelin, 1791)	1	1	19	0.5
Lucinidae	<i>Radiolucina amianta</i> (Dall, 1901)		*2	33-43	1.5
Ungulinidae	<i>Diplodonta notata</i> Dall & Simpson, 1901		2	40-43	1.5

Ungulinidae	<i>Diplodonta nucleiformis</i> (Wagner, 1840)	1	*5	15-43	5
Ungulinidae	<i>Diplodonta punctata</i> (Say, 1822)	1	6	15-47	10.5
Ungulinidae	<i>Phlyctiderma semiasperum</i> (Philippi, 1836)	*2	*8	15-43	6
Chamidae	<i>Arcinella cornuta</i> Conrad, 1866	*2	*10	12.5-47	8.5
Chamidae	<i>Chama congregata</i> Conrad, 1833	*1	*5	20-40	6.5
Chamidae	<i>Chama macerophylla</i> Gmelin, 1791	1	*7	15-45	12.5
Chamidae	<i>Chama radians</i> Lamarck, 1819		*2	22-40	2.5
Lasaeidae	<i>Orobitella floridana</i> (Dall, 1899)		1	15	0.5
Leptonidae	<i>Pythinella cuneata</i> (Verrill & Bush, 1898)		*3	8.5-11.2	106
Sportellidae	<i>Basterotia quadrata</i> (Hinds, 1843)		2	15-15	2
Carditidae	<i>Glans dominguensis</i> (d'Orbigny, 1853)		*1	43	2
Carditidae	<i>Pleuromeris tridentata</i> (Say, 1826)	*4	*23	11-103	91
Carditidae	<i>Pteromeris perplana</i> (Conrad, 1841)	1	*9	11.2-43	16
Astartidae	<i>Astarte crenata subequilatera</i> G.B. Sowerby II		1	43	1.5
Astartidae	<i>Astarte nana</i> Dall, 1886		3	33-43	3.5
Crassatellidae	<i>Crassinella dupliniana</i> (Dall, 1903)		1	47	1
Crassatellidae	<i>Crassinella lunulata</i> (Conrad, 1834)	*3	*14	8.5-43	21.5
Crassatellidae	<i>Eucrassatella speciosa</i> (A. Adams, 1852)		*1	40	2.5
Cardiidae	<i>Trachycardium muricatum</i> (Linnaeus, 1758)		3	4.9-22	1.5
Cardiidae	<i>Dinocardium robustum</i> (Lightfoot, 1786)	1	3	4.9-18	2
Cardiidae	<i>Laevicardium laevigatum</i> (Linnaeus, 1758)	3	*8	14-45	3.5
Cardiidae	<i>Laevicardium pictum</i> (Ravenel, 1861)	*4	*17	11.2-47	65
Cardiidae	<i>Nemocardium peramabile</i> (Dall, 1881)	1	3	11-19	3
Mactridae	<i>Mulinia lateralis</i> (Say, 1822)		*5	8.5-40	16.5
Mactridae	<i>Spisula raveneli</i> (Conrad, 1831)		*4	11.2-15	3.5
Pharidae	<i>Ensis megistus</i> Pilsbry & McGinty, 1943		2	22-40	1.5
Pharidae	<i>Ensis minor</i> Dall, 1900	1	*5	15-37	5.5
Tellinidae	<i>Angulus sybariticus</i> (Dall, 1881)	*3	*15	8.5-40	39
Tellinidae	<i>Angulus tenellus</i> (A.E. Verrill, 1874)		*1	13.4	1
Tellinidae	<i>Angulus texanus</i> (Dall, 1900)		1	11.2	1
Tellinidae	<i>Angulus versicolor</i> (DeKay, 1843)	1	*4	14-33	3
Tellinidae	<i>Eurytellina alternata</i> (Say, 1822)		*1	8.5	1
Tellinidae	<i>Macoma brevifrons</i> (Say, 1834)		*2	13.4-15	1.5
Tellinidae	<i>Macoma tenta</i> (Say, 1834)		1	15	1
Tellinidae	<i>Merisca aequistriata</i> (Say, 1824)		*5	15-40	3.5
Tellinidae	<i>Phyllodina squamifera</i> (Deshayes, 1855)		*1	90	1.5
Tellinidae	<i>Strigilla mirabilis</i> (Philippi, 1841)		*4	11.2-17.5	8
Tellinidae	<i>Tellinella listeri</i> Roding, 1798	*2	*5	18-40	6
Semelidae	<i>Abra aequalis</i> (Say, 1822)		2	22-30	1
Semelidae	<i>Ervilia concentrica</i> (Holmes, 1860)	*4	*17	8.5-103	114
Semelidae	<i>Semele bellastrata</i> (Conrad, 1837)	*3	*9	14-40	53
Semelidae	<i>Semele purpurascens</i> (Gmelin, 1791)		*1	15	1
Semelidae	<i>Semelina nuculoides</i> (Conrad, 1841)	1	*5	15-43	13
Trapezidae	<i>Coralliophaga coralliophaga</i> (Gmelin, 1791)	1	1	18	0.5
Veneridae	<i>Chione elevata</i> Say, 1822		2	15-30	1.5
Veneridae	<i>Chione mazyckii</i> Dall, 1902		1	30	0.5
Veneridae	<i>Cyclinella tenuis</i> (Récluz, 1852)		*1	43	1
Veneridae	<i>Gemma gemma</i> (Totten, 1834)		2	15-47	64.5
Veneridae	<i>Gouldia cerina</i> (C.B. Adams, 1845)	*1	*12	11.2-43	45
Veneridae	<i>Lirophora latilirata</i> (Conrad, 1841)	2	*5	18-43	9.5
Veneridae	<i>Macrocallista maculata</i> (Linné, 1758)	*3	*12	12.5-43	12.5

Veneridae	<i>Macrocallista nimbosa</i> (Lightfoot, 1786)		*1	15	1.5
Veneridae	<i>Mercenaria campechiensis</i> (Gmelin, 1791)		1	33	0.5
Veneridae	<i>Pitar simpsoni</i> (Dall, 1889)		1	22	0.5
Veneridae	<i>Puberella intapurpurea</i> (Conrad, 1849)	*4	*13	11.2-33	39.5
Veneridae	<i>Timoclea grus</i> (Holmes, 1858)		*2	30-33	1.5
Veneridae	<i>Transenella stimpsoni</i> Dall, 1902		*3	33-43	5.5
Petricolidae	<i>Cooperella atlantica</i> Rehder, 1943	*1	*3	15-33	3
Petricolidae	<i>Petricolaria pholadiformis</i> (Lamarck, 1818)		1	17.5	1
Myidae	<i>Paramya subovata</i> (Conrad, 1845)		1	15	0.5
Corbulidae	<i>Caryocorbula caribaea</i> (d'Orbigny, 1853)		*1	43	1
Corbulidae	<i>Caryocorbula chittyana</i> (C. B. Adams, 1852)		1	31	0.5
Corbulidae	<i>Caryocorbula contracta</i> (Say, 1822)		*8	11.2-103	13
Corbulidae	<i>Caryocorbula cf. cymella</i> (Dall, 1881)		*1	43	1
Corbulidae	<i>Caryocorbula dietziana</i> C.B.Adams, 1852	1	*3	11.2-43	3.5
Corbulidae	<i>Varicorbula limatula</i> (Conrad, 1846)		*3	33-43	2
Corbulidae	<i>Varicorbula philippii</i> (E.A. Smith, 1885)		1	43	0.5
Pholadidae	<i>Jouannetia quillingi</i> Turner, 1955		1	13.4	1
Lyonsiidae	<i>Lyonsia hyalina</i> Conrad, 1831		*1	14	1
Pandoridae	<i>Pandora trilineata</i> Say, 1822	*1	*5	10-40	10.5
Thraciidae	<i>Thracia cf. phaseolina</i> Lamarck, 1822		1	13.4	0.5
Thraciidae	<i>Thracia conradi</i> Couthouy, 1838		1	90	0.5
Periplomatidae	<i>Periploma leanum</i> (Conrad, 1831)		1	14	1
Periplomatidae	<i>Periploma margaritaceum</i> (Lamarck, 1801)	1	1	18	0.5
Verticordiidae	<i>Trigonulina ornata</i> d'Orbigny, 1842		2	13.4-90	1.5
Cuspidariidae	<i>Cuspidaria obesa</i> (Lovén, 1846)		1	43	0.5
Scaphopoda					
Dentaliidae	<i>Antalis taphrium</i> Dall, 1889		3	22-47	5
Dentaliidae	<i>Paradentalium americanum</i> (Chenu, 1843)		1	10	2
Dentaliidae	<i>Dentalium laqueatum</i> Verrill, 1885		1	30-90	4
Dentaliidae	<i>Graptacme calamus</i> Dall, 1889		2	31-47	4
Dentaliidae	<i>Graptacme eborea</i> (Conrad, 1846)	2	3	15-20	4
Gadilidae	<i>Polyschides tetraschistus</i> (Watson, 1879)		2	40-43	2
Gadilidae	<i>Polyschides tetrodon</i> (Pilsbry & Sharp, 1898)		2	30-33	2
Gastropoda					
Fissurellidae	<i>Diodora cayenensis</i> (Lamarck, 1822)	1	4	15-31	5
Fissurellidae	<i>Lucapinella limatula</i> (Reeve, 1850)		1	30	1
Turbinidae	<i>Arene tricarinata</i> (Stearns, 1872)	1	12	11-45	25
Turbinidae	<i>Eulithidium thalassicola</i> (Robertson, 1958)		2	43-45	4
Turbinidae	<i>Turbo castanea</i> Gmelin, 1791	1	*3	14-20	7
Calliostomatidae	<i>Calliostoma pulchrum</i> (C.B.Adams, 1850)		1	14	1
Calliostomatidae	<i>Calliostoma yucatecanum</i> Dall, 1881	1	*14	11.2-47	23
Litiopidae	<i>Litiopa melanostoma</i> Rang, 1829	1	1	20	1
Cerithiidae	<i>Cerithium atratum</i> (Born, 1778)	2	7	8.5-33	9
Modulidae	<i>Modulus modulus</i> (Linnaeus, 1758)	1	4	18-43	5
Turritellidae	<i>Torcula acropora</i> Dall, 1889	4	18	11-43	100
Turritellidae	<i>Vermicularia knorri</i> (Deshayes, 1843)		1	47	1
Littorinidae	<i>Littoraria irrorata</i> (Say, 1822)		1	11.2	1
Barleeiidae	<i>Barleeia tincta</i> Guppy, 1895		1	40	1
Vitrinellidae	<i>Circulus multistriatus</i> (A.E. Verrill, 1884)	*1	*1	19	1

Vitrinellidae	<i>Cyclostremiscus beui</i> (P.Fischer, 1857)	1	3	19-43	4
Caecidae	<i>Caecum carolinianum</i> Dall, 1892		1	43	2
Caecidae	<i>Caecum cooperi</i> S. Smith, 1860		*1	43	2
Caecidae	<i>Caecum imbricatum</i> Carpenter, 1858		*2	33-36	2
Caecidae	<i>Caecum pulchellum</i> Stimpson, 1851		1	15	1
Strombidae	<i>Strombus alatus</i> Gmelin, 1791	1	5	11.2-22	10
Calyptraeidae	<i>Bostrycapulus aculeatus</i> (Gmelin, 1791)		1	31	1
Calyptraeidae	<i>Calyptraea centralis</i> (Conrad, 1841)	4	*15	11-43	43
Calyptraeidae	<i>Cheilea equestris</i> (Linnaeus, 1758)		1	14	1
Calyptraeidae	<i>Crepidula fornicata</i> (Linné, 1758)	2	*6	12.5-40	15
Calyptraeidae	<i>Crepidula plana</i> Say, 1822	*1	*4	13.4-90	6
Calyptraeidae	<i>Crucibulum striatum</i> (Say, 1826)		1	40	2
Xenophoridae	<i>Xenophora conchyliophora</i> (Born, 1780)		*6	33-47	11
Vermetidae	<i>Petalococonchus erectus</i> (Dall, 1888)		2	13.4-37	2
Cypraeidae	<i>Erosaria acicularis</i> (Gmelin, 1791)		1	47	1
Ovulidae	<i>Simnialena uniplicata</i> (G.B.Sowerby II, 1849)		*2	13.4-17.5	2
Naticidae	<i>Naticarius canrena</i> (Linnaeus, 1758)		*12	11.2-47	23
Naticidae	<i>Neverita duplicata</i> (Say, 1822)	1	7	8.5-22	7
Naticidae	<i>Polinices porcellanus</i> (d'Orbigny, 1839)	2	14	18-40	59
Naticidae	<i>Sigatica carolinensis</i> (Dall, 1889)		4	8.5-43	4
Naticidae	<i>Sinum maculatum</i> (Say, 1831)	1	1	19	1
Naticidae	<i>Sinum perspectivum</i> (Say, 1831)		1	11.2	1
Naticidae	<i>Tectonatica pusilla</i> (Say, 1822)	3	*13	8.5-47	40
Cassidae	<i>Cassis madagascariensis</i> Lamarck, 1822		3	8.5-40	3
Cassidae	<i>Cypraecassis testiculus</i> (Linnaeus, 1758)		1	47	1
Cassidae	<i>Semicassis granulata</i> (Born, 1778)		*6	33-47	6
Ranellidae	<i>Cymatium cingulatum</i> (Lamarck, 1822)		4	43-47	38
Ranellidae	<i>Cymatium krebisii</i> (Mörch, 1877)		1	45	1
Ranellidae	<i>Cymatium parthenopeum</i> (von Salis, 1793)		*2	45-47	17
Cerithiopsidae	<i>Seila adamsii</i> (H.C.Lea, 1845)	*2	*5	15-43	6
Triphoridae	<i>Marshallora nigrocincta</i> (C.B. Adams, 1839)		1	43	1
Epitoniidae	<i>Cirsotrema dalli</i> Rehder, 1945		*5	37-45	6
Epitoniidae	<i>Depressiscula nautlae</i> (Mörch, 1875)		*3	14-47	3
Epitoniidae	<i>Epitonium albidum</i> (d'Orbigny, 1842)	*1	*1	19	1
Epitoniidae	<i>Epitonium angulatum</i> (Say, 1831)		4	33-43	5
Epitoniidae	<i>Epitonium candeanum</i> (d'Orbigny, 1842)		1	43	1
Epitoniidae	<i>Epitonium multistriatum</i> (Say, 1826)		6	8.5-47	6
Epitoniidae	<i>Epitonium occidentale</i> (Nyst, 1871)		*2	11-12.5	2
Epitoniidae	<i>Epitonium championi</i> Clench & Turner, 1952	1	*5	10-19	6
Epitoniidae	<i>Epitonium foliaceicosta</i> (d'Orbigny, 1842)		1	33	1
Epitoniidae	<i>Epitonium krebisii</i> (Mörch, 1875)		4	11.2-47	5
Epitoniidae	<i>Epitonium novangliae</i> (Couthouy, 1838)		1	47	1
Epitoniidae	<i>Epitonium rupicola</i> (Kurtz, 1860)		3	8.5-12.5	4
Epitoniidae	<i>Opalia pumilio</i> (Mörch, 1875)		1	31	1
Eulimidae	<i>Melanella</i> sp. cf. <i>Eulimostraca</i> sp.B Redfern 340	1	2	20-43	2
Eulimidae	<i>Melanella hypsela</i> (A.E. Verrill & Bush, 1900)	*2	*2	18-19	2
Eulimidae	<i>Melanella jamaicensis</i> (C.B. Adams, 1845)		1	12.5	1
Eulimidae	<i>Niso aeglees</i> Bush, 1885	1	*9	17.5-43	11
Muricidae	<i>Calotrophon ostrearum</i> (Conrad, 1846)	1	2	14-20	3
Muricidae	<i>Chicoreus florifer dilectus</i> (A. Adams, 1855)		*2	15-40	2
Muricidae	<i>Eupleura caudata</i> (Say, 1822)	*3	*5	12.5-20	7

Muricidae	<i>Haustellum rubidum</i> (F.C.Baker, 1897)		1	43	1
Muricidae	<i>Murexiella levicula</i> (Dall, 1889)		2	40-43	3
Muricidae	<i>Stramonita haemastoma floridana</i> (Conrad, 1837)		2	22-45	2
Buccinidae	<i>Antillophos candeanus</i> (d'Orbigny, 1842)		1	90	1
Buccinidae	<i>Hesperisternia multangulus</i> (Philippi, 1848)		1	17.5	1
Melongenidae	<i>Busycon sinistrum</i> Hollister, 1954		4	31-47	3
Melongenidae	<i>Busycotypus canaliculatus</i> (Linnaeus, 1758)		1	90	1
Melongenidae	<i>Busycotypus spiratus</i> (Lamarck, 1816)		1	47	1
Nassariidae	<i>Ilyanassa obsoleta</i> (Say, 1822)	1	3	10-20	7
Nassariidae	<i>Ilyanassa trivittata</i> (Say, 1822)	1	4	4.9-37	6
Nassariidae	<i>Nassarius acutus</i> (Say, 1822)		*6	4.9-40	125
Nassariidae	<i>Nassarius albus</i> (Say, 1826)		*10	30-47	21
Nassariidae	<i>Nassarius consensus</i> (Ravenel, 1861)		*7	33-47	21
Nassariidae	<i>Nassarius vibex</i> (Say, 1822)		*1	90	1
Fascioliariidae	<i>Fasciolaria liliun hunteria</i> (G.Perry, 1811)	*1	*2	13.4-20	2
Fascioliariidae	<i>Pleuroploca gigantea</i> (Kiener, 1840)		1	11.2	1
Columbellidae	<i>Astyris raveneli</i> (Dall, 1889)		1	43	1
Columbellidae	<i>Astyris lunata</i> (Say, 1826)	2	*9	8.5-90	134
Columbellidae	<i>Costoanachis translirata</i> (Ravenel, 1861)	4	*22	8.5-47	123
Columbellidae	<i>Suturoglypta iontha</i> Ravenel, 1861		*1	14	1
Columbellidae	<i>Nassarina glypta</i> (Bush, 1885)		2	33-43	5
Columbellidae	<i>Parvanachis obesa</i> (C.B.Adams, 1845)		1	11	1
Olividae	<i>Oliva reticularis</i> Lamarck, 1811		1	90	1
Olividae	<i>Oliva sayana</i> Ravenel, 1834	*1	*5	11.2-18	6
Olividae	<i>Olivella floralia</i> (Duclos, 1844)	3	*21	8.5-43	102
Olividae	<i>Olivella mutica</i> (Say, 1822)	4	*27	8.5-90	216
Olividae	<i>Olivella nivea</i> (Gmelin, 1791)	1	1	18	1
Olividae	<i>Olivella</i> sp. aff. <i>tunquina</i> (Duclos, 1835)		2	33-37	2
Marginellidae	<i>Dentimargo aureocinctus</i> (Stearns, 1872)		3	33-103	4
Marginellidae	<i>Prunum amabile</i> authors non (Redfield, 1852)	1	*7	14-43	11
Marginellidae	<i>Prunum apicinum</i> (Menke, 1828)		*3	12.5-30	7
Marginellidae	<i>Prunum hartleyanum</i> (Schwengel, 1941)		7	10-43	21
Marginellidae	<i>Prunum roscidum</i> (Redfield, 1860)	1	3	20-33	4
Costellariidae	<i>Vexillum wandoense</i> (Holmes, 1860)	*1	*1	19	1
Cancellariidae	<i>Axelella smithii</i> (Dall, 1888)		1	47	2
Cancellariidae	<i>Cancellaria reticulata</i> (Linnaeus, 1767)	4	5	12.5-20	8
Cancellariidae	<i>Tritonoharpa lanceolata</i> (Menke, 1828)		2	30-47	3
Drilliidae	<i>Cerodrillia simpsoni</i> (Dall in Simpson, 1887)		2	11.2-43	2
Drilliidae	<i>Cerodrillia bealiana</i> Schwengel & McGinty, 1942	1	7	20-45	8
Drilliidae	<i>Drillia cydia</i> (Bartsch, 1943)	2	6	15-43	8
Drilliidae	<i>Splendrillia moseri</i> (Dall, 1889)		2	45-103	4
Terebridae	<i>Terebra concava</i> (Say, 1826)	*3	*15	8.5-103	46
Terebridae	<i>Terebra dislocata</i> (Say, 1822)	*1	*10	4.9-47	18
Terebridae	<i>Terebra protexta</i> (Conrad, 1846)	*3	*6	14-103	9
Turridae	<i>Cochlespira radiata</i> (Dall, 1889)		*1	103	1
Turridae	<i>Crassispira fuscescens</i> (Reeve, 1845)	1	1	20	1
Turridae	<i>Inodrillia</i> cf. <i>a vira</i> Bartsch, 1943		*8	11-45	13
Conidae	<i>Brachycythara biconica</i> (C.B. Adams, 1850)		1	30	1
Conidae	<i>Conus anabathrum</i> Crosse, 1865	1	*13	12.5-47	21
Conidae	<i>Conus stearnsii</i> Conrad, 1869	4	*12	12.5-43	34
Conidae	<i>Cryoturris cerinella</i> (Dall, 1889)		3	17.5-103	3

Conidae	<i>Cryoturris fargoii</i> McGinty, 1955	1	1	20	1
Conidae	<i>Glyphoturris quadrata</i> (Reeve, 1845)		1	30	1
Conidae	<i>Ithythythara lanceolata</i> (C.B.Adams, 1850)		2	11-33	2
Conidae	<i>Kurtziella atrostyla</i> (Tryon, 1884)		5	8.5-33	15
Conidae	<i>Kurtziella cerina</i> (Kurtz & Stimpson, 1851)		1	17.5	1
Conidae	<i>Kurtziella dorvilliae</i> (Reeve, 1845)	1	1	18	1
Conidae	<i>Kurtziella limonitella</i> (Dall, 1884)		3	8.5-11.2	19
Conidae	<i>Platycythara elata</i> (Dall, 1889)		1	43	1
Conidae	<i>Rubellatoma rubella</i> (Kurtz & Stimpson, 1851)		3	18-25	11
Architectonicidae	<i>Heliacus bisulcatus</i> (d'Orbigny, 1842)		2	37-43	3
Pyramidellidae	<i>Odostomia laevigata</i> (d'Orbigny, 1841)		*1	13.4	1
Pyramidellidae	<i>Petitilla crosseana</i> (Dall, 1885)		1	90	1
Pyramidellidae	<i>Pyramidella suturalis</i> H.C. Lea, 1843		*4	8.5-15	6
Pyramidellidae	<i>Turbonilla interrupta</i> (Totten, 1835)	1	1	20	1
Pyramidellidae	<i>Turbonilla krebsii</i> (Mörch, 1875)		1	43	1
Acteonidae	<i>Acteon candens</i> Rehder, 1939		4	8.5-103	6
Acteonidae	<i>Rictaxis punctostriatus</i> (C.B. Adams, 1840)		1	8.5	1
Cylichnidae	<i>Acteocina candeii</i> (d'Orbigny, 1841)	1	2	18-43	2
Cylichnidae	<i>Acteocina lepta</i> Woodring, 1928		1	43	1
Philinidae	<i>Philina sagra</i> (d'Orbigny, 1841)		1	43	1
Retusidae	<i>Pyrunculus caelatus</i> (Bush, 1885)		1	43	1
Retusidae	<i>Retusa sulcata</i> (d'Orbigny, 1841)		1	43	1
Cavoliniidae	<i>Diacavolinia longirostris</i> (Blainville, 1821)	*2	*10	15-103	25
Arminidae	<i>Armina mulleri</i> (von Ihering, 1886)		*1	14	1
Cephalopoda:					
Ommastrephidae	<i>Illex illecebrosus</i> (Lesueur, 1821)		*1	17.5	5

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