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Marine Macroinvertebrate Diversity of St. Catherines Island, Georgia

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ABSTRACT

St. Catherines Island is one of several barrier islands lining the coast of Georgia, USA. This island is among the least recently anthropogenically impacted of the Georgia Sea Islands, but had not previously been examined in detail for coastal invertebrate macrofauna. From 1992 through late 1998 a coastal survey was conducted that examined the diverse marine invertebrate fauna of St. Catherines Island. Salt marshes, sand flats, mid- to low-energy sand beaches, beach wood debris, tidal creeks, shallow benthos, and artificial hard substrata (including docks) were qualitatively sampled for macroinvertebrates. Over 340 species were identified. Crustaceans composed close to 40% (14% amphipods; 15% decapods), polychaetes 17.5%, and molluscs about 25% of all species recovered. These results are compared to the few other relevant studies from the United States mid-Atlantic Coast.

INTRODUCTION

The coast of Georgia, USA, has a wide array of productive coastal habitats with varied anthropogenic input. Among the barrier islands dotting the Georgia coast, St. Catherines Island is a relatively pristine island with a rich human history and a strong record of paleontological and geological study (Morris and Rollins, 1977; Thomas et al.,

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1978; Kennedy and Pinkoski, 1987; Sherrod et al., 1989). To date, however, there has been only a single effort at a comprehensive study of living marine intertidal organisms of St. Catherines Island. Morris and Rollins (1977) offered a brief overview of the intertidal species found along this island and speculated on the extant community relationships to the island's paleoecology. Their study was admittedly not an attempt to completely describe the intertidal communities of St. Catherines Island but instead an effort to examine a few intertidal associations and relate these to paleontological communities. Thus, these authors concentrated on a few selected communities and associated representative species. Similarly, Fierstien and Rollins (1987) discussed some macroinvertebrate associations on the island associated with the distribution of the marsh periwinkle snail *Littorina irrorata*. With the rediscovered interest in biodiversity as a key indicator of the ''health'' of our environment (Schlesinger et al., 1994), we surveyed the infaunal and epifaunal marine invertebrates associated with the intertidal and shallow subtidal perimeter of St. Catherines Island.

The exact nature of biodiversity has been variously interpreted. Haila and Kouki (1994) and Haila and Margules (1996) discuss the evolution and usage of the term as it includes genotypes, population diversity within ecosystems, and variation of ecosystems at a landscape level. In this paper we will use a very basic definition of biodiversity as advanced by Wilson (1992) as biological diversity at the species level. This type of interpretation facilitates comparisons to other studies and among habitats, although it does not take into account evenness, dominance, or other skewed features of the communities.

The value of studying biodiversity rests with our abilities to monitor changes through time that could reflect overall environmental shifts. This is alluded to in a study of the subrecent intertidal assemblages of diatoms on St. Catherines Island (Sherrod et al., 1989). The authors note the problems associated with ''ecological noise'' in short-term studies. Coile and Jones (1988) published a checklist of the vascular plants of St. Catherines, noting the relatively low diversity compared to other regional barrier islands. They suggested that this reduced diversity is a result of extensive deer grazing and feral swine rooting as well as the islands history as a cattle grazing site (1945–1975) and historic sea cotton plantation (see Thomas et al., 1978, for a summary of the island's history and usage). While these events could certainly have a very real impact on terrestrial communities of the island, the impact to marine-based communities, if any, is unknown. Because there are few reports to act as baselines for coastal Georgia diversity, it is difficult to interpret the relative diversity of St. Catherines marine invertebrate macrofauna. Howard and Frey (1975) did a ''reconnaissance'' study of coastal Georgia estuarine channels. In box cores taken during their survey they found 73 species, 51 of which were also found on the nearby shelf by Dörjes (1977). A few years earlier Howard and Dörjes (1972) discussed animal-sediment associations on Sapelo Island, Georgia, beaches. Here they found 50 species of macrofauna with crustaceans composing 36% and polychaetes 38% on the muddier Nannygoat Flat, while sandier Cabretta Flat had 28% polychaetes and 40% crustaceans composing the macrofauna. Howard and Reineck (1972) delineated that 268 species of macrofaunal species from a Georgia beach to offshore transect. In that survey molluscs, polychaetes, and crustaceans dominated in terms of abundance. A brief review of some of these early studies was presented by Dörjes (1977). Aside from unpublished reports and popular field guide literature (e.g, Ruppert and Fox, 1988), these studies, and that by Morris and Rollins (1977) noted above, represent all the published diversity-based marine invertebrate studies for coastal Georgia. Here we have attempted to assemble a more complete species diversity listing as found in marine habitats on St. Catherines Island. This study, as far as discerned, can act as a qualitative baseline for comparable Georgia barrier islands and as a checklist for Georgia coastal macroinvertebrates.

METHODS

COLLECTION TECHNIQUES: Samples were variously collected by hand, dipnet, shovel and sieve (0.5-mm mesh), 2.4-m semiballoon trawl, net sledge, small box core, and yabby pump. All living specimens were recovered and note taken of empty shells retained. We made no attempt to quantify samples, although we did note relative abundance (in particular, quantitatively dominant species) within each habitat studied. A correlative study that involved quantitative transects of many of the island beaches will be published separately. Specimens recovered were preserved in 5–10% formalin for 1–7 days, washed in running tap water and transferred for storage to 70% ethanol or 40% isopropanol. All collection sites are detailed in results.

Our qualitative data allowed a comparison with one of the few other compilations of coastal Georgia invertebrates. We used a Bray-Curtis similarity index using PRIMER version 4.0 (Plymouth Routines in Multivariate Ecological Research; Carr 1997) to compare our species list with that compiled by Howard and Frey (1975a, 1975b). Taxa identified only to levels above genus were eliminated from the database for this analysis. Taxa identified only to the same genus in both surveys were scored similar. The faunal list of Howard and Frey (1975) includes compilations from other invertebrate surveys of coastal Georgial, including their work on or near Sapelo Island.

VOUCHER SPECIMENS**:** Representative specimens are cataloged in the invertebrate collections of the American Museum of Natural History. Parallel collections have also been placed on St. Catherines Island and in the invertebrate collection of Montclair State University.

RESULTS

COLLECTION SITES: From 1992 through late 1998 we sampled a wide range of diverse intertidal and shallow subtidal habitats along St. Catherines Island (fig. 1). With few exceptions, salinities during this time period at all sites remained relatively constant, varying only between 28 and 33.5 ppt. In April 1993 salinity at the Main Dock (Walburg Creek), however, reached a low of 26 ppt. The highest salinities recorded were 35 ppt at Seaside Dock in November 1992 and the northwest edge of Flag Pond in November 1993. Extreme salinities apparently reflected periods of substantial or minimal rain. Brief descriptions of the sites sampled follow (the abbreviation for each site used in taxonomic table 1 is in parentheses):

ST. CATHERINES SHOAL (B): St. Catherines Shoal is a large ramp margin sand body situated at the northeast margin of St. Catherines Island and has been, for the past decade, partially emergent at high tide and sparsely vegetated. The shoal consists predominantly of fine-grained quartz sand dispersed southward by ebb tidal flow through St. Catherines Sound and then northward by fair weather storms and longshore drift. The complex sedimentary dynamics of this shoal, as well as others associated with the Georgia Sea Islands, has been discussed by Oertel and Howard (1972), Oertel (1977), and Pottinger (1996). The marine habitats associated with St. Catherines Shoal are extremely ephemeral, coincident with rapid changes in dimension and extent of the sand shoal body. In general, the north-facing portion of the shoal is a marginal ramp abutting the deeply scoured sound, and the southern extremity consists of a mosaic of shallower sand spits and bars. The southern margin of this shoal is actively trawled seasonally by shrimpers and could be the most anthropogenically impacted of all marine habitats around the island.

ENGINEERS POINT (E): The northernmost margin of the island, Engineers Point, is separated from Ossabaw Island by St. Catherines Sound and displays pronounced marine habitat heterogeneity. The northeastern portion of Engineers Point is an expansive, relatively low-energy, rippled quartz sand flat somewhat protected by St. Catherines Shoal to the south. Ripple troughs accumulate organic rich muds from abundant fecal matter, vegetative detritus, and occasional exposure of the subjacent relict marsh sediment. The width of this rippled sand flat has changed dramatically in concert with the changing sedimentological dynamics of St. Catherines Sound. In the 1970s this flat was over 200 meters wide at low tide, but since that time has become highly constricted (Morris and Rollins, 1977; Oertel, 1977; Fierstien and Rollins, 1987). The northern extremity of

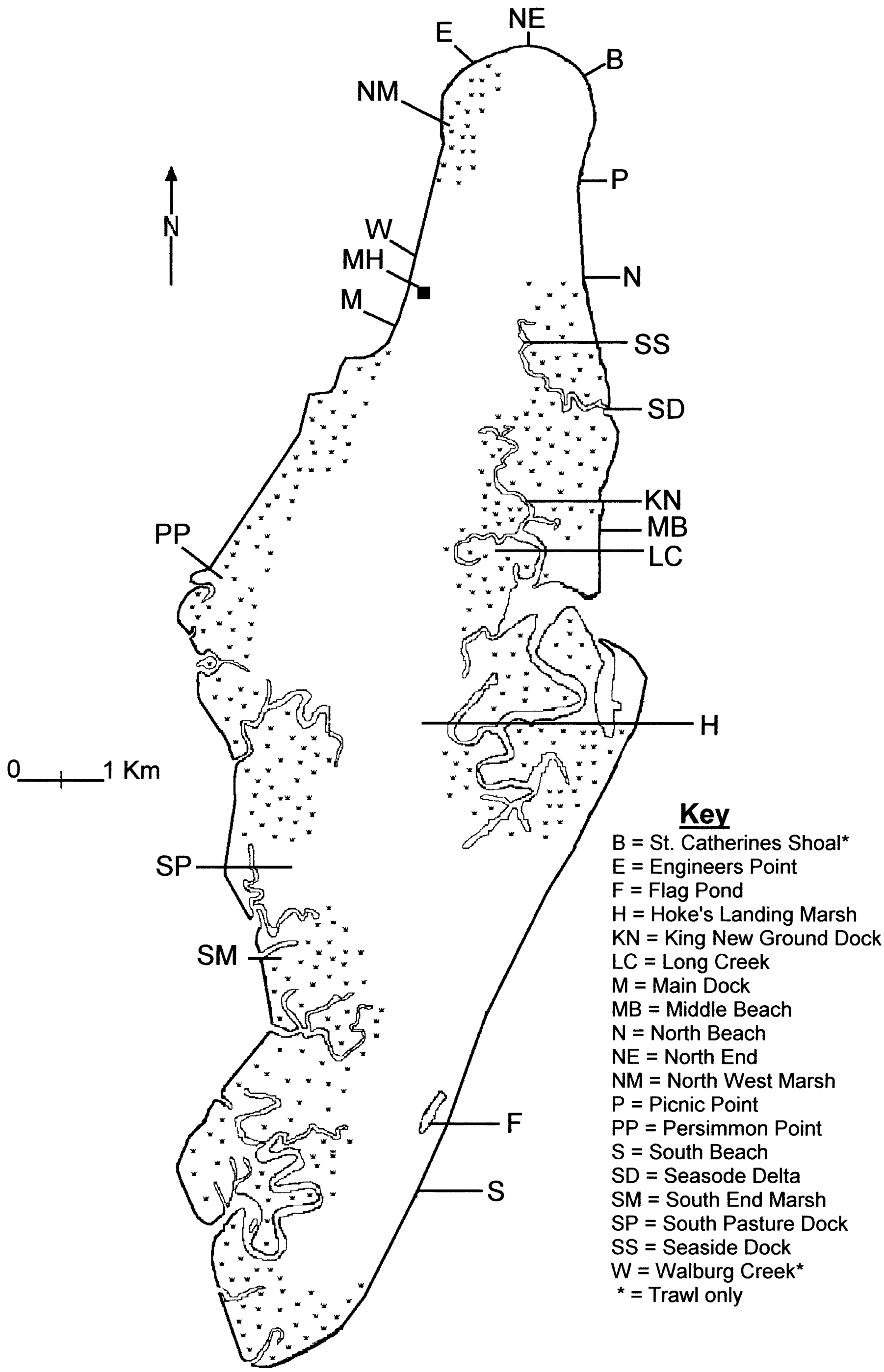

Fig. 1. Schematic map of St. Catherines Island showing all sampling sites except Necessary Creek. Necessary Creek drains Walburg Island, immediately to the west of St. Catherines, and forms the western boundary of Walburg Creek. Walburg Island is less than 0.3 km west of St. Catherines; the open Atlantic is to the east of St. Catherines Island. Stippled areas represent the extensive marshes of the island. The key to sites located on this map is the same as the key for table 1. MH = Main House.

Engineers Point, adjacent to St. Catherines Sound, is blunted by periodic erosional tidal scour, and supports a narrower intertidal zone, frequently studded by fallen trees eroded from the forested island core. These patches of ''skeletal forest'' provide a high to low intertidal, epifaunal wood ground habitat for several invertebrate species that require hard substratum. Scoured pools at the base of some of this wood debris offers tidal refugia for other invertebrates as well as small fish.

The protected northwest margin of Engineers Point opens into a moderately narrow sandy tidal flat, terminated by Northwest Marsh about 1 km south of the Island's northern tip. The substratum ranges from fine- to medium-grained quartz sand with notable amounts of organic matter (fecal pellets and detritus). Occasional sand aprons thinly veneer deposits of relict marsh mud (Morris and Rollins, 1977). Near the margin of the small tidal creek draining Northwest Marsh, the Engineers Point intertidal supports spotty development of marsh grass (*Spartina alterniflora*) and oyster (*Crassostrea virginica*) patches fringing the bank of Walburg Creek. Southward along Walburg Creek a fringing marsh with high mud content abruptly dominates the intertidal zone, along with patches of living oysters and wash-over accumulations (fans) of disarticulated oyster valves.

PICNIC POINT (P): About 1.5 km south of the northeast extremity of the island a chenier plain draped with dunes and beach ridges abruptly narrows to a steep bluff (Picnic Point) eroded into the Pleistocene core. Until Hurricane Hugo in 1989, this portion of the Island shoreline was rapidly retreating due to wave erosion. Since 1989, however, three nascent and vegetated beach ridges have aggraded against Picnic Point Bluff (Pottinger, 1996). These remarkably rapid shoreline changes appear to have had little effect upon the character of the intertidal zone, which remains a moderately wide, gently sloping quartz sand beach.

LONG CREEK (LC): South of King New Ground Dock, Long Creek is a muddy-banked, narrow, tortuous creek with shallow point bars densely populated by hard clams and adjoining steeper *Spartina* marsh fronts with extensive fiddler crab (*Uca*) populations. Occasional oyster bars dot the creek's margin.

NORTH BEACH (N): North Beach extends from Engineers Point east southward for about 3 km to Seaside Inlet, one of two major tidal inlets that punctuate the eastern margin of the island. Most of North Beach typifies the seaward strandlines of the Georgia Sea Islands, divisible into nearly horizontal (1° slope) narrow backshore and gently sloping (2°) wider foreshore segments (Frey and Howard, 1988). Ephemeral ridge and runnel features are commonly developed at high angles to the strandline. Sorted angular, fine-grained sands predominate, with local concentrations of black heavy minerals. The northern segment of North Beach backs St. Catherines Shoal and fronts a mosaic of beach ridges topped by eolian dunes. This beach ridge sequence extends southward for about 1.5 km to Picnic Point Bluff, grading into a stretch of open sandy beach in front of an actively eroding portion of the island Pleistocene core. At this point the beach is densely strewn with toppled trees sloughing from the forested island core, and outliers of eroding headland protrude from the beach as a palmetto palosol (Morris and Rollins, 1977, Station # 1; Frey and Basan, 1981). The southern half (about 1.5 km) of North Beach consists of fine-grained quartz sand and compacted semiconsolidated relict marsh mud representing the trailing edge of a rapidly migrating facies mosaic that has retreated at an average rate of 3.8 m per year for about the last 50 years (Rollins et al., 1990; Goodfriend and Rollins, 1998). Along this portion of North Beach, over-wash sands episodically breach the low barrier dunes and extend into a living salt marsh westward of the beach. Both the palmetto paleosol and the relict marsh muds serve as firm grounds for many marine invertebrates. Erosional liberation of ''fossil'' skeletal material from the relict marsh muds noticeably increase the carbonate content of this portion of North Beach. Other than rare shell lag accumulations, the silicoclastic beaches of the Georgia Sea Islands rarely contain more than 3–5% calcium carbonate (Frey and Howard, 1988). As North Beach grades to Seaside Inlet, the large inlet shoal and longshore drift wafts sand along the shoreface and seaward into a wide intertidal sand flat. Temporal changes in the ebb tidal dynamics alternately extend blanketing lobes of sand northward up North Beach and southward along Middle Beach. Consequently, living salt marsh fringing the tidal inlet is repeatedly destroyed and regenerated.

MIDDLE BEACH (MB) AND SOUTH BEACH (S): Middle Beach, between Seaside and McQueens Inlets, and South Beach (south of McQueens Inlet) are generally similar to the southern half of North Beach. All are exposed mid- to high-energy quartz sand beaches with gently sloping narrow backshore and wider foreshore segments. All locally display ridge and runnel systems, exposures of relict marsh muds, fallen trees, and dune-topped barrier beaches fronting live *Spartina alterniflora* dominated salt marsh. A 1-km-long portion of South Beach is backed by Flag Pond (F), formerly a freshwater body impounded by a narrow tree-lined barrier beach, which in March 1993 was breached during a violent single storm. A small tidal inlet flooded the impoundment, and since then Flag Pond rapidly developed into a salt marsh.

WALBURG CREEK (W): The northwestern portion of St. Catherines Island abuts a 0.5-km-wide tidal creek (Walburg Creek) that serves a part of the Intracoastal Waterway. Walburg Creek turns 90° to the north as it approaches the island, isolating a block of salt marsh named Walburg Island. Near its point of inflection against the island core, Walburg channel is over 15 m deep. The creek adjacent to the island was sampled with trawl, grab, and net sledge.

NECESSARY CREEK (NC): Necessary Creek is a relatively narrow, serpentine tidal creek that drains the majority of the interior of Walburg Island salt marsh and is a tributary to Walburg Creek about 2 km west of St. Catherines Island's main dock. Salt marshes represent the most areally extensive portion of coastal Georgia's marine intertidal habitats and are developed between neap mean high water and spring mean high water (Frey and Basan, 1981; Fierstien and Rollins, 1987). In turn, the salt marshes of the southeastern US constitute the largest area of coastal wetlands in North America. Georgia tidal creeks, including Necessary Creek, experience a mean tidal amplitude of 2.4 m, and tidal flow is strongly ebb dominated. At low tide, Necessary Creek displays high-banked levees adorned with tall *Spartina alterniflora*, channel thalwegs with thin, fine-grained sand veneers over thick deposits of organic-rich gray to black mud. Oyster patches and dams are locally developed along the channel bottoms and margins and the mouths of smaller feeder tributaries. Elongated and elevated point bars of silt and sand extend in the direction of ebb flow, and sloughs of soft mud are sandwiched between bar and channel levees. Smaller gut and tributary tidal creeks, such as Necessary Creek, represent lower-energy sheltered marsh environments, compared to large tidal creeks such as Walburg Creek. Smaller gut creeks often do not completely empty during low tide intervals due to intricate meander systems and drainage obstacles such as oyster dams.

FLOATING DOCKS: No exposures of well-consolidated bedrock exist along coastal Georgia, and hard substratum is thus at a premium in Georgia marine and estuarine environments. On St. Catherines Island hard marine substratum consists only of limited development of sandy ''beach rock'' in marsh areas prone to freshwater drainage from the Island core, ''firm grounds'' of semiconsolidated relict marsh muds along portions of the sea-facing beaches, ''wood grounds'' of fallen trees and driftwood, other floating debris, and man-made structures such as pilings, trunks, and docks. We sampled four floating docks along the island, two from the east side, and two from the west side. PVC pipes and flat plates, acting as settlement substrata, were positioned at some of these docks as part of a separate study on biofouling and these data are qualitatively incorporated into this biodiversity survey. The epifouling study will be published separately. The small erosional tidal pools at the base of the ''woodgrounds'' on South Beach were also sampled.

The Main Dock (M), the largest dock on St. Catherines, is located on the northwestern margin of the Island and accommodates most of the research and logistical vessels. The northern half of this floating dock is under a wooden protective boathouse and thus shadowed. The other half of this dock is continuously exposed to sunlight. The main dock is situated parallel to the flow of Walburg Creek. Swift currents are common along the dock pilings, especially during ebb flow.

The smaller South Pasture Dock (SP) is located on the southwest side of the Island surrounded by a low-lying *Spartina* marsh. The dock was damaged and partially detached during a storm in 1996.

King New Ground Dock (KN) and Seaside Dock (SS) are much smaller than the Main Dock and experience proportionally much less boat traffic. They are located on the eastern margin of the island on moderately small meandering tidal creeks with steep mud banks. Seaside Dock is well inland but along the main tidal creek to Seaside Inlet. King New Ground Dock is on Cracker Tom Creek, which empties into McQueen's Inlet.

THE FAUNA: Table 1 is a complete listing of all macroinvertebrate species recovered, organized within higher taxa, along with available common names and sites of collection. The table also includes a few species collected in other studies from along the island (especially by one of us, RHB); these are annotated for original citations. Tables 2 through 6 are species breakdowns by habitat and only show the more commonly collected or representative species. Figure 2 presents a relative distribution (by percentage) of higher macroinvertebrate taxa found on all St. Catherines Island sand beaches. Figure 3 indicates the relative numbers of major phyla on the island, while figure 4 shows total number of species per each higher taxon identified in table 1.

BEACHES (table 2): North, Middle, and South Beach are all exposed to direct oceanic influence. All are mid-energy beaches of quartz sand, although exposed peat mud banks represent historic marsh communities with in situ (in life position) remnants of populations of *Mercenaria mercenaria*, *Geukensia demissa*, and *Crassostrea virginica*, among others. Beach erosion has undermined trees and produces a ''skeletal forest'' of bark-stripped, prone, hard substratum. Infauna common to the sands of these sites represent a typical beach fauna of orbiniid polychaetes, haustoriid amphipods, and apodid holothoroideans. On higher-energy beaches it is common to find *Haloclava producta*, *Nereis succinea*, *Nephtys bucera*, *Neverita duplicata*, *Donax variabilis*, haustoriid amphipods, *Emerita talpoida*, and *Callichirus major* either in the intertidal or shallow subtidal zones. Shells and live specimens of the dwarf surfclam *Mulinia lateralis* frequently wash up on these beaches by the millions into the middle and higher tide reaches. The frequency of these occurrences must indicate substantial subtidal populations of this small bivalve. While these ''strandings'' are common, a remarkably large exhumation of *M. lateralis* occurred near Flag Pond in early October 1993. At this time live clams, at the surface or just beneath the beach sediment, were found at densities higher than 23,000/m^2 (Cleveland et al., personal obs.). The live clams were mixed with a large number of empty valves (live clams made up about 79–87% of the exhumed clams), indicating a stochastic, perhaps storm-based event, offshore. A subsample of these clams showed most to be sexually mature with ripe gonads.

Along lower-energy beaches (the more protected northwest end of the island including Engineers Point), we frequently encountered *Hydractinia echinata* (on shells occupied by hermit crabs), *Nereis succinea*, *Owenia fusiformis*, *Busycon carica*, *Busycoptypus canaliculatus*, *Oliva sayana*, *Sinum perspectivum*, *Terebra disolocata*, *Squilla empusa*, *Biffarius biformis*, *Lepidoa websteri*, *Menippe mercenaria*, *Pagurus acadianus*, *Mellita quinquiesperforata* (usually washed up on shore, frequently buried just beneath sand veneer), and *Sclerodactyla briareus*. Interestingly, in his own studies, R. Heard (personal commun.) found the most common small hermit crabs along lower-energy beaches of the Georgia sea isles to be *P. annulipes*, *P. longicarpus*, *P. pollicaris*, and *Clibanarius vittatus*. More quiescent beaches along the northeast tip of the Island had patches of *Diopatra cuprea*, whose external, emerged tubes were home for the blood brittle star *Hemipholis elongata*. Bivalves, mainly infaunal, composed 23% of the total beach species on St. Catherines Island (23). Gastropods composed 13.2%, and polychaetes 17.8%. Amphipods, dominated in terms of abundance by haustoriids, composed 12.5% of all St. Catherines Island

TABLE 1

Macroinvertebrates of St. Catherines Island, Georgia, Collected from Coastal Habitats, 1992–1998

Key to sites appears below. Sites represent locations where particular species are typically found but do not include all species localities. Common names are given where available. Comments on interspecific or other associations appear in lettered notes at the end of the table. Numbers of species in higher taxa are noted in brackets.

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
Porifera [9]																					
Adocia tubifera (George & Wilson, 1919)	Pink tubular sponge								X												X
Aplysilla longispina (George & Wilson, 1919)	Sulfur sponge					X															
Cliona celata Grant, 1826	Yellow boring sponge		X				X		X											X	
Halichondria bowerbanki (Burton, 1930)	Bread sponge																		X	X	
Haliclona sp.	Finger sponge					X															
Hymeniacidon heliophila (Parker, 1910)	Sun sponge					X													X		
Leucosolenia sp.	Organ-pipe sponge							X													
Lissodendoryx isodictylis (Carter, 1882)	Garlic sponge					X		X											X	X	
Microciona prolifera (Ellis & Solander, 1786)	Red beard sponge					X													X	X	
Cnidaria [25]																					
HYDROZOA [10]																					
Bougainvillia rugosa Clarke, 1882	Bougainvillia hydroid					X		X		X						X			X	X	
Campanularia sp.[A]	Campanularian hydroid	X				X															
Eudendrium carneum Clarke, 1882	Stick hydroid							X													
Garveia sp.	Rope grass							X													
Hydractinia echinata Fleming, 1828	Snail fur	X	X							X		X									X
Lovenella gracilis Clarke, 1882[B]	Lovenellid hydroid		X						X	X			X			X					
Obelia geniculata (Linne, 1758)													X								
Physalia physalis (Linné, 1759)	Portuguese man-of-war								X												
Podocoryne carnea Sars, 1846						X															
Tubularia crocea (L. Agasiz, 1862)	Tubularian hydroid							X											X		
SCYPHOZOA [3]																					
Aurelia aurita (Linné, 1758)	Moonjelly		X						X	X											
Chysaora quinquecirrha (Desor, 1848)	Sea nettle	X	X																		
Stomalophus melagris Agassiz, 1862	Cannonball jelly																				X

(continued)

Key to sites:

B	St. Catherines Shoal (trawled behind shoal)	KN	King New Ground Dock	N	North Beach	P	Picnic Point	SM	South End Marsh
E	Engineer Point	LC	Long Creek	NC	Necessary Creek	PP	Persimmon Point	SP	South Pasture Dock
F	Flag Pond	M	Main Dock	NE	North End	S	South Beach	SS	Seaside Dock
H	Hoke's Landing Marsh	MB	Middle Beach	NM	North West Marsh	SD	Seaside Delta	W	Walburg Creek (trawled)

TABLE 1—(*Continued*)

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
ANTHOZOA [12]																					
Astrangia danae Agassiz, 1847	Star coral																				X
Bunodosoma cavernata Bose, 1802[C]	Warty anemone								X												
Calliactis tricolor (LeSueur, 1817)	Hermit crab anemone	X								X											
Diadumene leucolena (Verrill, 1866)	Ghost anemone									X											
Edwardsia elegans Verrill, 1869[2]	Burrowing anemone		X																		
Haliactis sp.[1]									X												
Haliplanella luciae (Verrill, 1898)	Orange-striped anemone					X		X	X										X	X	
Haloclava producta (Stimpson, 1856)	Burrowing anemone		X																		
Leptogorgia virgulata (Lamarck, 1815)	Sea whip		X							X	X										
Nematostella cf. *vectensis* Stephenson, 1935	Burrowing anemone								X												
Paranthus rapiformis (LeSueur, 1817)	Sea onion					X		X		X											
Renilla reniformis (Pallas, 1766)	Sea pansy	X							X												
Ctenophora [2]																					
Beroe ovata Chamisso & Eysenhardt, 1821	Pink comb jelly								X												X
Mnemiopsis leidyi A. Agassiz, 1865	Sea walnut	X							X												X
Bryozoa [6]																					
Alcyonidium hauffi Marchus, 1839	Rubbery bryozonan	X						X		X	X										
Amathia distans Busk, 1866	Spiral bryozoan									X										X	
Anguinella palmata van Beneden, 1845	Ambiguous bryozoan																			X	
Membranipora tenuis Desor, 1848	White crust	X	X					X				X									
Schizoporella unicornis (Johnston, 1847)	Orange crust								X												
Zoobotryon verticillatum (delle Chiaje, 1828)	Bushy bryozoan															X					
Platyhelminthes [5]																					
TURBELLARIA																					
Bdelloura candida (Girard, 1850)	Limulus leech		X						X	X											
Coronodena mutabilis (Verrill, 1973)	Mutable flatworm					X															
Euplana gracilis (Girard, 1850)	Slender flatworm							X													
Polycladida sp.						X		X													
Stylochus ellipticus (Girard, 1850)	Oyster flatworm					X		X	X							X					
Nemertinea [5]																					
Carinoma tremaphoros Thompson, 1900	Burrowing ribbon worm																X				
Lineus socialis (Leidy, 1855)	Social lineus								X												
Nemertopsis bivittata (delle Chiaje, 1841)									X												
Tetrastemma vermiculus (Quatrefages, 1846)	Four-eyed nemertean					X															
Tubulanus pellucidus (Coe, 1895)	Tube nermertean					X		X		X									X	X	

TABLE 1—(*Continued*)

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
Annelida [64]																					
POLYCHAETA [63]																					
Ampharetidae sp.			X																		
Amphitrite cirrata Mueller, 1771	Ornate worm					X			X										X		
Amphitrite johnstoni Malmgren, 1866	Johnston's ornate worm							X													
Amphitrite ornata (Leidy, 1855)	Spaghetti worm					X		X		X									X	X	
Amphitritidae sp.																			X		
Arabella iricolor (Montagu, 1804)	Opal worm								X	X											
Brania clavata (Claparede, 1863)								X											X	X	
Brania sp.						X															
Capitella sp.						X															
Capitella cf. *capitata* (Fabricius, 1780)	Capitellid threadworm		X					X		X						X					
Ceratonereis longicirrata (Webster, 1879)						X		X											X	X	
Ceratonereis sp.																			X		
Cirratulidae sp.						X													X	X	
Cirroformis grandis (Verrill, 1873)	Orange fringed worm		X																		
Cistenides gouldii (Verrill, 1873)	Trumpet worm							X													
Clymenella torquata (Leidy, 1855)	Bamboo worm																	X			
Demonax micropthalmus (Verrill, 1873)	Fan worm									X									X		
Diopatra cuprea (Bosc, 1802)	Plumed worm	X	X							X											
Drilonereis magna Webster & Benedict, 1887	Threadworm								X							X					
Euchone elegans Verrill, 1873	Fanworm					X		X											X		
Glycera americana Lelidy, 1855	Bloodworm								X	X											
Glycera dibranchiata Ehlers, 1868	Blood worm							X	X	X	X					X					
Haploscoloplos fragilis (Verrill, 1873)									X	X											
Haploscoloplos robustus (Verrill, 1873)									X	X											
Heteromastus filiformis (Claparède, 1864)									X												
Hydroides dianthus (Verrill, 1873)	Limy tube worm								X												
Kinbergonuphis jenneri (Gardiner, 1975)	Soda straw worm								X												
Kinbergonuphis microcephala (Hartman, 1944)			X													X					
Lepidonotus sublevis Verrill, 1873D	Twelve scaled worm								X												
Lepidonotus variabilis Webster, 1879	Twelve scaled worm																			X	
Lumbrineris tenuis Verrill, 1873									X	X						X	X				
Magelona phyllisae Jones, 1963									X							X					
Microspio pigmenta Reisch, 1959						X															
Nemerata sp.						X													X		
Nephtys bucera Ehlers, 1868	Shimmy worm		X						X	X						X					

TABLE 1—(*Continued*)

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
Nephtys picta Ehlers, 1868	Shimmy worm		X						X	X											
Nereis succinea Frey & Leuckart, 1847	Clam worm		X			X		X		X		X							X	X	
Nereis virens Sars, 1835	Clam worm		X																		
Ophelia sp.									X												
Orbinia ornata (Verrill, 1873)	Ragged worm															X					
Orbinia riseri (Pettibone, 1957)									X												
Owenia fusiformis delle Chiaje, 1841	Shingle tube worm	X	X																		
Phyllodoce fragilis Webster, 1879	Green oyster worm		X																X		
Phyllodoce mucosa Oersted, 1843	Paddle worm		X				X		X												
Poecilocheatus johnsoni (Hartman, 1939)[2]																					
Polydora caulleryi Mesnil, 1897	Whip mud worm					X															
Polydora ligni Webster, 1879	Polydora mud worm					X															
Polydora socialis (Schmarda, 1861)	Mud worm					X														X	
Polydora websteri Hartman, 1943	Oyster mud worm					X													X		
Polyodontes lupinus (Stimpson, 1856)	Sea wolf					X															
Potamilla neglecta Sars, 1851	Fan worm					X													X		
Sabella melanostigma Schmarda, 1861	Feather duster worm					X		X													
Sabellaria floridana Hartman, 1944	Mason worm								X	X						X					
Sabellidae sp.						X		X											X	X	
Schistomeringos rudolphi (delle Chiaje, 1828)	Ghost worm							X													
Scoloplos rubra (Webster, 1879)									X												
Scolelepis squamata (Müller, 1806)	Palp worm															X	X				
Syllides setosa Verrill, 1882								X													
Syllis gracilis Grube, 1840								X													
Syllis sp.						X		X											X	X	
Terebellidae sp.						X													X	X	
Trypanosyllis sp.																			X		
Websterinereis tridentata (Webster, 1879)						X															
ECHIURIDA																					
Thalassema hartmani (Fisher, 1947)[2]																					
Mollusca [88]																					
GASTROPODA [38]																					
Acteocina canaliculata (Say, 1822)[1]	Channeled barrel bubble								X												
Aeolidia papillosa (Linné, 1761)	Shag-rug aeolis		X					X												X	
Astyris lunata (Say, 1826)	Lunar dovesnail					X													X	X	

TABLE 1—(*Continued*)

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
Boonea impressa (Say, 1822)	Impressed odostome		X					X													
Busycon carica (Gmelin, 1791)	Knobbed whelk		X						X		X	X				X					
Busycon carica eliceans (Montfort, 1810)	Kiener's whelk															X					
Busycon contrarium (Conrad, 1840)	Lightening whelk		X							X		X									
Busycotypus canaliculatus (Linné, 1758)	Channeled whelk		X						X	X		X				X					
Costanachis avara (Say, 1822)	Greedy dove snail		X																		
Cratena pilata (Gould, 1870)	Striped nudibranch							X											X	X	
Crepidula convexa Say, 1822	Convex slippersnail		X						X	X											
Crepidula fornicata (Linné, 1758)	Common Atlantic slippersnail		X						X	X		X				X					X
Crepidula plana Say, 1822	Eastern white slippersnail	X	X						X	X		X									
Doridella obscura Verrill, 1870	Obscure corambe					X		X									X				
Epitonium sp.	Wentletrap															X					
Epitonium angulatum (Say, 1830)[1]	Angulate wentletrap								X												
Epitonium humphreysi (Kiener, 1838)	Humphrey's wentletrap									X											
Epitonium rupicola (Kurtz, 1860)[1]	Brown-banded wentletrap								X												
Eupleura caudata (Say, 1822)	Thick-lip drill											X									
Hastula cinerea (Gmelin, 1791)	Gray auger		X							X											
Ilyanassa obsoleta (Say, 1822)	Eastern mudsnail		X	X	X		X				X						X				X
Ilyanassa trivittata (Say, 1822)	Threeline mudsnail											X				X					
Littorina irrorata (Say, 1822)	Marsh periwinkle		X		X		X			X	X	X	X		X	X		X			
Littorina ziczac (Gmelin, 1791)	Zebra periwinkle									X											
Melampus bidentatus Say, 1822	Common marsh snail				X				X				X	X				X	X		
Nassarius vibex (Say, 1822)	Bruised nassa	X	X																		
Natica pusilla Gould, 1841[1]	Southern miniature natica								X							X					
Neverita duplicata (Say, 1831)	Shark eye	X	X						X	X		X				X					
Oliva sayana Ravenel, 1834	Lettered olive		X									X									
Olivella mutica (Say, 1822)	Variable drwarf olive								X								X				
Olivella nivea (Gmelin, 1791)[1]	West Indian dwarf olive								X												
Parvanachis obesa (C. B. Adams, 1845)	Fat dovesnail		X					X	X		X									X	
Simnialena uniplicata (Sowerby, 1848)	Single toothed simnia										X										
Sinum perspectivum (Say, 1831)	White baby-ear								X	X						X					
Siphonaria alternata Say, 1826	Say's false limpet	X								X				X							
Siphonaria pectinata (Linné, 1758)	Striped false limpet													X							
Terebra dislocata (Say, 1822)	Eastern auger		X						X												
Urosalpinx cinerea (Say, 1822)	Atlantic oyster drill		X																		

TABLE 1—(*Continued*)

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
BIVALVIA [48]																					
Abra aequalis (Say, 1822)[1]	Common Atlantic ark								X												
Anadara brasiliana (Lamarck, 1819)	Incongruous ark								X												
Anadara ovalis (Bruguiere, 1789)	Blood ark					X			X							X					
Anadara transversa (Say, 1822)	Transverse ark								X												
Atrina rigida (Lightfoot, 1786)*	Stiff pen shell															X					
Atrina serrata Sowerby, 1825*	Sawtooth pen shell															X					
Bankia gouldi (Bartsch, 1908)[E]	Gould shipworm					X		X		X											
Barnea truncata (Say, 1822)	Atlantic mud-piddock									X											
Brachidontes exustus (Linné, 1758)[F]	Scorched mussel							X		X				X					X		
Corbula swiftiana C. B. Adams, 1852	Box clam		X																		
Crassostrea virginica (Gmelin, 1791)	Eastern oyster		X			X													X	X	
Cyrtopleura costata (Linné, 1758)	Angelwing								X	X											
Dinocardium robustum (Lightfoot, 1786)	Giant Atlantic cockle								X												
Diplodonta punctata (Say, 1822)*	Atlantic diplodon		X																		
Diplothyra smithii Tryon, 1862	Oyster piddock										X										
Divaricella quadrisulcata (d'Orbigny, 1842)*	Cross-hatched lucine															X					
Donax parvulus Philippi, 1849	Coquina																X				
Donax variabilis Say, 1822	Variable coquina		X						X	X		X				X					
Dosinia discus (Reeve, 1850)	Disk dosinia									X											
Ensis directus Conrad, 1834	Atlantic jackknife							X													
Ervilia concentrica (Holmes, 1860)	Concentric ervilia		X																		
Gemma gemma (Totten, 1834)	Amethyst gemclam															X					
Geukensia demissa (Dillwyn, 1817)	Ribbed mussel		X	X							X	X	X		X			X			
Hiatella arctica (Linné, 1767)	Arctic hiatella		X																		
Ischadium recurvum (Rafinesque, 1820)	Hooked mussel															X					
Lyonsia hyalina Conrad, 1831*	Glassy lyonsia								X												
Martesia cuneiformis (Say, 1822)	Wedge piddock								X												
Mercenaria mercenaria (Linné, 1758)	Northern quahog		X				X		X		X	X									
Mercenaria mercenaria notata Say, 1822	Hard clam		X																		
Modiolus americanus (Leach, 1815)	American horsemussel					X										X			X		
Modiolus modiolus squamosus Beauperthuy, 1967	Northern horsemussel															X					
Mulinia lateralis (Say, 1822)	Dwarf surfclam		X						X	X											
Noetia ponderosa (Say, 1822)	Ponderous ark								X												
Nucula proxima Say, 1822	Atlantic nut clam		X																		
Petricola pholadiformis Lamarck, 1818	False angelwing								X							X					

TABLE 1—(*Continued*)

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
Polymesoda caroliniana (Bosc, 1801)	Carolina marshclam														X						
Raeta plicatella (Lamarck, 1818)*	Channeled duckclam															X					
Rupellaria typica (Jones, 1844)	Atlantic rupellaria									X											
Solen viridis Say, 1821	Green razor		X							X											
Sphenia antillensis Dall & Simpson, 1901	Antillean sphaenia		X							X											
Spisula solidissima (Dillwyn, 1817)	Atlantic surfclam								X												
Tagelus plebius (Lightfoot, 1796)*	Stout tagelus								X												
Tellina aequistriata Say, 1824	Striate tellin															X					
Tellina agilis Stimpson, 1857	Agile tellin								X	X											
Tellina alternata Say, 1822	Alternate tellin								X							X					
Tellina iris Say, 1822[I]	Iris tellin								X												
Tellina texana Dall, 1900	Say's tellin		X																		
Trachycardium muricatum (Linné, 1758)*	Yellow pricklycockle															X					
CEPHALOPODA [2]																					
Lolliguncula brevis (Blainville, 1823)	Atlantic brief squid	X	X								X	X									X
Octopus vulgaris Lamarck, 1798	Common octopus									X											
Arthropoda [130]																					
CHELICERATA—MEROSTOMATA																					
Limulus polyphemus (Linné, 1758)	Horseshoe crab		X						X	X											
CHELICERATA—PYCNOGONIDA [4]																					
Achelia spinosa (Stimpson, 1853)						X		X											X	X	
Callipallene brevirostrum (Johnston, 1837)	Long-necked sea spider					X		X													
Nymphon grossipes (Fabricius, 1778)								X													
Tanystylum orbiculare Wilson, 1878	Ringed sea spider					X		X											X	X	
CRUSTACEA [7]																					
CIRRIPEDIA																					
Balanus amphitrite Darwin, 1854	Striped barnacle		X																		
Balanus balanoides (Linné, 1767)	Northern rock barnacle		X			X	X														
Balanus eburneus Gould, 1841	Ivory barnacle		X			X		X											X		
Chthamalus fragilis Darwin, 1854[G]	Fragile barnacle		X					X		X											
Conchoderma virgatum (Spengler, 1790)[H]	Striped goose barnacle															X					
Conopea galeata (Linné, 1771)	Seawhip barnacle		X							X											
Lepas anatifera Linné, 1758[I]	Gooseneck barnacle															X					

TABLE 1—(*Continued*)

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
AMPHIPODA [48]																					
Acanthohaustorius millsi Bousfield, 1965			X						X	X						X					
Acanthohaustorius shoemakeri Bousfield, 1965									X												
Aeginella spinosa Boeck, 1861	Skeleton shrimp								X												
Ameroculodes sp.[2]									X												
Amphiporeia virginiana Shoemaker, 1933			X							X											
Ampithoidae sp.								X											X	X	
Ampithoe longimana Smith, 1874	Long-antennaed tube-builder							X													
Batea catharensis Muller, 1865																					X
Caprella equilibra Say, 1818	Skeleton shrimp					X		X											X	X	
Corophium archerusicum Costa, 1857								X		X											
Corophium insidiosum Crawford, 1937			X			X		X						X					X	X	
Corophium lacustre Vanhoffen, 1911	Slender tube-builder					X															
Corophium tuberculatum Shoemaker, 1934[1]									X												
Cymadusa compta (Smith, 1874)	Wave-diver tube-builder					X		X											X		
Dulichiella appendiculata (Say, 1881)	Big clawed amphipod					X		X											X	X	
Eobrolgus spinosus (Holmes, 1903)									X												
Gammarus mucronatus Say, 1818	Spine-backed scud					X			X	X									X	X	
Gammarus palustris Bousfield, 1969	Scud																		X	X	
Gammarus tigrinus Sexton, 1939	Scud								X												
Gammarididae sp.																				X	
Haustorius canadensis Bousfield, 1962	Beach digger		X						X	X			X								
Hyperia galba (Montagu, 1813)	Big-eyed amphipod		X								X										
Indunella sp.[1]									X												
Jassa falcata (Montagu, 1808)	Mottled tube maker							X													
Lembos websteri Bate, 1862						X		X											X	X	
Melita nitida Smith, 1873										X						X				X	
Microdeutopus gryllotalpa Costa, 1853						X		X											X	X	
Microprotopus ranei Wigley, 1966								X													
Neohaustorius biarticulatus Bousfield, 1965	Sand-digger									X						X					
Neohaustorius schmitzi Bousfield, 1965									X												
Netamelita barnardi McKinney, Kailke & Holland, 1978						X		X													
Orchestia grillus Bosc, 1802	Saltmarsh beach-hopper		X																		
Paracaprella pusilla Mayer, 1890																			X		
Paracaprella tenuis Mayer, 1903	Skeleton shrimp					X		X								X			X	X	

TABLE 1—(*Continued*)

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
Parahaustorius longimerus Bousfield, 1965									X	X						X					
Parapleustes aestuarius Watling & Maurer, 1979						X		X											X	X	
Photis pugnator Shoemaker, 1945						X		X													
Photidae sp.																					
Podocerus sp.								X													
Pontogeneia sp.																					
Proboloides holmesi Bousfield, 1973								X													
Protohaustorius deichmannae Bousfield, 1965									X												
Pseudohaustorius caroliniensis Bousfield, 1965									X												
Stenothoe minuta Holmes, 1903	Seed amphipods					X		X												X	
Synchelidium americanum Bousfield, 1973										X											
Talitridae sp.					X																
Trichophoxus sp.			X																		
Unicola irrorata Say, 1818																			X		
ISOPODA [13]																					
Ancinus depressus (Say, 1818)	Thorn isopod								X												
Bopyrid sp.[J]										X											
Chiridotea caeca (Say, 1818)	Sand isopod								X	X						X					
Cleantiodes planicauda (Benedict, 1899)																					X
Cyathura polita (Stimpson, 1855)			X									X									
Cymothoa excisa Perty, 1839		X																			
Edotea triloba (Stimpson, 1818)	Mounded-back isopod								X												
Exosphaeroma diminuta Menzies & Frankenberg, 1966										X											
Ligia exotica Roux, 1828	Wharf roach		X			X		X								X			X	X	
Limnoroa tripunctata Menzies, 1951	Southern gribble							X													
Lironeca ovalis (Say, 1818)			X																		
Probopyrus pandalicola (Packard, 1879)	Shrimp parasite																		X		
Sphaeroma quadridentata Say, 1818	Sea pill bug								X	X						X					
TANAICEA																					
Hargeria rapax (Harger, 1879)								X													
CUMACEA [2]																					
Leptocuma minor Calman, 1912[K]			X																		
Oxyurostylis smithi Calman, 1912[l]									X												

TABLE 1—(*Continued*)

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
MYSIDACEA																					
Heteromysis formosa Smith, 1873[L]	Red opossum shrimp								X	X						X				X	
STOMATOPODA [2]																					
Coronis scolependra Latreille, 1828	Mantis shrimp															X					
Squilla empusa Say, 1818	Common mantis shrimp	X	X																		
DECAPODA [50]																					
Acetes americanus carolinae Hanse, 1933	Long eyed sergestid shrimp		X																		X
Albunea paretii Guérin-Ménevile, 1853	Slender-eyed mole crab		X																		
Alpheus sp.	Snapping shrimp									X											
Armases cinereum (Bosc, 1802)	Wharf crab				X	X		X	X										X		
Callianassa biformis Biffar, 1971	Ghost shrimp		X						X	X											
Callianassa major Say, 1818	Ghost shrimp									X											
Callinectes sapidus Rathbun, 1896	Blue crab		X		X	X	X	X			X		X		X	X			X		X
Callinectes similis Williams, 1966	Lesser blue crab		X																		
Clibanarius vittatus (Bosc, 1802)	Striped hermit crab		X							X											
Dyspanopeus sayi (Smith, 1869)	Say's mud crab							X											X	X	
Eurypanopeus depressus (Smith, 1869)	Flatbacked mud crab		X			X													X	X	
Eurytium limosum (Say, 1818)	Broadbacked mud crab		X																		
Hepatus epheliticus (Linné, 1763)	Dolly varden								X												
Hexapanopeus angustifrons Benedict & Rathbun, 1891						X		X	X										X	X	
Lepidopa websteri Benedict, 1903	Square-eyed mole crab		X						X							X					
Libinia dubia H. Milne Edwards, 1834	Six-spined spider crab								X												
Libinia emarginata Leach, 1815	Nine-spined spider crab	X																			
Megalobranchium soriatum (Say, 1818)	Eroded porcelain crab																			X	
Menippe mercenaria (Say, 1818)	Florida stone crab		X			X		X	X												
Microphrys sp.	Spider/decorator crab																				X
Neopanope cf. *texana* (Stimpson, 1859)								X													
Ocypode quadrata (Fabricius, 1787)	Ghost crab		X						X	X						X					
Ogyrides alphaerostris (Kingsley, 1880)	Long-eyed shrimp								X												
Ogyrides hayi Williams, 1981	Long-eyed shrimp															X					
Ovalipes ocellatus (Herbst, 1799)	Lady crab	X	X									X									
Pagurus annulipes (Stimpson, 1860)			X																		
Pagurus acadianus Benedict, 1901	Acadian hermit crab		X																		
Pagurus longicarpus Say, 1817	Long-clawed hermit crab	X	X							X		X				X					
Pagurus pollicaris Say, 1817	Flat-clawed hermit crab	X																			

TABLE 1—(*Continued*)

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
Palaemonetes intermedius Holthuis, 1949	Grass shrimp							X													
Palaemonetes pugio Holthuis, 1949	Common grass shrimp		X			X		X											X	X	
Palaemonetes vulgaris Say, 1818	Common shore shrimp		X	X		X		X											X	X	
Panopeus herbstii H. Milne-Edwards, 1834	Atlantic mud crab		X			X		X													
Penaeus aztecus Ives, 1891	Brown shrimp																				X
Penaeus duorarum Burkenroad, 1939	Pink shrimp		X								X	X									X
Penaeus setiferus (Linné, 1767)	White shrimp																				X
Persephona mediterranea (Herbst, 1794)	Mottled purse crab									X											
Petrolisthes armatus (Gibbes, 1850)	Porcelain crab								X												
Petrolisthes galathinus (Bosc, 1802)	Cherry-striped porcelain crab		X			X		X								X					
Pinnixa chaetopterana (Stimpson, 1860)	Parchment worm crab		X						X	X						X					
Pinnixa cylindrica (Say, 1818)	Pea crab		X														X				
Pinnixa cristata Rathbun, 1900	Pea crab		X							X											
Pinnixa sayana (Stimpson, 1860)	Pea crab		X																	X	
Pinnotheres osteum Say, 1817	Oyster pea crab		X						X												
Portunus depressifrons (Stimpson, 1859)	Flat-browed crab											X									
Rhithropanopeus harrissi (Gould, 1841)	White-fingered mud crab							X												X	
Uca minax (LeConte, 1855)	Red-jointed fiddler crab																	X			
Uca pugilator (Bosc, 1802)	Sand fiddler crab				X													X			
Uca pugnax (Smith, 1870)	Marsh fiddler crab				X						X							X			
Upogebia affinis (Say, 1818)	Flat-browed mud shrimp								X							X					
INSECTA																					
COLLEMBOLA																					
Anurida maritima Guérin, 1836[M]	Oyster springtail									X											
Echinodermata [9]																					
ECHINOIDEA [2]																					
Mellita quinquiesperforata (Leske, 1778)	Sand dollar	X	X						X												
Arbacea punctulata (Lamarck, 1816)	Purple sea urchin							X													
ASTEROIDEA [2]																					
Asterias forbesi (Desor, 1848)	Common sea star																				X
Luidia clathrata (Say, 1825)	Slender sea star																				X
OPHIUROIDEA [2]																					
Hemipholis elongata (Say, 1815)	Blood brittlestar								X	X			X								
Ophiothrix angulata (Say, 1825)[N]	Spiny brittle star																			X	

TABLE 1—(*Continued*)

Taxon	Common name	B	E	F	H	KN	LC	M	MB	N	NC	NE	NM	P	PP	S	SD	SM	SP	SS	W
HOLOTHUROIDEA [3]																					
Leptosynapta tenuis (Ayres, 1851)	White synapta		X						X	X											
Petamera pulcherrima (Ayres, 1851)										X											
Sclerodactyla briareus (LeSueur, 1824)	Brown sea cucumber									X											
Hemichordata [2]																					
Balanoglossus aurantiacus (A. Agassiz, 1873)	Golden acorn worm								X												
Saccoglossus kowalevskii (A. Agassiz, 1873)	Kowalevsky's acorn worm								X												
Chordata [4 nonvertebrates]																					
UROCHORDATA																					
Aplydium stellatum (Verrill, 1871)	Sea pork									X											
Clavelelina oblonga Herdman, 1880	Light bulb tunicate							X													
Corella borealis Traustedt, 1886)								X													
Molgula manhattensis (DeKay, 1843)	Sea grapes					X		X	X										X	X	

* Shell only.

[1] Collected by Rollins and West (1997).

[2] Collected by R. Heard in St. Catherine's Sound; *Ameroculodes* sp. is a small species. This is probably the new species in preparation for publication by R. Heard.

[A] This campanularian hydroid was found growing in bushy tufts on the surf clam *Spisula solidissima.* Note that the latter is probably the subspecies *S. solidissima similis,* a form that is found south of Cape Hatteras. *S. raveneli* is found in the southernmost range of *S. solidissima* but the validity of this species is in question (Cargnelli et al., 1999).

[B] *Lovenella gracilis* is commonly found growing on the coquina clam *Donax variabilis.*

[C] The anemone *Bunodosoma cavernata* was found only on driftwood.

[D] Found within the outer whorl in shells of *Busycon* occupied by the hermit crab *C. vittatus.*

[E] *Bankia gouldii* and *Sphenia antillensis* found in driftwood.

[F] *Brachidontes exustus,* juveniles found on driftwood.

[G] Small acorn barnacle, *Chthamalus fragilis* found growing on isopod *Sphaeroma quadridentata.*

[H] Striped gooseneck barnacle *Conchoderma virgatum* found on beached green sea turtle, *Chelonia viridis.*

[I] Gooseneck barnacles *Lepas anatifera* common on driftwood.

[J] Heard (personal commun.) notes at least 10 common bopyrids and probably another 5 less common species along the Georgia coast. Some of their hosts include *Palaemonetes, Ogyrides, Panopeus, Uca, Upogebia,* and *Alpheus.*

[K] Heard (personal commun.) has also found the cumaceans *Mancuma altera, Spilocuma watlingi,* and *Leucon americanum* along subtidal and lower intertidal protected Georgia sea island beaches.

[L] Perhaps seasonally based, *Heteromysis formosa* is the only mysid we recovered during our survey. Heard (personal commun.) has commonly found species of *Neomysis* and *Americamysis* along the Georgia coast.

[M] These springtails were found supratidally in water trapped in empty shells of the bivalve *Sphenia.*

[N] These small brittlestars (*H. elongata*) were only found associated with the exposed portion of the tubes of the polychaete *Diopatra cuprea.*

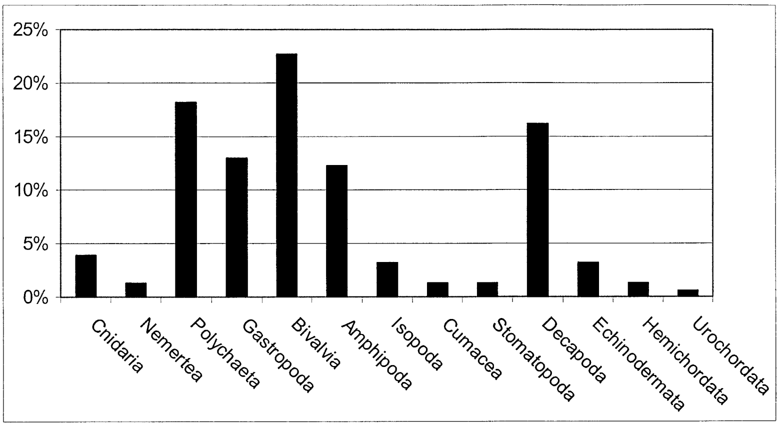

Fig. 2. Relative percentages of 154 beach taxa on all sampled St. Catherines Island beaches (Engineers Point, North, Middle, and South Beach).

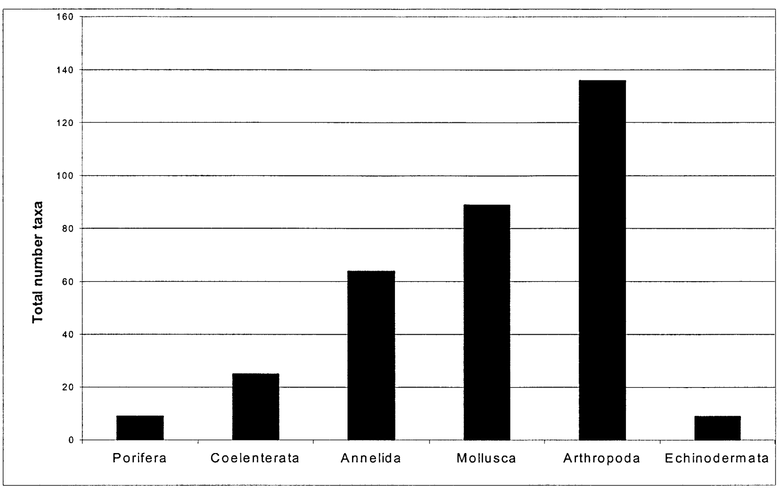

Fig. 3. Comparative numbers of taxa collected within major phyla on St. Catherines Island.

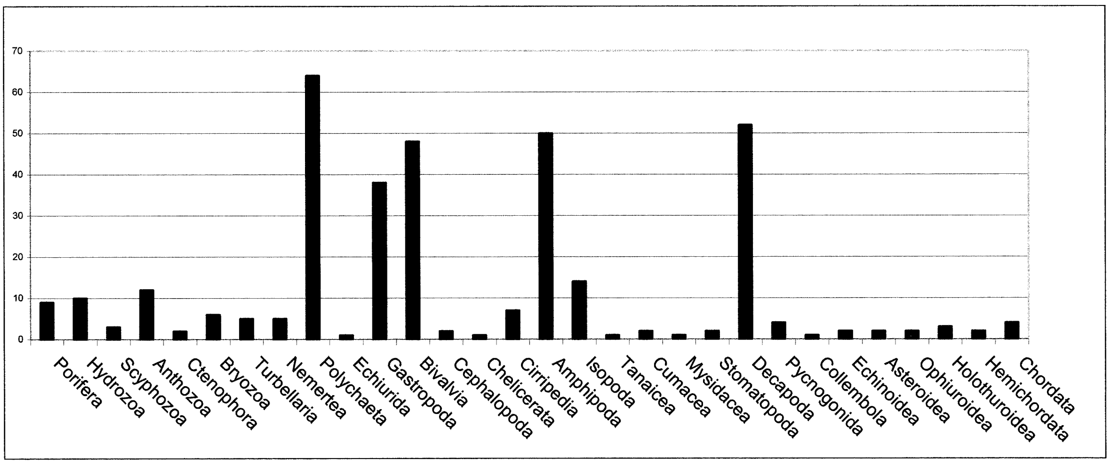

Fig. 4. Total number species per higher taxon (taxonomic levels indicated in table 1).

TABLE 2

Common Beach Fauna of St. Catherines Island, Georgia

''Common'' fauna are here defined as organisms typically found year-round in or on beach habitats. Epifauna found on beach inhabitants are noted along with host. L, in low energy portions of beach (sand flat); H, in higher energy (swash) zone of beach; I, ranges intertidal zone; ST, subtidal (usually found on beach after storms or collected live just subtidally). No label indicates that the species was found across a wide range of beach zones.

Acanthohaurstorius millsi H
Acteocina canaliculata I,L,ST
Albunea paretii H
Ampelisca verrilli L
Ampithoe longimana
Anadara brasiliana ST
Anadara transversa ST
Arabella iricolor L
Balanoglossus aurantiacus L
Biffarius biformis L
Busycon carica
Busycotypus canaliculatus
Calliactis tricolor (on hermit-crab-inhabited shells)
Callichirus major L
Chiridotea caeca I,ST
Clibanarius vittatus I,ST
Coronis scolependra I,ST
Costanachis avara ST
Cyathura polita ST
Cymothoa excisa ST
Dinocardium robustum ST
Donax variabilis H
Edotea triloba ST
Emerita talpoida H
Glycera americana I
Haploscoloplos robustus H
Hargeria rapax I,ST
Hemipholis elongata (with *Diopatra* tube) I,L
Lepidopa websteri H
Leptosynapta tenuis L
Lineus socialis I,ST
Lovenella gracillis (on *Donax*) H
Mellita quinquiesperforata ST
Mercenaria mercenaria L
Mulinia lateralis ST
Nematostella vectensis L
Nereis succinea
Neverita duplicata ST
Oliva sayana I,ST
Olivella nivea ST
Orbinia ornata
Ovalipes ocellatus ST
Owenia fusiformis I
Oxyurostylis smithi ST
Pagurus annulipes ST
Pagurus longicarpus ST
Parathus rapiformis ST
Persephona mediterranea ST
Saccoglossus kowaleveskii L
Sclerodactyla briareus I,ST
Scololepis squamata I
Sinum perspectivum ST
Solen viridis L
Spisula solidissima L
Squilla empusa ST
Tagelus plebius L
Terebra dislocata I,L

TABLE 3

Common Marsh (*Spartina alterniflora* dominant flora) Fauna of St. Catherines Island

Distributional or behavioral notes for some taxa are included. ''Common'' as defined in table 2.

Callinectes sapidus	common in flooded marsh only, otherwise subtidal
Geukensia demissa	infaunal, typically clumped along *Spartina* roots
Littorina irrorata	vertically migratory (tidal) on *Spartina*
Melampus bidentatus	found under wood or matted organic debris
Nereis succinea	often associated with wood debris on marsh surface, specimens usually relatively small
Orchestia grillus	common along bases of *Spartina*, evident at low tide
Palaeomontes vulgaris	common in flooded marsh
Panopeus herbstii	
Uca pugilator	high localized densities along sandier banks
Uca pugnax	

TABLE 4

Common Dock Fauna of St. Catherines Island

''Common'' as defined in table 2. While we found *Corophium insidiosum* among the most common amphipods on these docks, Heard (personal commun.) finds *C. lacustre* and *C. acherusicum*, among the most common amphipods occurring in Georgia estuaries, typically in upper mesohaline fouling communities.

Achelia spinosa	*Hiatella arctica*
Aeolidia papillosa	*Lembos websteri*
Amphitrite ornata	*Ligia exotica*
Anadara ovalis	*Limnoroa tripunctata*
Armases cinereum	*Membranipora tenuis*
Balanus eburneus	*Menippe mercenaria*
Bankia gouldi	*Microciona prolifera*
Barnea truncata	*Microprotopus raneyi*
Bougainvillia rugosa	*Modiolus americanus*
Brachidontes exustus	*Molgula manhattensis*
Caprella equilibra	*Neopanope* cf. *texana*
Ceratonereis longicirrata	*Nereis succinea*
Cliona celata	*Palaemonetes vulgaris*
Corophium insidiosum	*Paracaprella tenuis*
Crassostrea virginica	*Parvanachis obesa*
Cratena pilata	*Petrolisthes galathinus*
Crepidula fornicata	*Polydora websteri*
Dulichiella appendiculata	*Potamilla neglecta*
Eudendrium carneum	*Sabella melanostigma*
Eurypanopeus depressus	*Schizoporella unicornis*
Halichondria bowerbanki	*Stenothoe minuta*
Haliplanella luciae	*Tanystylum orbiculare*
Hexapanopeus angustifrons	*Tubularia crocea*

beach fauna. Decapod crustaceans made up 16.4% of all beach species.

In early October 1990 we also observed a mass exhumation of the burrowing shrimp *Upogibia affinis* along the southern portion of North Beach. During this event there was an unusually large spring tide (with a range of 9.3 m) leading a northward-moving tropical storm. During the same event we noted hundreds of juvenile *Busycon carica* and *B. carica eliceans* clustered in large patches along the beach. Most of the *U. affinis* stranded on the beach appeared unable to reburrow into the substratum, and perished through dessication or predation.

In all, about 66.5% of taxa recovered from beaches sampled on St. Catherines Island were polychaetes, gastropods, bivalves, and amphipods (fig. 2).

''HARD SUBSTRATA'' (table 4): Floating docks of St. Catherines Island are typically densely colonized by sponges, hydroids, barnacles, and chlorophyte algae (e.g., *Enteromorpha* sp., *Spongilla* sp.). PVC pipe and plate studies show that fouling communities at the Main Dock and King New Ground Dock were dominated by the barnacle *Balanus eburneus* and corophiid amphipods. Skoog (1996) found *Bougainvillia rugosa* to be abundant during summer months, but were replaced in the winter by the hydroid *Tubularia crocea*. Similar hydroid population trends have been recorded by Cain (1987) along floating docks in Beaufort, South Carolina. Species diversity was significantly higher within the protection of the PVC tube interiors throughout the winter months than on the exposed exterior of the tubes (Skoog, Prezant, Toll, Rollins, personal obs.). Diversity tended to increase along exposed portions of the docks during summer months. During summer months *Haliplenella luciae* and *Bougainvillia rugosa* dominated PVC pipe interiors at protected sites, while in the winter this shifted to *Balanus eburneus*, *Tubularia crocea*, and various bryozoans and tunicates. *Crassostrea virginica*, the American oyster, was found only on pipes in exposed areas. Sponges also were

TABLE 5

Fauna Commonly Associated with Oyster (*Crassostrea virginica*) Bars Along St. Catherines Island

These fauna include epibionts (Ep), endobionts (En), crevice dwellers (C), mud tube dwellers (T), oyster predators (Pr) or oyster parasites (Pa), deposit feeders (D), filter feeders (F), scavengers (Ss), and generalized predators of small invertebrates (P). ''Common'' as defined as in table 2.

Amphitrite cirrata C,D	*Gammarus mucronatus* C	*Phyllodoce fragilis* C,P
Amphitrite ornata C,D	*Geukensia demissa* (juveniles) C,F	*Pinnotheres osteum* En,Pr
Ancinus depressus C,S	*Haliplanella luciae* Ep,P	*Polydora ligni* Ep,F
Astyris lunata C	*Hexapanopeus angustifrons* C,S,P	*Polydora websteri* En,F
Balanus eburneus Ep,F	*Hydroides dianthus* Ep,F	*Potamilla neglecta* Ep,F
Boonea impressa Pa	*Membranipora tenuis* Ep,F	*Rhithropanopeus harrissi* C,S,P
Corophium insidiosum C,T	*Menippe mercenaria* C,SP,P	*Sabella melanostigma* Ep,F
Cymadusa compta C	*Nereis succinea* C,S,P	*Stylochus ellipticus* Pr (of oyster spat)
Diplothyra smithii En,F	*Nereis virens* C,S,P	*Tubulanus pellucidus* C,P
Doridella obscura Ep,P	*Panopeus herbstii* C,S,P	*Urosalpinx cinerea* Pr
Eurypanopeus depressus C,P,S		

more abundant in exposed locations. Flat PVC plates hung just below the water surface at the Main Dock usually had large populations of the hydroid *Tubularia crocea* (especially in cooler months), a species typically lacking from more protected King New Ground Dock. The hydroids typically had dense populations of caprellid and corophiid amphipods. PVC plates, also in the summer, were dominated by the solitary tunicate *Molgula manhattensis*. The dock hydroids were also a common home to the shag-rug aeolis nudibranch *Aeolidia papillosa,* whose coiled egg masses are not unusual among the hydroids during summer months. The feather blenny *Hypsoblennius hentz* was also commonly found among the epifauna of docks. The wooden supports of our fouling plates were, after about 20 months in the water, totally eaten away by the shipworm (bivalve) *Bankia gouldi*. The protected docks on the inner reaches of the island often had complex communities of sponges comprising at least six species.

TABLE 6

Common Fauna Associated with ''Skeleton'' Trees (''woodground'') Along Beach Intertidal Zones of St. Catherines Island

Species marked with an * are unique to this habitat on the island in our survey. The list does not include species found in the ephemeral pools that sometimes exist at the base of the stranded trees. ''Common'' as defined in table 2.

Amphitrite ornata	*Limnoroa tripunctata*
Anadara ovalis	*Littorina ziczac**
Armases cinereum	*Membranipora tenuis*
Balanus eburneus	*Menippe mercenaria*
Bankia gouldi	*Petrolisthes galathinus*
Brachidontes exustus	*Potamilla neglecta*
Crassostrea virginica	*Schizoporella unicornis*
Hiatella arctica	*Siphonaria pectinata**
*Ischadium recurvum**	

The skeleton forest of intertidal woodgrounds on Middle and North Beach housed wood crabs (*Sesarma cinereum*) as well as the zebra periwinkle (*Littorina ziczac*) and the pulmonate snail *Siphonaria alternata* (table 6). The sessile fauna on tree remains included tightly packed barnacles and small-ribbed mussels. The sea pillbug *Sphaeroma quadridentata* was a common surface inhabitant of the wood, while the southern gribble isopod *Limnoroa tripuntata* produced extensive borings within the wood. Small tidal pools at the base of some of these eroded tree remains were home to scavenging hermit crabs and deposit-feeding terebellid polychaetes (*Amphitrite ornata*). The striped anemone *Haliplanella luciae* is among St. Catherines most common anemones, found regularly on driftwood and those tree remains found in the low to mid tidal reaches, as well as in tide pools. The warty anemone *Bunodosoma cavernata*, rare in our collections, was found on the island just once in our sampling period. This single specimen was recovered on a piece of driftwood from Middle Beach. Driftwood was also a common habitat for the deposit-feeding terebellid polychaete *Amphitrite johnstoni*, which was found in crevices on wood debris where it created muddy tube homes.

MARSHES (table 3): On St. Catherines Island marshes had large populations of the sand fiddler crab *Uca pugilator*, but overall diversity within these marshes was low. Within the vegetated regions of the marshes, aside from fiddler crabs, were large populations of the ribbed marsh mussel *Geukensia demissa*, found buried and byssally attached along the roots of *Spartina alterniflora*. Small populations of the coffee bean snail *Melampus bidentatus* were found, typically under protected mats of stranded wood or algae and under needle rush wracks. Various xanthid mud crabs also were relatively common along with occasional nereid polychaetes.

The muddy point bars of the marsh creeks housed large infaunal populations of the hard clam *Mercenaria mercenaria*. Soft (mud) sediment hard clams tended to be larger and older than those found within sandy sediments of higher-energy environments (e.g. Engineers Point). In soft sediments of the point bars, hard clams were found buried to depths exceeding 25 cm. The muddy point bars were also typically covered with extensive populations of the mud snail *Ilyanassa obsoleta*. Along these creek banks were occasional small to large oyster bars. These bars were also home to numerous smaller invertebrate species associated with the oyster *Crassostrea virginica* (table 5). The latter included small xanthid crabs, pyramidellid gastropods, small orange-striped anemones, and predatory oyster drills. The parasitic oyster mosquito (snail) *Boonea impressa* was nowhere abundant on the oyster reefs and oyster patches of the island, but could consistently be found in small numbers along the ''lip'' of at least some members of each oyster population, especially in sandier habitats (e.g. Engineers Point). Oyster beds were also home to the bright green delicate paddle worm *Phyllodoce fragilis*. This worm was found within the crevices of the oyster reefs, where it likely scavenges food or occasionally preys on small invertebrates. The entire family of brightly colored phyllodocid polychaetes has few predators. Most potential predators of these paddleworms are repelled by the phyllodocids' copious mucus secretions that contain some, to date, unidentified repellent (Prezant, 1980).

More than 50% of the species found on the oyster bars are considered crevice dwellers, occupying the numerous interstices created by the irregularly growing oysters (table 5). Diverse feeding types were represented in this complex community, ranging from deposit-feeding polychaetes (*Amphitrite ornata*) to filter-feeding barnacles (*Balanus eburneus*) to carnivorous turbellarians (*Tubulanus pellucidus*), and a variety of scavenging crabs. Various oyster predators and parasites were also common on the bars (e.g. *Urosalpinx cinerea*, *Boonea impressa*).

BRAY-CURTIS INDEX: A total survey comparison was made with the summative work of Howard and Frey (1975). The latter authors compiled a coastal and near coastal marine invertebrate list that included works of Heard and Heard (1971) and Dörjes (1977). A similarity index comparison of our work compared to that of Howard and Frey (1975) showed a 40% similarity.

DISCUSSION

Dörjes (1977) surveyed and reviewed the marine macrobenthic communities of Sapelo Island, Georgia, including salt marshes, point bars, estuarine inlets, beaches and flats, shoals, and the near shelf benthos, although about 20 years previous to our study that survey represented the best comparative work of a Georgia sea island. Sapelo Island is adjacent to St. Catherines, and Dörge's work represents the most comprehensive study of comparable locations.

Salt marshes represent diverse microhabitats, from creek banks to high marshes, from densely vegetated low marshes to nonvegetated barrens. The nonvegetated mud banks of Sapelo Island salt marshes were dominated by *Crassotrea virginica*, *Illyanassa obsoleta*, and *Diopatra cuprea*. On St. Catherines Island mud banks also had large populations of oysters (*C. virginica*) and mud snails (*I. obsoleta*) but did not have dense populations of the polychaete *Diopatra cuprea*. Dörjes (1977) also noted large populations of *Upogebia affinis* and *Heteromastus filiformis* on Sapelo Island, both uncommon in St. Catherines Island creek/marsh mud banks (although *U. affinis* is eratically common on low-energy beaches and *H. filiformis* can regularly be found on these same beaches). Higher up on the banks, in the marsh barrens, only fiddler crabs are abundant on both island. On both Sapelo and St. Catherines Islands *Crassostrea virginica*, *Geukensia demissa*, *Littorina irrorata*, *Sesarma reticulatum*, *Nereis succinea*, and various mud and fiddler crabs are common inhabitants of the marsh proper. *Melampus bidentatus*, a common marsh snail of more northerly marshes, is not abundant in Georgia sea island marshes, though locally common in some marsh locations on St. Catherines. The differences in marsh fauna reported by Dörjes (1977) and in our report are minimal and probably reflect differences in time (season) or methods of collection.

Point bars are common features of Georgia coastal creeks. These small mud and/or sand bars are relatively uniform in habitat and typically lack angiosperms of any type. Dörjes (1977) noted that point bars in general will have few species with large populations and few if any endemic species. On St. Catherines Island point bars have semiprotected muddy habitats that are prime sites for the large hard clams *Mercenaria mercenaria* as well as the mud snails *Illyanassa obsoleta*. *M. mercenaria* is a commercially important bivalve in Georgia (Walker and Heffernan, 1990a, 1990b). Near-surface anaerobic muds tend to inhibit many macrofaunal species. In addition to anaerobic sediments, periodic shifting of these bars is at least partially responsible for low diversity. In some of these anaerobic muds, hard clam (*M. mercenaria*) and ribbed mussel (*G. demissa*) shells have undergone significant pyritization in living animals (Clark and Lutz, 1980). Living pyritized clams have been found not only within point bar muds on St. Catherines, but also in back levee, low marsh areas (DeLillo, 1998). The significance of pyritization in extant and extinct populations, as well as possible mechanisms underlying the pyritization process, is discussed by DeLillo (1998).

More than 50% of the common macroinvertebrate fauna found within or on oyster bars of St. Catherines Island are considered crevice dwellers, living in the complex interstices created by the irregular growth patterns of oysters. These crevice dwellers are afforded significant protection from transient fish predators, although numerous resident predators coinhabit these crevices (e.g. various xanthid crabs, phyllodocid and nereid polychaetes, etc.; see table 5). The oyster bar community of St. Catherines Island is typical of those reported for southern Atlantic coasts (see Fox and Ruppert, 1985). Dense populations of oysters tend to inhibit settlement and establishment of other large sessile or sedentary macrofauna through preemptive competition (Sutherland and Karlson, 1977). Thus, while crevice dwellers can take advantage of the habitat created by the oysters, few other large ‘‘settlers’’ can become established in this community. Heard (personal commun.) has commonly found the amphipods *Gammarus palustrus* and *Parhaylae hawaiensis* (Danna, 1853) on oyster reefs along Sapelo Island and Wassaw Island, and on Savannah Beach.

Interesting comparisons to loose sediment coastal habitats can be drawn from Dörjes' data on beach-related tidal flats. On Sapelo Island, Nannygoat Flat is a protected bight with low water energy and rich organic sediments. Cabretta Flat, on the other hand, merges landward with the beach, but seaward is protected by an intertidal shoal. Nevertheless, northern and southern channels allow tidal flow across the flat at regular intervals. Thus, Cabretta Flat has lower organic sandy sediments than Nannygoat Flat. The hydrodynamic regime on Cabretta Flat accounts for the huge number of amphipods found in this site. About 40% of all species on Cabretta Flat are crustaceans, while only 28% are polychaetes. On the other hand, on Nannygoat Flat 36% are crustaceans and 38% are polychaetes. The number of polychaete species and population sizes, reflect an increase in small particle sediments. Only *Heteromastus filiformis* and *Ilyanassa obsoleta* were found on Nannygoat Flat by Dörjes, while similarly, *Oliva sayana*, *Callichirus major*, and several haustauriid amphipod species were found only on Cabretta. On St. Catherines Island we found *Heteromastus filiformis* and *Oliva sayana* on beach habitats. *Ilyanassa obsoleta* was, however, similarly only found in low-energy, high organic environments. Dörges noted that protected muddy flats and point bars had similar communities on Sapelo Island, although mud flat species abundance was higher. We found flats on St. Catherines to have higher diversity than point bars along tidal creeks.

We found 154 species of macroinvertebrates on St. Catherines Island beaches. For comparison, Rakocinski et al. (1991) found 107 species of macroinvertebrates on 3 barrier islands along the northern Gulf of Mexico. Of these, 23 species composed 97% of all taxa recovered. While there is overlap in the northern Gulf of Mexico beaches and those of St. Catherines (e.g. *Nepthys bucera*, *Scolelepis squamata*, *Donax variabilis*, *Ancinus depressus*, *Exoshaeroma diminutum*, *Emerita talpoida*, etc.), there is a much wider difference in overall species recovered. In a few cases there are congeners that form parallel populations on St. Catherines beaches and those of the northern Gulf of Mexico (e.g. *Leptosynapta tenuis* and *Leptosynapta crassipatina*). The beach fauna of nearby Sapelo Island, however, is quite similar to that of St. Catherines. In both cases, beaches are dominated by *Donax variabilis*, *Callichirus major*, *Scololepis squamata* (*S. agilis* on Sapelo), various haustoriid amphipods, and (along the high beach up to the dune and into the swale) *Ocypode quadrata*. Several of the upper offshore species reported by Dörjes (1977) were found intertidally or just subtidally on St. Catherines. These include *Hemipholis elogata*, *Cistenides gouldii*, *Tellina texana*, *Biffarius biformis*, *Glycera americana*, *Owenia fusiformis*, and *Oxyurostylis smithi*. We found the brittlestar *H. elongata* only associated with the exposed portions of the tube of the polychaete *Diopatra cuprea*. Again, methods of collection, sieve size, and/or season could explain differences in recovered taxa. Because the islands are adjacent, it is unlikely that any major differences in fauna from similar habitats will be significant.

Howard and Frey (1975) characterized the estuarine environments along coastal Georgia. In doing so they recovered representatives of 73 species and relatively low abundances (the authors account for this by noting limited sampling protocol that included too large a sieve mesh). Nevertheless, they noted that of the 73 species collected, 37% were annelids (27 species), 22% arthropods (16 species) and 15% were molluscs (11 species). It is interesting to note that in terms of abundance, annelids account for 57% of the animals collected, arthropods accounted for 11.9%, and molluscs only 4.7%. Echinoderms, which composed only 2.7% of species collected (a total of two species), accounted for 14.4% of total specimens collected. In our study (including a far wider array of sampled habitats) over 340 species of macroinvertebrates were collected, with crustaceans alone accounting for about 40% of the total taxa. Polychaetes accounted for 17.5% and molluscs about 25% of species recovered. The relative abundances of higher taxa are more in line with those reported by Howard and Dörjes (1972) and Dörjes (1977) for crustaceans of Cabretta Flat (36% or 50 species). We recovered, percentwise, fewer polychaete taxa and more molluscan taxa than similar regional studies.

Of the macroinvertebrates they found in their entire Georgia coast study, Howard and Frey (1975), recovered 20 (17 identified to species) from the St. Catherines Sound benthos. These included the species in the list below.

Abra aequalis
*Alcyonidium polyoum**
Arabella iricolor
Caprella equilibra
*Cerebratulus lacteus**
Cistinides gouldii
Clymenalla torquata
Diopatra cuprea
Hemipholis elongata
Leptogorgia virgulata
Lyonsia hyalina
Molgula manhattensis
Mulinia lateralis
Nassarius vibex
Nephtys picta
Nereis succinea
Orbinia ornata
Solen viridis

The two species indicated by asterisks were not found in the present study. *Cerebratulus lacteus* is a large nemertean, often found swimming in the water column and easily fragmented upon recovery. It is likely this is not a particularly rare ribbon worm found along St. Catherines, but our sampling protocol failed to recover any specimens. *Alcyonidium polyoum* is a rubbery bryozoan, difficult to separate taxonomically from *A. hauffi* (recovered in our study). The difficulty in identification of these taxa calls for further systematic study of this group of Bryozoa along the Georgia coast. Howard and Frey (1975) also noted a St. Catherines Sound undescribed species of *Cerebratulus*, an unidentified sipunculid, and an undescribed balanoglossid. Nevertheless, there appears to be little in their estuarine study not also recovered in our present study. Heard (personal commun.) also notes that two species of *Leptogorgia* are found in Georgia: *L. virgulata* and *L. setosa*. *L. virgulata* is a more euryhaline, clearwater species, while *L. setosa* can tolerate mesohaline, turbid estuarine waters.

Overall, arthropods as a phylum dominated in terms of total number of taxa we recovered on St. Catherines Island (fig. 3). In other studies this was not necessarily the case and likely reflects specific collection sites (especially intertidal vs. subtidal). Knott et al. (1983) examined benthic invertebrates along coastal South Carolina transects that extended to depths of 5 m. Of the 223 species they collected, 88 occurred intertidally. Overall, polychaetes dominated in numbers and species. On St. Catherines Island polychaetes also dominated when lower taxa are examined (fig. 4; lower taxa defined here as above genus but below phylum; as designated in table 1). Knott et al. (1983) attributed the dominance of polychaetes to the moderate wave energy of the habitats studied. In all, polychaetes composed 40% of the species and 60% of total abundance, while amphipods made up 17% of species and 22% of abundance, bivalves 13.5% of species and 12% abundance, and decapods 7.6% of species and $<$1% abundance. Snails, isopods, and echinoderms together compose about 13% of species but less than 1% abundance. The relatively high diversity of this beach transect is in part a result of a newly placed jetty. Within intertidal areas *Scolelepis squamata*, *Neohaustorius schmitzi*, and *Donax variabilis* dominated. Subtidally, again to 5-m depth, *Spiophanes bombyx*, *Scolelepis squamata*, *Protohaustorius deichmannae*, *Acanthohaustorius millsi*, and *Tellina* sp. were dominant. These fauna are quite similar to beach fauna recovered along St. Catherines Island. However, relative percentages of the major taxa again differ, with polychaetes on St. Catherines composing only 17.5% of total island fauna and 17.8% of beach fauna (fig. 2). Amphipods of St. Catherines Island beaches comprise 12.5% of the species recovered. Molluscs offer the highest diversity in terms of species numbers on St. Catherines beaches, accounting for 36.2% of all beach species (13.2% gastropods, 23% bivalves). Decapod crustaceans compose 16.4% of the beach species. These relative percentages are in stark contrast to the polychaete and amphipod species dominance and low numbers of gastropod taxa in the Knott et al. South Carolina study. Additionally, Knott et al. (1983) recorded only 88 intertidal species compared to 152 on St. Catherines Island. It is possible the difference in total number of taxa accounts for the large relative difference in percent of noted taxa. A longer duration and more intensive effort along the intertidal of St. Catherines Island uncovered a greater number of species. Thus, without a comparable study along the South Carolina beach, no valid comparisons can be made. Similarly, without a more comprehensive subtidal effort along the St. Catherines Island coast, comparisons with the 205 subtidal species recovered along South Carolina by Knott et al. (1983) could be misleading.

One of the many interesting habitats on the Island is the woodland of toppled (via beach erosion) skeleton trees stranded on the northern and southern beaches. These woodgrounds offer a complex intertidal and spray zone habitat for desiccation-resistant fauna. Many authors have discussed the relationship of complex physical structures (especially as found in rocky intertidal zones) to biodiversity (Fletcher and Underwood, 1987; Walters and Wethey, 1996; Beck, 1998). The wide array of microhabitats associated with this intertidal woodground (e.g. protected and unprotected flat surfaces, eroded pits and depressions, crevices and cracks in the wood proper, protected nooks at limb branching, etc.) offers a heterogeneous habitat not commonly available on beach habitats. In addition to crevice dwellerings (e.g. small anenomes, isopods, nudibranchs) where dehydration is limited because of protection within narrow, water-retaining nooks, the pulmonate snail *Siphonaria pectinata* is a common surface resident on these wood habitats. The periwinkle *Littorina ziczac* is also occasionally found on these wood substrata, usually aligned within surface fissures or cracks. *L. ziczac* is more common in regions south of Georgia (Ruppert and Fox, 1988).

We know of no comparable qualitative effort to survey the coastal marine invertebrate fauna of a Georgia barrier island, thus making direct comparisons difficult. Nevertheless, to obtain some notion of faunal overlap, we performed a Bray-Curtis similarity index comparing our data set with the summative set of Howard and Frey (1975). The authors performed their own survey, but added the taxa also found by Heard and Heard (1971) and Dörjes (1977). In all, Howard and Frey (1975) listed 315 taxa from North and South Newport Rivers, Sapelo Island, and St. Catherines and Sapelo Sounds. The total similarity in the invertebrate faunal lists was 40%, with a total of 497 taxa identified between all studies. Differences in similarity clearly reflect differences in collection efforts, times of collections, specific collection localities, field techniques, plus the fact that Dörjes (1977) list includes shelf biota and thus deeper water species.

This study, however, represents a multiyear qualitative examination of the marine macroinvertebrate fauna of St. Catherines Island, Georgia. A quantitative beach study will be reported separately, as will a temporal quantitative study of fouling plate epifauna. It is important to note that long-term quantitative variation is common in near-shore marine and estuarine environments (Holland, 1985). Even among the dominant species recovered, temporal variation in relative abundance is a well-known phenomenon (Flint and Younk, 1983). Periodic appearances of huge numbers of the dwarf surfclam *Mulinia lateralis* and the flat-browed mud shrimp *Upogebia affinis* on the beaches of St. Catherines Island have been noted during the present study. These can result from an array of stochastic environmental changes, many of which are very short-lived (e.g. storm surges). In fact, Holland (1985) reviews some of this annual variation among shallow marine communities. For both *M. lateralis* and *U. affinis* exhumations of these types could end up depositing such large numbers of organisms on beach surfaces that desiccation and shorebird predation could impact localized populations. However, it is likely that within a brief period the high reproductive potential of these organisms will allow rapid recruitment back into the decimated region. Overall, it is important to take any biotic listing as a portion of a temporal continuum. With time, even without human inteference, environments change. Some habitats are seasonally ephemeral and organisms' life cycles are temporally suited to these local conditions. Thus, differences in species lists over the short-term could have little or no significance. However, baseline studies allow us to monitor short term changes that are natural along with environmental shifts. Perhaps more importantly, they also allow us to eventually distinguish natural from artificially induced changes if we have a sufficient temporal baseline. The possible impact of the highly active shrimping activity adjacent to these Georgia barrier islands has yet to be specifically studied for possible impact in benthic and nearby communities. Van Dolah et al. (1991), however, examined the effects of shrimp trawling on soft-bottom benthic communities along portions of the South Carolina coast. They found that there were similar species present before and after trawling, with no ''consistent differences'' in diversity, abundance or composition of pre- and post-trawling sites. They pointed out, however, that these results were for soft-bottom benthos, and other research points to significant damage when trawls are drawn over hard (epifaunal) benthic communities. Aside from oyster reefs, all natural benthic communities adjacent to and along St. Catherines Island are soft-bottom.

The listing of macroinvertebrates offered here for St. Catherines Island represents the first multiyear approximation of the diverse coastal fauna of this relatively unimpacted barrier island. Baseline qualitative studies and archival collections allow us to witness the natural or anthropogenically induced fluidity of species presence or absence over time. It is, however, imperative that we pursue additional *quantitative* assessment to monitor short-and-long term changes of macrobenthos in coastal habitats. Even in light of macrofaunal mobility and stochastic shifts in populations, the majority of organisms in coastal habitats, even variable estuarine habitats, remain stable over short periods of time (Hewitt et al., 1997). While during the course of this four-year study we found relatively few additional taxa, we have not surveyed meiofauna nor assessed the viability of individual populations through time. Recent and ongoing quantitative assessments within narrow geographic boundaries that have a wide array of relatively unspoiled habitats, though seemingly late in the game, still hold promise to offer insight into the ecology of relatively natural environments. St. Catherines Island offers this luxury and can serve as a model environment for comparative baseline studies. Ongoing quantitative studies of the island communities will allow comparisons with environmentally similar but more heavily anthropogenically impacted coastal regimes.

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REFERENCES

Beck, M.W. 1998. Comparison of the measurement and effects of habitat structure on gastropods in rocky intertidal and mangrove habitats. Marine Ecologial Progression Series 169: 165–178.

Cain, E.A. 1987. Potential effect of floating dock communities on a South Carolina estuary. Journal of Experimental Marine Biology and Ecology 108: 83–91.

Cargnelli, L.M., S.J. Griesbach, D.B. Packer, and E. Weissberger. 1999. Atlantic surfclam, *Spisula solidissima*, life history and habitat characteristics. NOAA Technical Memoires NMFS-NE-142: 13 pp.

Carr, M.R. 1997. PRIMER user manual: Plymouth routines in multivariate ecological research. Plymouth, Plymouth Research Laboratory: 91 pp.

Clark, A.H., and R.A. Lutz. 1980. Pyritization in the shells of living bivalves. Geology 8: 268–271.

Coile, N.C., and S.B. Jones, Jr. 1988. Checklist of the vascular flora of St. Catherines Island, Georgia. American Museum Novitates 2920: 1–14.

Dahlberg, M.D., and R.W. Heard, III. 1969. Observations on elasmobranchs from Georgia. Quarterly Journal Florida Academy of Sciences 32: 21–25.

Dahlberg, M.D., and E.P. Odum. 1969. Annual cycles of species occurrence, abundance, and diversity in Georgia estuarine fish populations. American Midland Naturalist 83: 382–392.

DeLillo, N.J. 1998. Iron sulfide formation and the in vivo pyritization of *Mercenaria mercenaria* (Linnaeus) in the salt marshes of St. Catherines Island, Georgia. Ph.D. dissertation, University of Pittsburgh, 349 pp.

Dörjes, J. 1971. Georgia coastal region, Sapelo Island, U.S.A.: sedimentology and biology. VII. Distribution and zonation of macrobenthic animals. Senckenbergiana maritima 4: 183–216.

Dörjes, J. 1977. Marine macrobenthic communities of the Sapelo Island, Georgia Region. *In* B. C. Coull (editor), Ecology of Marine Benthos: 399–421. Colombia: University of South Carolina Press.

Fierstien, J.F., and H.B. Rollins. 1987. Observations on intertidal organism associations of St. Catherines Island, Georgia. II. Morphology and distribution of *Littorina irrorata* (Say). American Museum Novitates 2873: 1–31.

Fletcher, W.J., and A.J. Underwood. 1987. Interspecific competition among subtidal limpets: effects of substratum heterogeneity. Ecology 68: 387–400.

Flint, R.W., and J.A. Younk. 1983. Estuarine benthos: long-term community structure variations, Corpus Christi Bay, Texas. Estuaries 6: 126–141.

Fox, R.S., and E.E. Ruppert. 1985. Shallow-water Marine Benthic Macroinvertebrates of South Carolina: species identification, community composition and symbiotic associations. Belle W. Baruch Library in Marine Science 14: 329 pp.

Frey, R.W., and P. B. Basan. 1981. Taphonomy of relict Holocene salt marsh deposits, Cabretta Island, Georgia. Senckenbergiana maritima 13: 111–155.

Frey, R.W., and J.D. Howard. 1988. Beaches and beach-related facies, Holocene barrier islands of Georgia. Geologial Magazine 125(6): 621–640.

Goodfriend, G.A., and H.B. Rollins. 1998. Recent barrier beach retreat in Georgia: Dating exhumed salt marshes by aspartic acid racemization and post-bomb radiation. Journal of Coastal Research 14(3): 960–969.

Haila, Y., and J. Kouki. 1994. The phenomenon of biodiversity in conservation biology. Annales Zoologici Fennici 31: 5–18.

Haila, Y., and C.R. Margules. 1996. Survey research in conservation biology. Ecography 19: 323–331.

Hewitt, J.E., R.D. Pridmore, S.F. Thrush, and V.J. Cummings. 1997. Assessing the short-term stability of spatial patterns of macrobenthos in a dynamic estuarine system. Limnology and Oceanography 42(2): 282–288.

Holland, A.F. 1985. Long-term variation of macrobenthos in a mesohaline region of Chesapeake Bay. Estuaries 8: 93–113.

Howard, J.D., and J. Dörjes. 1972. Animal-sediment relationships in two beach-related tidal flats; Sapelo Island, Georgia. Journal of Sedimentary Petrology 42: 608–623.

Howard, J.D., and R.W. Frey. 1975. Estuaries of the Georgia coast, U.S.A.: sedimentology and biology. II. Regional animal-sediment characteristics of Georgia estuaries. Senckenbergiana maritima 7: 33–103.

Howard, J.D., and H.E. Reineck. 1972. Georgia coastal region, Sapelo Island, U.S.A.: sedimentology and biology. VIII. Conclusions. Senckenbergianna maritima 4: 217–222.

Kennedy, S.K., and R. Pinkoski. 1987. Source of tidal creek sand on a tide-dominated Barrier island, St. Catherines Island, Georgia –Fourier shape analysis. Journal of Coastal Research 3: 475–483.

Knott, D.M., D.R. Calder, and R.F. Van Dolah. 1983. Macrobenthos of sandy beach and nearshore environments at Murrels Inlet, South Carolina, U.S.A. Estuarine Coastal and Shelf Science 16: 573–590.

Morris, R.W., and H.B. Rollins. 1977. Observations on intertidal organism associations on St. Catherines Island, Georgia. I. General description and paleoecological implications. Bulletin of the American Museum of Natural History 159(3): 87–128.

Oertel, G. F. 1977. Geomorphic cycles in ebb deltas and related patterns of shore erosion and accretion. Journal of Sedimentary Petrology 47: 1121–1131.

Oertel, G.F., and J.D. Howard. 1972. Water circulation and sedimentation at estuary entrances of the Georgia coast. *In* D.J.P. Swift, D.B. Duane, and O.H. Pilkey (editors), Shelf sediment transport: process and pattern: 411–427. Stroudsburgh, PA: Dowden, Hutchinson and Ross.

Pottinger, J.E. 1996. Origin and development of beach ridges on St. Catherines Island: Impact of storm events. M.S. thesis, University of Pittsburgh, 101 pp.

Prezant, R.S. 1980. An antipredator mechanism of the polychaete *Phyllodoce mucosa* with notes on similar mechanisms in other potential prey. Fisheries Bulletin 77: 605–616.

Rakocinski, C., R.W. Heard, T. Simons, and D. Gledhill. 1991. Macroinvertebrate associations from beaches of selected barrier islands in the northern Gulf of Mexico: important environmental relationships. Bulletin of Marine Science 48(3): 689–701.

Rollins, H.B., R.R. West, and R.M. Busch. 1990. Hierarchical genetic stratigraphy and marine paleoecology. *In* W. Miller, III (editor), Paleocommunity temporal dynamics: the long term development of multispecies assemblagies. Paleontological Society Special Publication. 5: 273–308.

Rollins, H.B., and R.R. West. 1997. Taphonomic constraints on even horizons: Short-term averaging of *Anadara brasiliana* valves, St. Catherines Island, Georgia. *In* C.C. Brett and G.C. Baird (editors), Paleontological events: stratigraphic, ecological, and evolutionary implications: 41–56. New York: Columbia University Press.

Ruppert, E.E., and R.S. Fox. 1988. Seashore Animals of the Southeast. Columbia: University of South Carolina Press, 429 pp.

Schlesinger, R.C., D.T. Funk, P.L. Roth, and C.C.

Myers. 1994. Assessing changes in biological diversity over time. Natural Areas Journal 14: 235–240.

Sherrod, B.L., H.B. Rollins, and S.K. Kennedy. 1989. Subrecent intertidal diatoms from St. Catherines Island, Georgia: taphonomic implications. Journal of Coastal Research 5: 665–667.

Skoog, S.Y. 1996. Feeding mechanisms, food acquisition, and habitat selection of *Caprella equilibra* and *Paracaprella tenuis*, at St. Catherines Island, Georgia. M.S. thesis, Indiana University of Pennsylvania, 83 pp.

Sutherland, J.P., and R.H. Karlson. 1977. Development and stability of the fouling community at Beaufort, North Carolina. Ecolological Monographs 47: 425–446.

Thomas, D.H., G.D. Jones, R.S. Durham, and C.S. Larsen. 1978. The anthropology of St. Catherines Island. I. Natural and cultural history. Anthropology Papers of the American Museum of Natural History 55: 155–248.

Van Dolah, R.F., P.H. Wendt, and M.V. Levisen. 1991. A study of the effects of shrimp trawling on benthic communities in two South Carolina sounds. Fisheries Research 12: 139–156.

Walker, R.L., and P.B. Heffernan. 1990a. Intertidal growth and survival of northern quahogs *Mercenaria mercenaria* (Linnaeus 1758) and Atlantic surf clams *Spisula solidissima* (Dillwyn 1817) in Georgia. Journal of the World Aquaculture Society 21(4): 307–313.

Walker, R.L., and P.B. Heffernan. 1990b. Plastic mesh covers for field growing of clams, *Mercenaria mercenaria* (L.), *Mya arenaria* (L.) and *Spisula solidissima* (Dillwyn), in the coastal waters of Georgia. Georgia Journal of Science 48: 88–95.

Walters, L.J., and D.S. Wethey. 1996. Settlement and early post-settlment survival of sessile marine invertebrates on topographically complex surfaces: the importance of refuge dimensions and adult morphology. Marine Ecolological Progress Series 137: 161–171.

Wilson, E.O. 1992. The diversity of life. Cambridge, MA: Harvard University Press.

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