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## Distribution of Ghost Shrimp; North Beach, St. Catherines Island, Georgia

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### ABSTRACT

The Carolinian Ghost Shrimp (*Callichirus major* Say 1818) inhabits the open sandy beaches of the Sea Islands of Georgia. Burrows of this fossorial thalassinidean are distributed along the foreshore from just above mid-tide level to the shallow subtidal, forming a narrow band of high-density burrow apertures called the burrow strand. Burrow distribution along North Beach was investigated by random quadrat sampling every 7.5 m from high-tide line to low-tide line for 4 km along transects spaced 100 m apart. The burrow strand has a steep shoreward (and a gentler seaward) gradient and exhibits variable densities along its length, peaking at approximately 15 burrows/m<sup>2</sup>. The Georgian Ghost Shrimp (*Callianassa biformis* Biffar 1970) inhabits sheltered, rippled, muddy-sand tidal flats in the lower foreshore, usually bordering sounds between the Sea Islands on the Georgia

coast. Burrows are distributed as a burrow strand parallel to the shore, but are somewhat more diffuse than those of the Carolinian Ghost Shrimp and reach much higher maximum densities (up to 483 burrows/m<sup>2</sup>). In unstable substrates burrow density of the Carolinian Ghost Shrimp is highly variable and generally reduced. Relict marsh muds, appearing along the lower beach of the erosive front of St. Catherines Island, prevent colonization of such areas by this animal. Burrow distribution is controlled shoreward by length of exposure, seaward by predation, and laterally by substrate grain size and stability. Use of Ghost Shrimp burrows in interpretation of the geologic record should be done with great caution because a broad spectrum of burrow morphologies can be produced by a single species and many species produce similar burrows.

### INTRODUCTION

Fossorial (burrowing) shrimp are among the most abundant and common macroinvertebrates in some modern environments,

but are seldom seen because of their infaunal, subterranean mode of life. Yet in the fossil record, callianassid claws and chelipeds are

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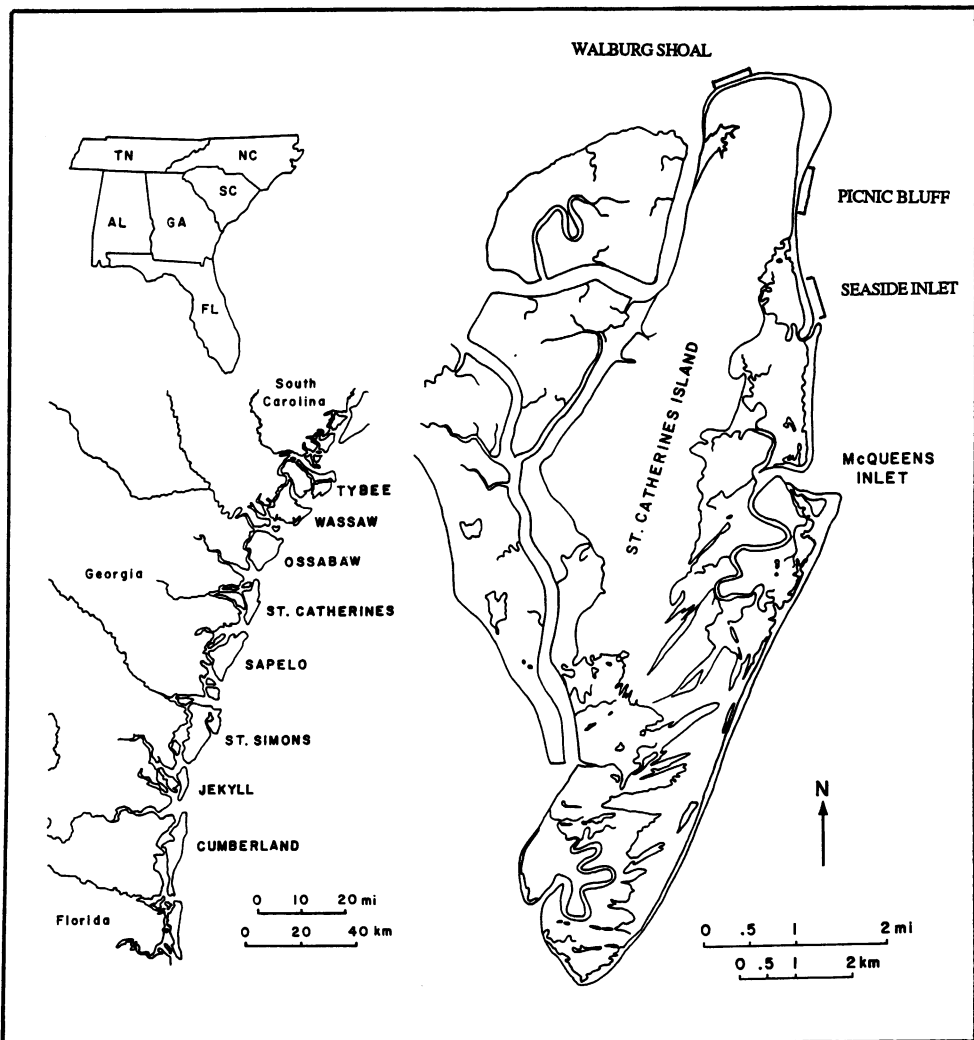


Fig. 1. Index map of the southeastern United States, Georgia coast, and St. Catherines Island, Georgia. (from Shadrui, 1990)

among the most common and abundant remains of decapod crustaceans. Research on the Carolinian Ghost Shrimp (*Callichirus major* Say 1818) was initiated in August of 1987, in order to assess that species' applicability as a model which could be used to compare fossil Cretaceous and Tertiary callianassid claws. This research was subsequently enlarged to include *Callianassa bifurmis* Biffar 1970, when it became apparent that the burrow distributions of these two species overlapped. The present research program originated as an investigation of the range of claw morphology exhibited by the

Carolinian Ghost Shrimp; it evolved into a study of the relative sizes, distribution, and ecology of Ghost Shrimp on three Georgia barrier islands, Tybee, St. Catherines, and St. Simon's (fig. 1).

The Carolinian Ghost Shrimp (fig. 2) was described and named *Callianassa major* by Say in 1818. Stimpson (1866) established a new genus, *Callichirus*, with *Callianassa major* as its type species. Manning and Felder (1986, 1991) reviewed the systematic usage of this species, indicating that it was considered by various authors to be a subgenus of *Callianassa*, a separate new genus, or a syn-

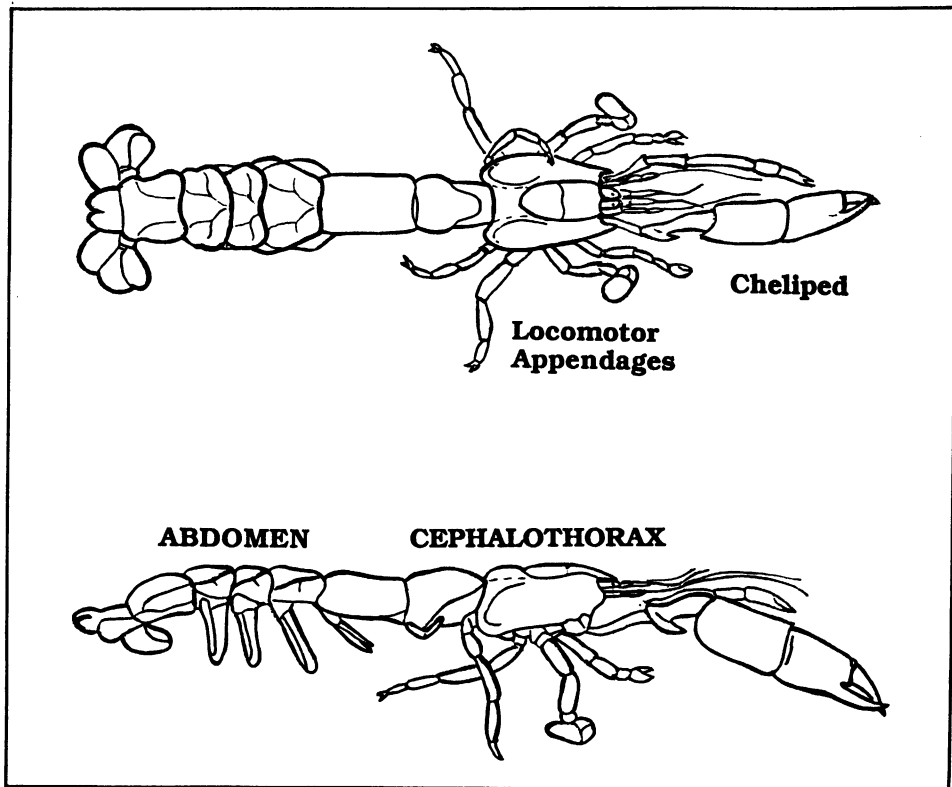


Fig. 2. General morphology of the Ghost Shrimp as depicted in dorsal and lateral views. (after Biffar, 1971)

onym of *Callianassa*. In a major systematic revision, Biffar (1971) reviewed its relationships to other callianassids of the southeastern United States. Manning and Felder (1986) reassigned it to *Callichirus*. Aspects of the ecology of the Carolinian Ghost Shrimp have been described by Lutz (1937), Pearse et al. (1942), Pohl (1956), Pryor (1975), Rodrigues (1976), Rodrigues and Suguio (1984), Rodrigues and Shimizu (1986), Rodrigues et al. (1986a, 1986b), Williams (1984), and Frey et al. (1978). Carolinian Ghost Shrimp were reported to reach densities of 1780 animals per acre on South Carolina beaches (Pohl, 1946: 75). They occur from Beaufort Inlet, North Carolina to Santa Catarina, Brazil (Rodrigues, 1983). Swinbanks and Leuternauer (1987) described the distribution of burrows of two other thalassinidean shrimp, *Callianassa californiensis* and *Upogebia pugetensis*, on the delta of the Fraser River. They reported the burrows to be segregated by sed-

iment type and that those of *C. californiensis* reached maximum densities of 350–450 burrow openings/m<sup>2</sup> at low intertidal levels.

The Georgian Ghost Shrimp, *Callianassa biformis*, described by Biffar (1970) from the south end of Sapelo Island, McIntosh County, Georgia, is known from South Carolina to Georgia but probably has a more extensive range. This diminutive ghost shrimp is commonly found from mid to low-tide levels in protected areas behind sand bars associated with sound channels where it burrows shallowly into ripple-marked muddy sand flats. Populations have been observed on the south end of Sapelo Island (type locality), on the south end of St. Simon's Island, on the north end of St. Catherines Island (this study), on the northern part of the McQueen Inlet ebb delta on St. Catherines Island, and at the mouth of Big Bay Creek, Edisto Island, South Carolina.

### ACKNOWLEDGMENTS

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### NATURAL HISTORY

#### DESCRIPTION

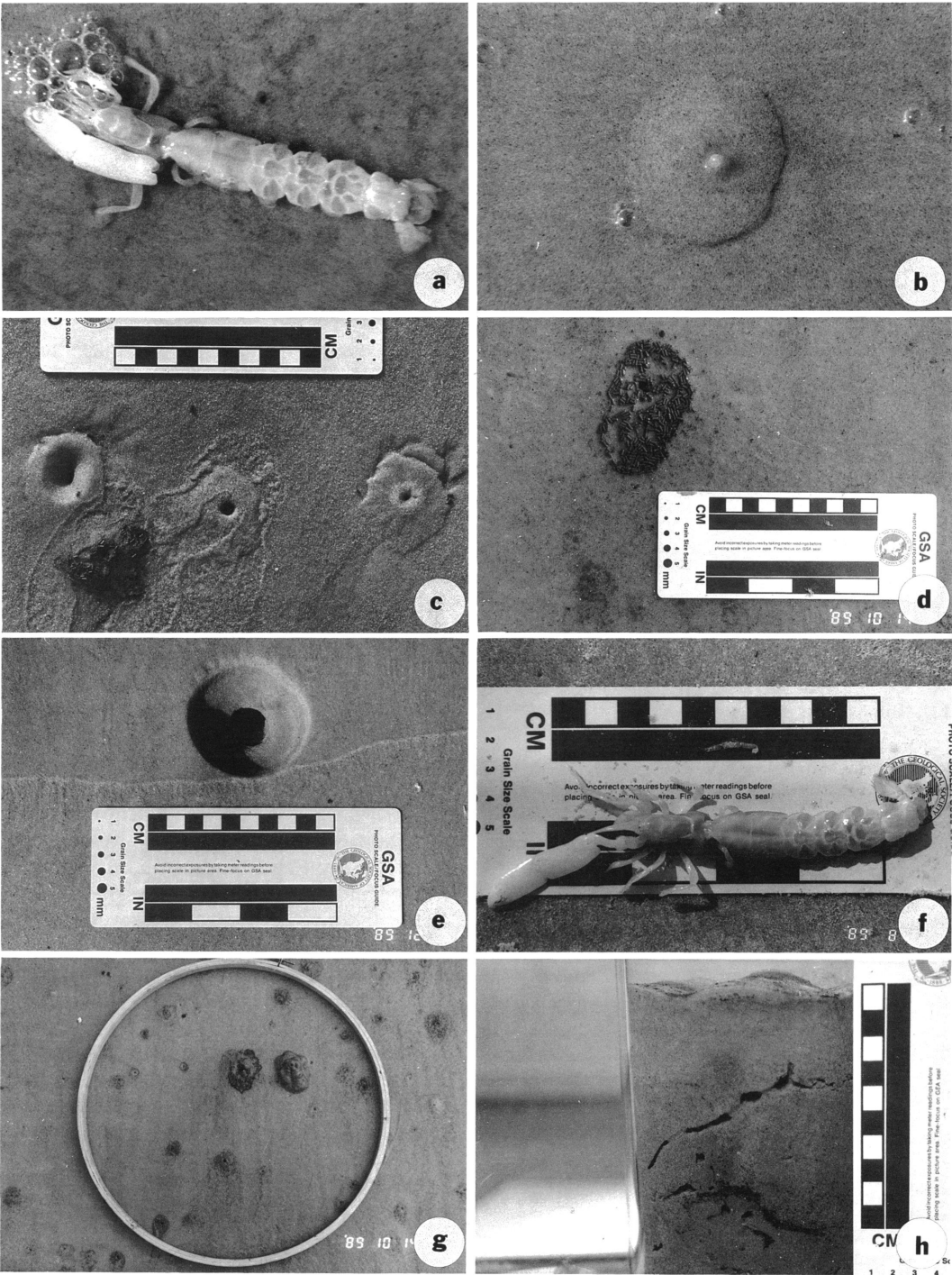
*The Carolinian Ghost Shrimp* is a medium-sized (30–100 mm) decapod crustacean beautifully adapted to its burrowing mode of life (fig. 2). The pale animal is elongate, dorsoventrally flattened, cylindrical, and lightly mineralized (fig. 3a). The cuticle is thin and flexible over most of its body which consists of a short cephalothorax, appendages, and an elongate abdomen. The cephalothorax is lightly sclerotized and flexible except for the anterior of the dorsal shield which forms a hardened dorsal disk. The locomotor appendages are attached to the sternum beneath the animal's carapace and consist of the

heavily mineralized chelipeds with well-developed claws and four pairs of locomotor appendages, the last much reduced and not fused to the other sternal somites. The abdomen consists of two very soft and flexible segments with very reduced pleopods used for reproduction, followed by three more highly mineralized segments with well-developed diaphragm-like pleopods, in turn followed by the hardened sixth segment and telson with attached uropods forming a tail fan.

The Carolinian Ghost Shrimp spends most of its life burrowed into the sand of beaches and sand flats (fig. 4) fronting the open ocean. Its presence on a beach is indicated by holes marking burrow mouth apertures (fig. 3c), which often exhibit water spouts or sand floods (fig. 3b) temporarily accumulating as volcano-like mounds (fig. 3c) often ringed by extruded rod-shaped black fecal pellets composed of mud (fig. 3d). Collapsed burrows (fig. 3e) occasionally form as the unstable beach sand caves into, or washes into, the underlying burrow. Few observations have been made of the animal outside its burrow (Pohl, 1946: 78; E. C. Bishop, 1988). The animal apparently feeds on detritus and particulates in water pumped through its burrow. It periodically extrudes masses of rod-shaped, cylindrical, channeled fecal pellets consisting largely of mud containing 3–10% organic carbon (Pryor, 1975: 1246). The composition of the fecal pellets indicates that these animals are actively ingesting large quantities of mud from some source. Because the open beach consists mostly of well-sorted quartz sand, the animal must ingest these large quantities of mud from the turbid coastal water being pumped through their burrows. The production of fecal pellets is copious and may result in the accumulation of stringers of pellets in ripple or runnel troughs and eventually in layers of mud in environments otherwise

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Fig. 3. Ghost Shrimp from St. Catherines Island, Georgia. **a**, Dorsal view of male Carolinian Ghost Shrimp (*Callichirus major*) released in beach runnel; **b**, Carolinian Ghost Shrimp burrow mouth on North Beach showing a flood of sand being pumped onto the beach by a ghost shrimp; **c**, four active burrows on North Beach showing open burrow mouths, sand mounds, and a ring of fecal pellets of Carolinian Ghost Shrimp; **d**, burrow mouth of Carolinian Ghost Shrimp showing sand mound capped by a ring of rod-shaped fecal pellets; **e**, collapsed mouth of Carolinian Ghost Shrimp burrow indicating diameter of major shaft; **f**, lateral view of Georgian Ghost Shrimp (*Callinassa biformis*) above a



Carolinian Ghost Shrimp to illustrate the difference in size of adults; g, active burrows of Georgian Ghost Shrimp on Walburg Creek Shoal showing great density, tiny size, and abundant fecal pellets (hoop diameter = 36 cm); h, active burrows of Georgian Ghost Shrimp (*Callianassa biformis*) in fossoria in aquarium.



Fig. 4. Photograph of *Callichirus major* burrow strand looking north at low tide along North Beach at Picnic Bluff, St. Catherines Island; 10 cm scale in foreground.

characterized by sand-sized quartz (Howard and Reineck, 1972: 92; Pryor, 1975).

Large numbers of Carolinian Ghost Shrimp were collected during single years on Tybee, St. Catherines, and St. Simon's islands, using a Yabby Bait Pump (Manning, 1975). These samples were analyzed by students Mike Klug and Ginny Millar at Georgia Southern College for completion of senior thesis requirements; specimens exhibited similar patterns of population structure, sexual composition (70% female, 30% male), and relative proportions of right and left handedness (52% left, 48% right). The lack of small juveniles (fig. 5) seems to indicate that recruitment occurs at a size of about 20 mm. However sampling along beach transects has demonstrated that specimens on the lower part of the beach consist primarily of smaller animals as well as a few large males. This pattern may indicate that larval animals settle and live subtidally. Posey (1986) demonstrated that the seaward edge of the distribution of *Callinassa californiensis* on the mid-tidal zone in Oregon was controlled by fish predation. Predation by sting rays may control the distribution of Carolinian Ghost Shrimp in Georgia, as well as recruitment of juveniles

into the populations. Thompson and Pritchard (1969), Swinbanks and Murray (1981), and Swinbanks and Luternauer (1987) stated that the upper limit of the distribution of *C. californiensis* is controlled by critical tide level which exposes the burrows for 3.2 to 7.8 days leading to anoxia in the burrow waters. Felder and Lovett (1989) described the habitat and some ecological parameters of *Callinassa louisianensis* Schmitt, 1935, in the northern Gulf of Mexico and mentioned that that species is included in the diet of the Whooping Crane.

Carolinian Ghost Shrimp reproduce sexually. The mechanism of sperm transfer is not known. Egg masses developing in the ovaries in the cephalothorax and abdomen are visible in the females throughout the fall and winter. In the spring (about mid-March) females begin to lay their eggs and carry the egg masses throughout the summer attached to the pleopods of their abdomens, primarily of the first two abdominal somites. The eggs hatch and the larvae enter a planktonic existence as is indicated by their abundance in plankton samples. Larval settlement into the substrate is an unknown process.

Samples collected on the Georgia coast have

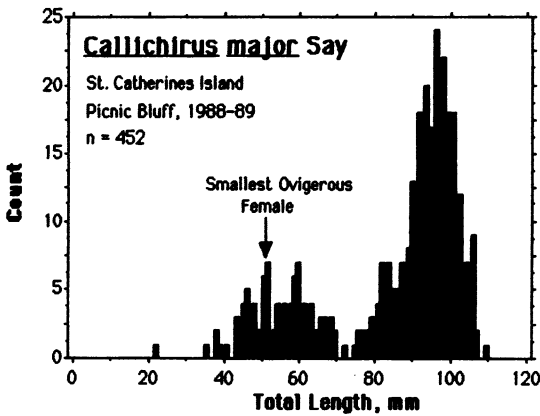


Fig. 5. Histogram of total length (rostrum to telson) of 452 specimens of *Callinectes major* collected at Picnic Bluff during 1988-89.

usually included a commensal crab, *Pinnixa cristata* Rathbun, which is very small, transversely elongate, and obviously adapted to cohabiting the burrows of Carolinian Ghost Shrimp. When females are ovigerous, small amphipods have been observed in the egg masses, presumably feeding on the eggs. Pohl (1946: 78) cited the presence of a bryozoan, *Acanthodesia tenuis* (Desor), encrusting the burrow wall and reiterated the observation made by Pearse in 1939, and by herself in 1944, of a small red commensal copepod, *Clausidium dissimile* Wilson, suggesting it might be the "curious parasite" found by Say (1818).

The burrowing mode of life has made Carolinian Ghost Shrimp difficult to capture and study. Previously they had to be captured by digging them out of the sand, cutting off their escape by blocking their burrow with a long spade, or tricking them by dropping sand or shell into the upper part of their burrow (Pohl, 1946: 71). The availability of a suction device called a Yabby Pump has revolutionized the sampling of fossorial infauna, allowing rapid capture of large samples (Manning, 1975: 318).

The Georgian Ghost Shrimp (*Callinassa biformis* Biffar 1970) resembles the Carolinian Ghost Shrimp but is differentiated by specific morphological details and by its much smaller size (fig. 3f). Ecologically the Georgian Ghost shrimp tends to inhabit lower intertidal sand flats in sheltered areas which are typically rippled, and contain a considerable

proportion of substratal mud. It is generally associated with abundant acorn worms, mud snails, hermit crabs, and other invertebrates. The burrows of the Georgian Ghost Shrimp are smaller, apparently shallower, and found in great densities of up to 483 burrows/m<sup>2</sup> on St. Catherines Island (fig. 3g, h).

The ecological ranges of Carolinian and Georgian Ghost Shrimp overlap on such sheltered tidal flats, although the respective burrows appear to be of different depth, effectively partitioning them from one another.

#### BURROWS

When removed from the substrate and released on an open sand surface, Carolinian Ghost Shrimp immediately begin to burrow, entering the substrate laterally, and disappearing beneath the surface within a few minutes. Placement of animals in aquaria (Pohl, 1946; GAB, this study) and in ant-farm-like frames (fossillorium) (Pohl, 1946) allowed the burrowing process to be studied in detail. Once beneath the sand, the Carolinian Ghost Shrimp constructs a widened area called a turnaround which allows the animal to reorient in order to more efficiently remove sand from the burrow (fig. 6). The burrow is then commonly constructed with several branches from the turnaround, some horizontal and some inclined at a steep angle to the horizontal. Carolinian Ghost Shrimp burrows in analogous Pleistocene ancient barrier island sediments (Howard and Scott, 1983: 176) indicate the burrows extend 3-5 m into the beach. Ancient burrows of analogous, but not necessarily conspecific, ghost shrimp from more ancient sediments (fig. 7) preserve similar morphologies and are assignable to the ichnogenus *Ophiomorpha*. Carolinian Ghost Shrimp burrows on the beach consist of three major parts: (1) a vertical upper constricted burrow aperture, (2) a nearly vertical main shaft, and (3) one or more approximately horizontal burrow mazes. The upper constricted burrow aperture is vertical, about 5 mm in diameter, and usually about 15-20 cm in length. It opens into the main burrow shaft which is vertical to inclined, several meters in length, and about 1-2 cm in diameter with periodic enlarged turnarounds and numerous horizontal and/or inclined branches. The lower part of the burrow is thought to consist of anastomosing, inter-





Fig. 6. Female Carolinian Ghost Shrimp turning around in turnaround chamber in aquarium. Rear of cephalothorax and thoracopods are visible at top and tucked-under abdomen below. Anterior of animal is to the right. Scale bar  $\approx$  1 cm.

connected, horizontal tunnels. Rodrigues and Suguio (1984) found close correlation between the size of the burrow and the size of the animal inhabiting it. Felder (personal commun.) has correlated the number of surficial burrow apertures with the number of burrow shafts to establish a closer estimate of the true population density. Ghost Shrimp probably spend most of their time in the lower part of the burrow, occasionally rising in the shafts to eliminate sand or waste. In unconsolidated sand the animal lines the burrow with a mucal-mud binding agent, packing mucus-laden pellets into the burrow walls, building a considerable burrow wall thickness, and imprinting a knobby texture onto the exterior of the burrow. When lithified, these burrows are assigned to the ichnogenus *Ophiomorpha*. Burrow morphology can vary dramatically in different sediment types as well as interspecifically (Frey et al., 1978). We emphasize that many burrow morphologies are constructed by a single species and similar

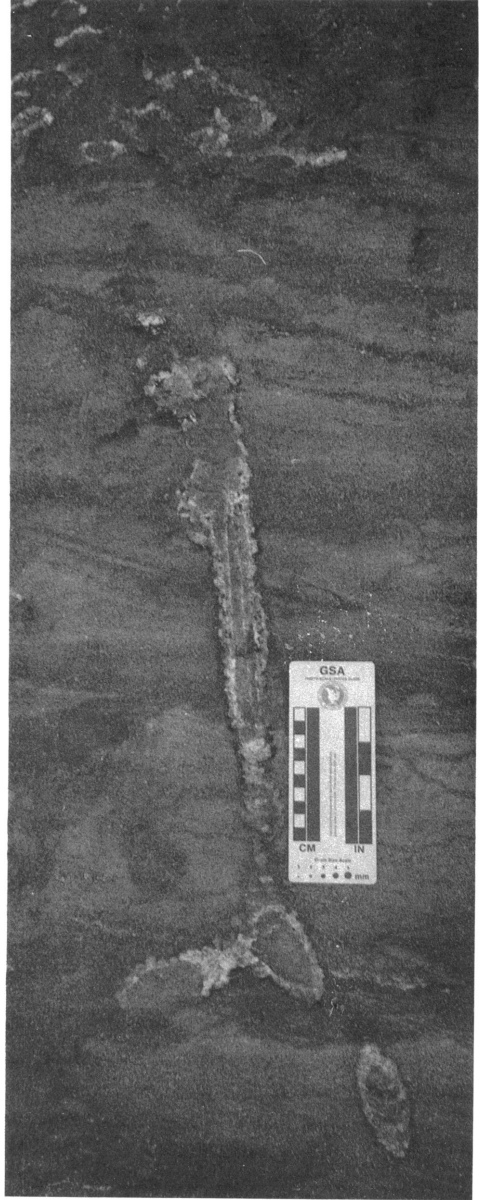


Fig. 7. Fossilized ghost shrimp burrows, assignable to the ichnogenus *Ophiomorpha*, exposed in a road cut through Eocene Tobacco Road Formation along Old River Road, Burke County, Georgia. Notice the vertical shaft parallel to the scale (10 cm on left) giving way to a turnaround and a more or less horizontal burrow branch at the bottom. Horizontal branches of other burrows show as oval or circular cross sections.



burrow morphologies are constructed by different species. Burrows occasionally collapse, forming chevronlike sedimentary structures (Frey et al., 1978). When erosional conditions scour a beach containing Carolinian Ghost Shrimp burrows, the burrows may be eroded to a level where the beach surface intersects the main shafts. When this occurs the main shaft is plugged and abandoned or a small, inclined shunt is constructed to the beach surface (Frey et al., 1978).

The burrows of different ghost shrimp species exhibit morphologies ranging from solitary burrows to communal burrow systems (Frey et al., 1978), necessitating great caution when interpreting Holocene and ancient ecological data (e.g., the interpretation of the ecology of *Callichirus major*, if based on what is known about the ecology of *Callianassa californiensis*, would lead to largely erroneous conclusions). Erickson and Sanders (1991) described Pleistocene burrows of the ghost shrimp, *Callichirus major*.

#### BURROW DISTRIBUTION

The density and distribution of burrows of the Carolinian Ghost Shrimp have been described by Pohl (1946), Pryor (1975), and Eric Bishop (1988). Pohl (1946: 74) found the maximum burrow density to lie just above mid-tide level "... in the quarter of the beach between the half-way and three-fourths mark. . ." Pryor (1975) cited Ghost Shrimp burrow mouth densities of up to 450/m<sup>2</sup> in tidal pools and protected shores of the Mississippi Sound [although these probably belonged to a smaller ghost shrimp such as *Callianassa biformis*]. Eric Bishop (1988) surveyed and contoured the distribution of Carolinian Ghost Shrimp burrow mouths on beaches at Tybee, St. Catherines, and St. Simon's islands, concluding that maximum burrow mouth development occurs on stable beaches just above mid-tide level. His study demonstrated variation in burrow distribution across and along the beach. The burrow density increases rapidly from 0 bpm<sup>2</sup> to a maximum just above the mid-tide level then decreases slowly to low densities along the low water level. The zone of highest density generally follows the beach trend just above mid-tide level, but this position changes with

physical conditions such as revetments, beach slope, steep sound channel walls, or presence of relict marsh sediment under the beach surface. The density of burrows varies along the beach, building into hill-like local density maxima separated by saddlelike minima but burrows are always present except where excluded by sedimentological factors cited above. On disturbed beaches (renourished beaches and ebb deltas) burrow density generally decreases dramatically: the distribution pattern broadens and becomes more dispersed. On normal, open oceanic beaches the burrow distribution occupies a continuous narrow zone about 50 m wide along the beach from below low-water level to just above mid-tide level. When contoured and plotted on a true scale map this pattern is stringlike, hence it can be referred to as the *burrow strand*.

The subtidal occurrence of the Carolinian and Georgian Ghost Shrimp has not been investigated in this project because turbid water conditions prohibit subtidal sampling. Reports from the literature (Dörjes, 1972; Frey et al., 1978) indicate that the Carolinian Ghost Shrimp occurs subtidally to a depth of a few meters on the forebeach and on shallow shoals.

Monitoring burrow mouth density on St. Catherines and St. Simon's islands over a two-year period has demonstrated the stability of the density distribution patterns. Only minor fluctuations were observed in burrow mouth density patterns except for one small area on North Beach, St. Catherines Island. That area, apparently underlain by relict marsh and veneered by beach sand (Morris and Rollins, 1977), experienced a dramatic decrease in burrow density from 1988 to 1989 over a 100 m stretch of beach. A general decrease in burrow density was observed over the same period on North Beach at St. Catherines and Old Village Beach at St. Simon's Island.

Burrows of the Georgian Ghost Shrimp (*Callichirus biformis*) are much smaller, typically ringed by muddy sand mixed with fecal pellets, and have smaller fecal pellets (fig. 4g). Depth (based on success in extracting these animals from shallow depths with a Yabby Pump and observation in an aquarium, fig. 3h) appears to be much less than that of *Callichirus major*. Burrow density data from the

north end of St. Catherines Island (fig. 11) indicate that the density increases from 0 bpm<sup>2</sup> just above the mid-tide line to 483 bpm<sup>2</sup> just above the low-tide line with a lateral distribution of abundant Georgian Ghost Shrimp along the shore for 700 m in an elongate hill-like pattern. The pattern of distribution appears to depend more on the presence of mud in the substrate than on other physical parameters.

## METHODOLOGY

### MAPPING BURROW DISTRIBUTION

A survey was made (fig. 8) on North Beach, St. Catherines Island, by using an iron stake near Picnic Bluff as a beginning point (point 0) from which 100 m intervals were surveyed to the north and to the south using a 100 m fiberglass tape. Points on the beach at high tide line were numbered 0, 1N, 2N, . . . , 20N and 0, 1S, 2S, . . . , 27S. Starting at the high-tide line (HTL), beach transects (called Line 0, Line 1N, etc.) were established at each of the surveyed points and laid out perpendicular to the shoreline across the beach from the high-tide line to the low-tide line. Stations were established at 7.5 m intervals along each line beginning at high-tide line (Station 1) and extending to the low-water level (both high- and low-tide levels fluctuate from day to day but are roughly comparable as all surveys were done during spring tides).

The highest (i.e., highest on the beach or closest to the high-tide line) Carolinian Ghost Shrimp burrow mouths were located on the beach and their position relative to the line of transect recorded. These burrows are normally easily recognized by their diameter (5 mm), by their periodic activity (water spouting, extrusion of sand floods, or extrusion of characteristic rod-shaped fecal pellets), or by their mucus lining manifested by a coherent collar of sand around the burrow mouth. Burrow occupancy was validated by periodically sampling with a Yabby Pump.

A round hoop with a  $\frac{1}{4}$  m<sup>2</sup> area was randomly tossed 16 times at each station along each transect from the first station below the highest burrow to the lowest station nearest the low-water line. Tosses were kept within half-station intervals of each point along the transect and within about 10 m of each point

along the strike direction of the beach. The 16 tosses were made in a crisscross pattern to assure four counts from each quadrant of the area around a station. Although not random in the sense of using a random number table to determine direction and distance of tosses, experience and consistency of resultant data indicate that the number of tosses and methodology more than adequately compensate for lack of randomness. Burrow density near each point was calculated by tabulating the total number of burrow mouths encircled by, or lying beneath, the hoop for each of 16 tosses and dividing the total by 4 [ $16 \text{ tosses} \times \frac{1}{4} \text{ m}^2 \text{ toss} \times \frac{1}{4} = \text{burrows/m}^2$  (bpm<sup>2</sup>)]. The data for all points along all lines were then contoured using a contour interval appropriate to the burrow density. The resultant map of burrow distribution is discussed under Results. Because of the greater density of burrows of the Georgian Ghost Shrimp it was impractical to use a  $\frac{1}{4}$  m<sup>2</sup> hoop (as it was virtually impossible to tabulate burrow counts in such a large area). Therefore, 10 tosses of a 14-in. diameter embroidery hoop having a surface area of 0.095 m<sup>2</sup> were used and the burrow density was calculated [ $10 \text{ tosses} \times 0.95 \text{ m}^2/\text{toss} \times 1/0.095 = \text{burrows/m}^2$ ].

## RESULTS

### BURROW DENSITY AND DISTRIBUTION

Carolinian Ghost Shrimp burrows on St. Catherines Island are distributed in a complex pattern that is controlled by physical conditions of exposure and substrate quality. Three detailed areas are presented here to help illustrate the distribution patterns observed on the north end of the island along North Beach (fig. 9), on Sea Side Ebb Delta (fig. 10), and on the Sound (fig. 11). On the middle and north end of North Beach, the pattern is characterized by a 2.5 km burrow strand from the Sound to the south end of the erosional bluff (Picnic Bluff) developed on the Pleistocene core of the island. Over this interval the burrow strand approximately follows the mid-tide line with a steep gradient on its shoreward side and gentler gradient on the seaward side (fig. 9). Burrow density ranges from 0 to 13.75 bpm<sup>2</sup> along the burrow strand with three nodes of max-

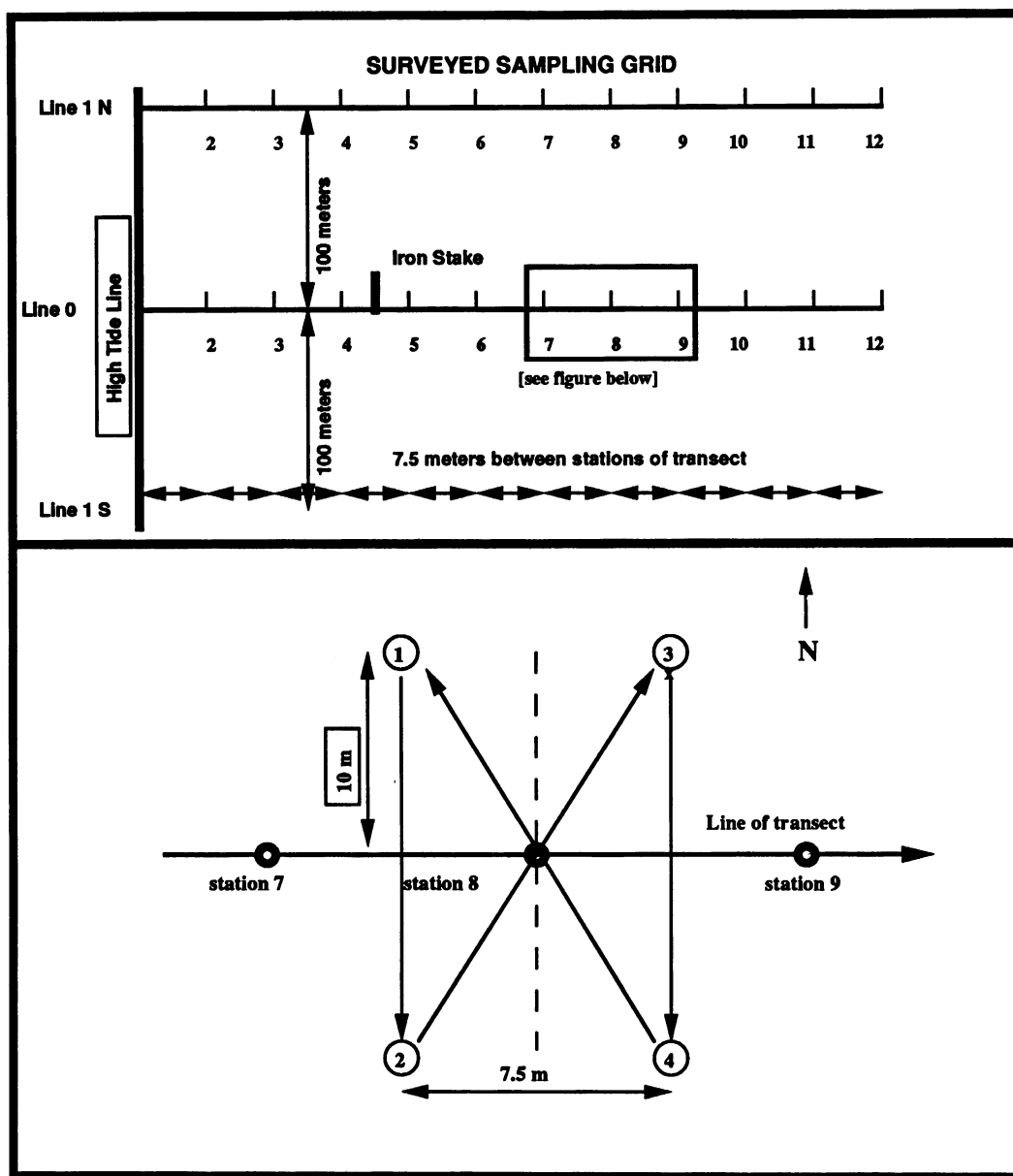


Fig. 8. Transect grid used in North Beach density surveys and hoop tossing pattern used to assure even sampling across sampling area.

imum density. Burrow density decreases dramatically at both ends of the distribution as it approaches St. Catherines Sound to the north and the relict marsh sediment exposed in front of Picnic Bluff on the older part of the island to the south. In the sound, Carolinian Ghost Shrimp are found along the steep channel wall, but are largely excluded from

the flat, rippled sandy tidal flats forming the ebb shoal along the north edge of the island. They then appear again in some abundance along the edge of the shoal near the low-water line and continue around the north end of the island where they cohabit the beach with a large population of Georgian Ghost Shrimp (*Callinassa biformis*).



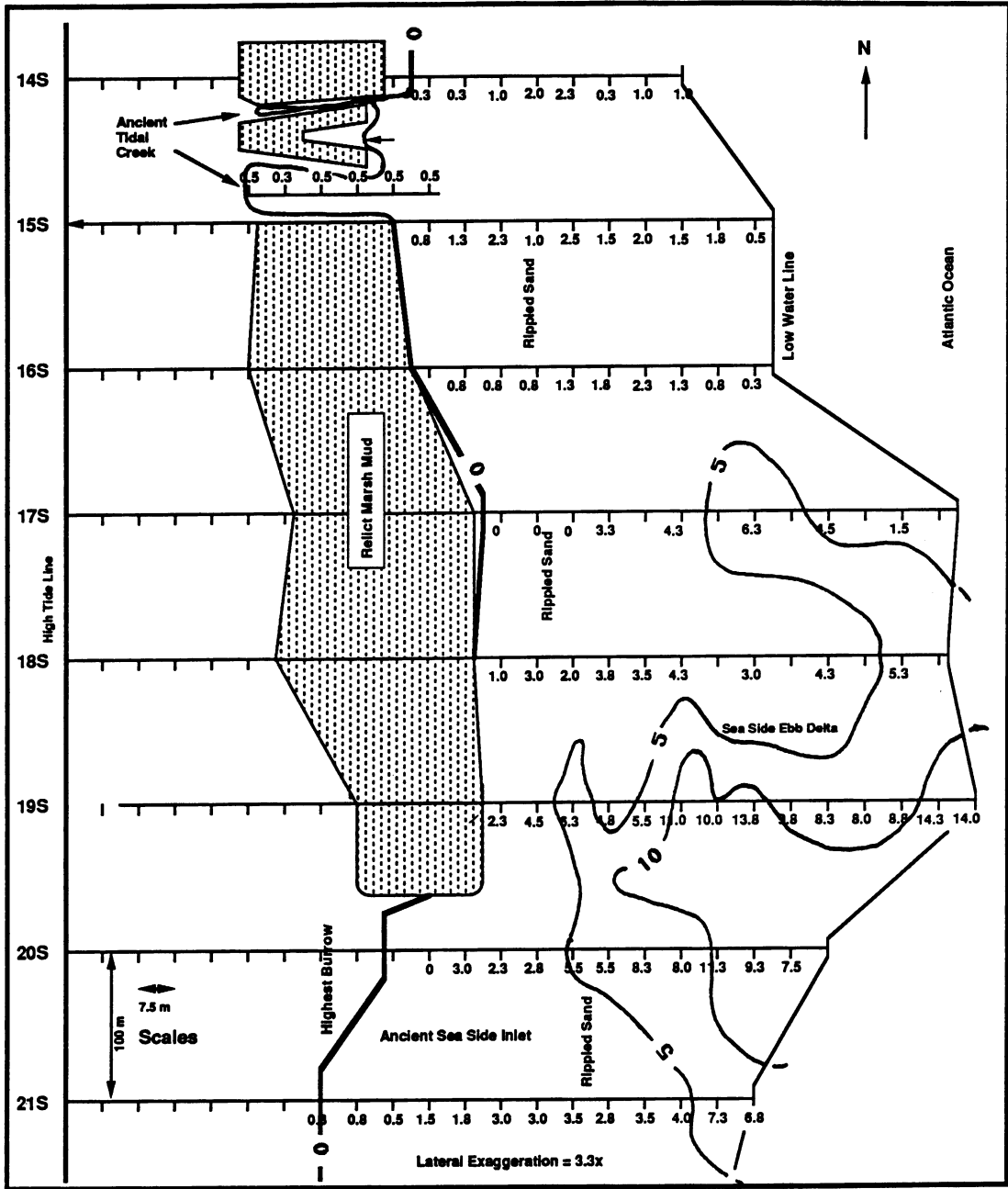


Fig. 10. Distribution of the Carolinian Ghost Shrimp (*Callichirus major*) along the south end of Black Hammock Spit and on part of Sea Side Inlet ebb delta. Relict marsh mud prevents the colonization of the mid-beach by Ghost Shrimp except while sand-filled ancient channels provide adequate substrate at the correct level. Burrow distribution on Sea Side ebb delta becomes diffuse and somewhat lowered, typical of distributions on unstable substrates. Contour interval is 5 burrows/m<sup>2</sup>. Note that the diagram is exaggerated 3.3× perpendicular to the beach.

the shore along the stretch of the Sound beach which has a muddy-sand substrate. Although present in small numbers along the entire length of the north end of the island, two major distributional peaks of Georgian Ghost Shrimp are present on sand tidal shoals at

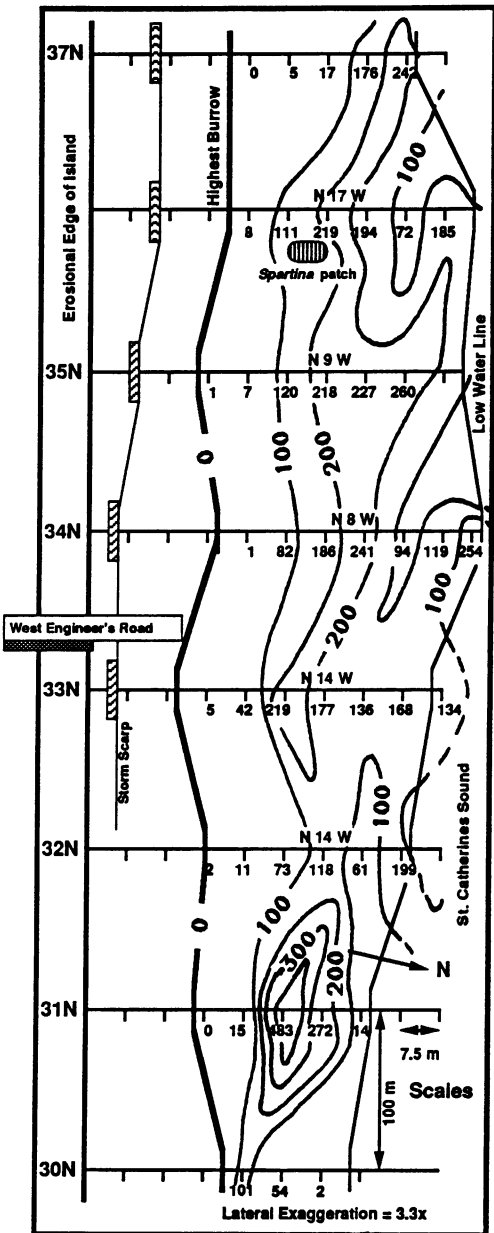


Fig. 11. Distribution of the burrows of the Georgian Ghost Shrimp (*Callinassa biformis*) on protected, rippled, muddy-sand substrate on Walburg Creek Shoal on the northwest shoulder of St. Catherines Island. The distribution of the burrows of Georgian Ghost Shrimp is tied more closely to muddy sands which tend to accumulate in current shadows on entrances to sounds. Contour interval is 100 burrows/m<sup>2</sup>. Note that the diagram is exaggerated 3.3× perpendicular to the beach.

the northwest (Engineer's Point) and the northeast "shoulders" of St. Catherines Island. The distribution at Engineer's Point (fig. 11) is well developed for over 700 m and is up to 50 m wide, consisting of three nodes of maximum density. Burrow density rapidly increases from 0 burrows/m<sup>2</sup> from just above mid-tide level to maximum densities of 483 burrows/m<sup>2</sup> just above normal low-tide level and begins to decrease more slowly to unknown densities in the subtidal waters of the Sound. The distributions of Carolinian and Georgian Ghost Shrimp overlap on Engineer's Point where Carolinian Ghost Shrimp burrows reach their highest density on the upper part of the beach and both are present on the middle and lower part of the beach.

## CONCLUSIONS

The burrows of the Carolinian and Georgian Ghost Shrimp on the north end of St. Catherines Island are characteristically distributed parallel to the strand line. These distributions can be related to available preferred substrate and to tidal exposure (fig. 12). The upper edge of the burrow strand lies just below the line of demarcation of the lowest of the monthly high-tide sequences which define long intervals of exposure twice each month. The lower edge of the burrow strand lies just below the line of demarcation of the highest low tide and just above the line of demarcation of the lowest low tide (subtidal line). This distribution pattern strongly suggests that the position of the burrow strand is controlled primarily by substrate and secondarily by length of exposure along its upper edge and perhaps by predation along its lower edge.

The following conclusions can be made regarding the distribution of ghost shrimp on St. Catherines Island:

1. The Carolinian Ghost Shrimp (*Callinectes major*) is the most abundant and nearly ubiquitous macroorganism on sandy, oceanic Georgia beaches.
2. Open ocean sand beaches are inhabited by the Carolinian Ghost Shrimp whose presence is indicated by active burrows.
3. Burrows of the Carolinian Ghost Shrimp reach their maximum density as a narrow

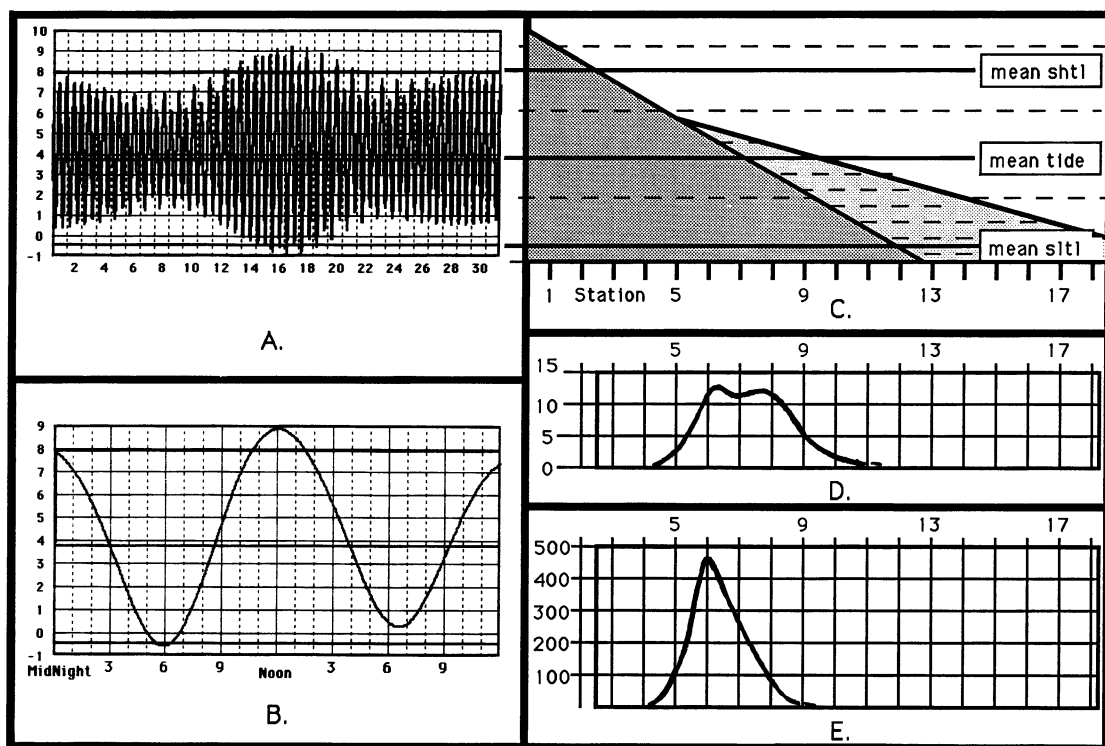


Fig. 12. Summary of distribution of St. Catherine's Ghost Shrimp relative to tidal parameters, particularly to mean lowest high spring tides (shtl) and mean highest low spring tides (sltl), and typical beach profiles on open beaches and protected tidal sand flat shoals. (A) Monthly tidal graph for September, 1989; (B) daily tidal graph for September 19, 1989; (C) idealized beach profiles for normal ocean beaches (stipple pattern) and muddy sand tidal flats (dashed stipple pattern); (D) typical abundance profile across the beach for distributions of Carolinian Ghost Shrimp (*C. major*); with number of individuals plotted on vertical axis against stations plotted on horizontal axis; and (E) typical abundance profile across the tidal flats of Georgian Ghost Shrimp (*C. bififormis*) with number of individuals plotted on vertical axis against stations plotted on horizontal axis. Tidal data produced using Nautasoft's "MacTides."

band, termed the "burrow strand," parallel to the mid-tide line on open ocean sand beaches.

4. Burrow patterns on unstable sand substrates become diffuse and generally less dense.

5. The Carolinian Ghost Shrimp is not found in areas where the beach is underlain by relict marsh muds, but Ghost Shrimp burrows may mark sand-filled ancient tidal creek channels.

6. Protected muddy, rippled sand substrates at entrances to sounds are inhabited by abundant Georgian Ghost Shrimp (*Callianassa bififormis*) whose presence is indicated by abundant, small, active burrows.

7. The distribution of the burrows of Carolinian Ghost Shrimp (*Callinectes major*) and the Georgian Ghost Shrimp (*Callianassa bififormis*) overlap.

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