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OBSERVATIONS ON THE BIOLOGY OF MUDSHRIMPS OF THE GENUS *CALLIANASSA* (ANOMURA: THALASSINIDEA) IN MISSISSIPPI SOUND[1]

by
Philip J. Phillips[2]

ABSTRACT

The apparent habitat isolation of the mudshrimps *Callianassa islagrande* Schmitt and *Callianassa jamaicense louisianensis* Schmitt (Anomura: Thalassinidea) in Mississippi Sound is a function of species-related differences in ability to burrow and survive in the significantly different substrates of each habitat. *C. islagrande* is found only in sand bottomed beaches of the offshore barrier islands, whereas *C. j. louisianensis* is found only in the muddy backwaters of the mainland and Deer Island. Both forms produce deep and extensive permanent or semipermanent burrows in their respective habitat and are probably of some significance in sediment turnover. Laboratory studies show that *C. j. louisianensis* can only burrow efficiently in mud and cannot burrow or survive in sand unless there is sufficient available mud with which this form constructs its burrow walls. The inability of *C. islagrande* to tolerate silt limits its ability to burrow and survive in mud. For this reason *C. islagrande* cannot inhabit the muddy inshore waters. The poor burrowing efficiency of *C. j. louisianensis* in sand is due to a mechanical inability to handle uncohesive sand grains. The foliaceous third maxillipeds and comparatively larger second and third pereipods of *C. islagrande* (compared with those of *C. j. louisianensis*) are adaptations to a sandy habitat, enabling greater burrowing efficiency per unit of effort. Adults and juveniles exhibited the same behavior patterns in aquarium studies. Settling juveniles probably exhibit the same behavior pattern as adults and juveniles.

INTRODUCTION

The purpose of this study was to determine whether substrate type is a factor influencing distribution of the thalassinid crustaceans, *Callianassa jamaicense louisianensis* Schmitt and *Callianassa islagrande* Schmitt, within Mississippi Sound. These forms produce extensive permanent or semipermanent burrows in the littoral and shallow neritic bottoms. Willis (1942) in a study of the mudshrimps of Grand Isle, Louisiana, found *C. islagrande* only in the clean shifting sand beaches facing the

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[1] Modified from a thesis submitted to the faculty of Mississippi State University in partial fulfillment of the requirements for the degree of Master of Science.

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Gulf of Mexico and *C. jamaicense* only in sheltered, mudbottomed backwaters. A similar situation occurs in Mississippi Sound, wherein *C. islagrande* is found only in the sandy beaches of the offshore barrier islands and *C. j. louisianensis* is found only in the muddy inshore beaches. Other than the original descriptions of these taxa (Schmitt 1935) and the report by Willis (1942), there have been no published studies on these callianassids. An unpublished master's thesis (Friedrichs 1955) for the most part consists of a reiteration of Schmitt's original descriptions, and does not contain any pertinent ecological observations.

COLLECTING STATIONS

1. Ocean Springs (Beach)
2. Marsh Point
3. Deer Island
4. Craveline Bay
5. Belle Fontaine
6. Biloxi (Beach)
7. Horn Island (West End)
8. Horn Island (near lagoon)
9. Horn Island (chimney)
10. Ship Island (Quarantine Station)
11. Ship Island (Fort Massachusetts)

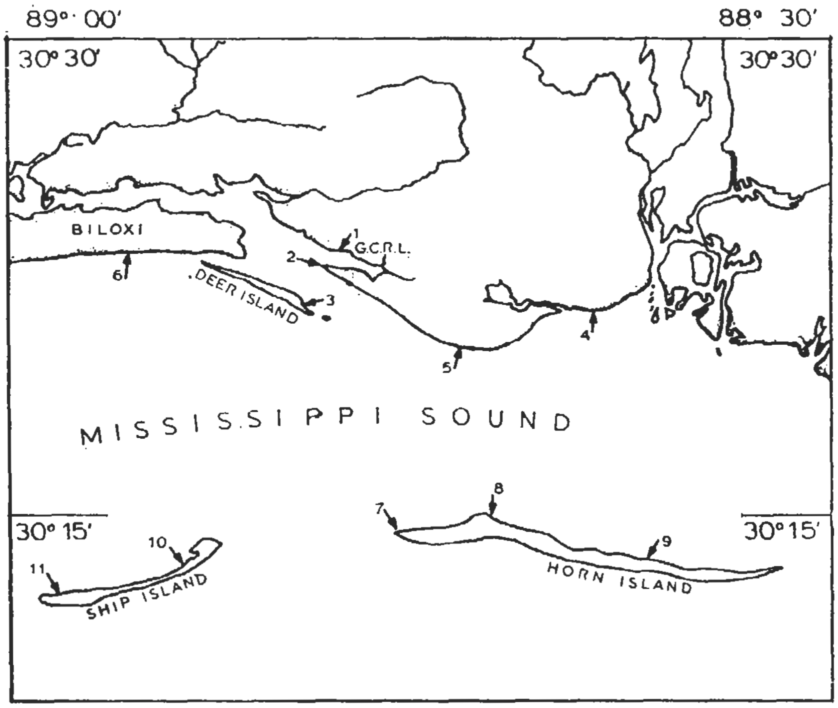

Figure 1
Mississippi Sound Collecting Stations

C. j. louisianensis was collected only at Stations 1 through 6.

C. islagrande was collected only at Stations 7 through 10.

METHODS AND MATERIALS

Collections:

Collections were made at selected stations in Mississippi Sound (Fig. 1). *C. islagrande* were taken only along the north beaches of Horn and Ship Islands, whereas *C. j. louisianensis* were found only along beaches of the mainland and Deer Island (Table 1, Fig. 1). Initial collections were made using sieve and shovel. Toward the latter part of this study a "yabby" pump (Fig. 2), essentially a hand coring device, was used to collect *C. j. louisianensis*. The use and construction of this pump was described by Hailstone and Stephenson (1961). After the cylinder is pushed into the substrate and extracted with the thumbholes closed, the core is released into a sieve and the mud-

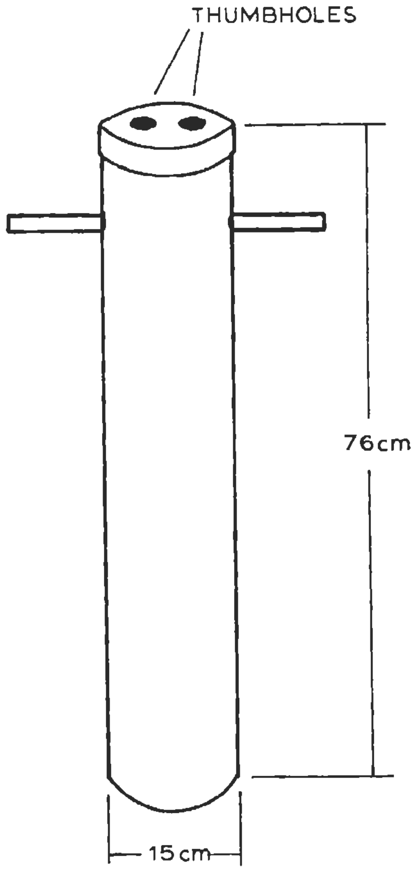

Figure 2
The "Yabby" Pump Used to Collect *C. j. louisianensis*

Table 1: Collection Data for Callianassid Crustaceans in the Mississippi Sound

A: **C. j. louisianensis**

Locality	Station	Date	Salinity (g/kg)	Tide	No. of Speci- mens	Number of Females w/Ripening Ovarian Eggs	
							Ovigerous*
Ocean* Springs Beach	1	1-24-67	4.6	low	4		
	1	2-9-67	12.2	low	2		
	1	2-10-67	12.2	low	3		
	1	2-13-67	11.9	low	7		
	1	2-14-67	12.0	low	3		
	1	3-17-67	16.7	low	5		
	1	3-27-67	20.6	high			
	1	6-19-67	25.0	high	6	1	
Marsh Point	2	2-16-67	10.6	high	8		
	2	2-21-67	14.0	low	3		
	2	2-24-67	12.0	high			
	2	3-3-67	21.6	high	1		
	2	3-8-67	19.0	low	30		
	2	4-3-67	20.8	high	10		
Marsh Point	2	4-17-67	22.8	high	10		
	2	4-24-67	25.0	low	20	1	
	2	4-27-67	24.0	low	17	2	
	2	6-17-67	23.0	low	6	1	
	2	6-22-67	25.0	high	41	6	3 (1 with early ova, 2 with eyespot ova)
Deer Island	3	2-27-67	17.2	high			
	3	3-3-67	24.0	high			
	3	4-11-67	22.3	high	2		
Graveline Bayou	4	3-13-67	15.6	high	3		
Belle Fontaine	5	3-13-67	17.6	high	2		
Biloxi Beach	6	6-13-67	28.0	low	3	1	
B: **C. islagrande:**							
Horn Island, west end	7	12-2-66	Not measured	low	12		
	7	3-1-67	22.5	high			
	7	3-18-67	24.0	high			
	7	3-22-67	29.4	high	7	2	
Horn Island, near lagoon	8	5-14-67	30.0	high	7		
Horn Island, Chimney	9	4-11-67	27.4	high	4		
	9	4-12-67	27.6	high	3	1	
Ship Island, Quarantine Station	10	3-20-67	30.0	high	15	3	
	10	4-2-67	30.0	low	37	3	
	10	4-22-67	28.2	low	103	9	3 with early ova
Ship Island, Fort Massachusetts	11	3-21-67	27.2	high			

*2 ovigerous females were collected 6-25-51 at Marsh Point; attached ova were at eyespot stage.

shrimps are recovered. The same spot is repeatedly sampled until no more mudshrimps are obtained. This pump is most successfully used on exposed mudflats and considerably less so in sand. The term "yabby" is the Australian common name for *Callianassa australiensis* Dana.

Callianassid collections are best made during periods of low tide with little or no surf action. This combination of factors was seldom encountered. Data for each collection (Table 1) include the following: location, salinity, tide, species, number of specimens and the gross gonadal condition of adult females. Salinity was measured with a sea water hydrometer corrected for temperature.

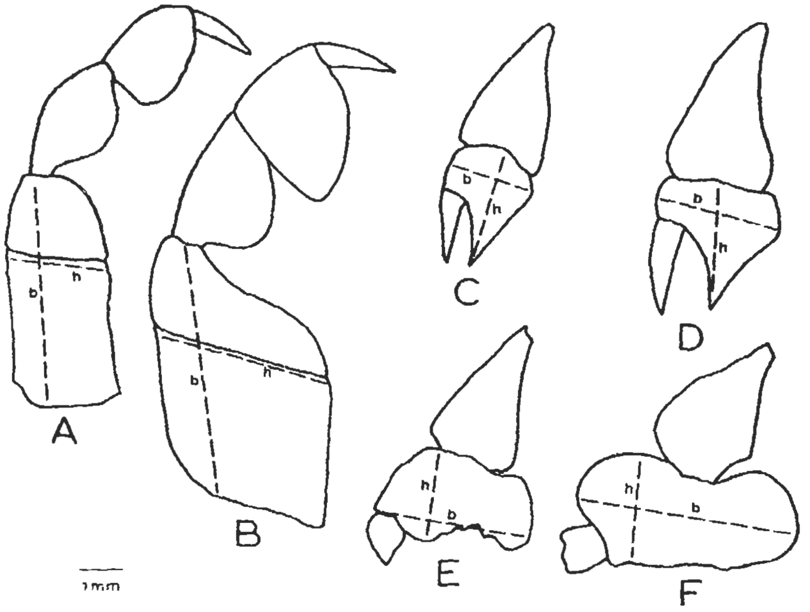

Figure 3

Burrowing Appendages of *C. j. louisianensis* and *C. islagrande*

A: Right third maxilliped of *C. j. louisianensis*.

B: Right third maxilliped of *C. islagrande*.

C: Right second pereiopod of *C. j. louisianensis*.

D: Right second pereiopod of *C. islagrande*.

E: Right third pereiopod of *C. j. louisianensis*.

F: Right third pereiopod of *C. islagrande*.

Lines "b" and "h" indicate the length and breadth of the merusischium on the third maxillipeds. Lines "b" and "h" indicate the propodal length and breadth on pereiopods.

The two species may be distinguished by differences in the shape of the third maxillipeds (Fig. 3) and uropodal endopodites. In *C. islagrande* the third maxillipeds are foliaceous and the uropodal endopodites are four times as long as broad. *C. j. louisianensis* has periform third maxillipeds and the uropodal endopodites are about one-and-one-half times as long as broad. Sex, in both species, was determined by examination of the first and second pairs of pleopods. The second pair of pleopods of the male are more than twice the length of the first, whereas the first and second pairs of pleopods in the female are of subequal length. Ripening ovarian eggs in adult females appear bright yellow to orange through the translucent abdominal exoskeleton. Ovigerous females are those having ova attached to the pleopodal setae. During their early development, ova attached to pleopodal setae are bright orange and these recently "berried" females may also have some bright orange ovarian eggs. More advanced ova, in the eyespot stage, have a dull yel-

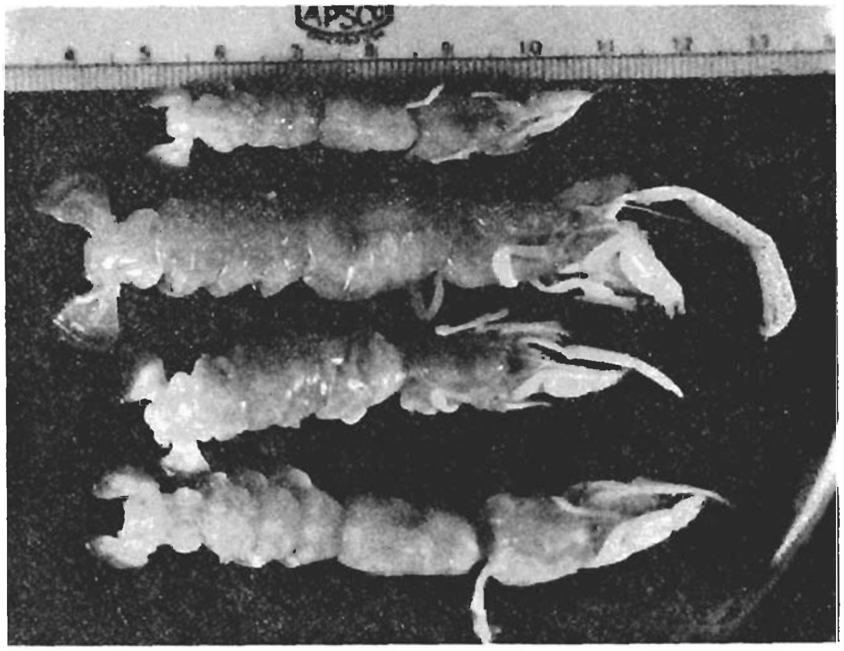

Figure 4

Sexual Dimorphism of the Major Cheliped in *C. islagrande*

The top and bottom specimens, females, have major chelipeds less than one-and-one-half times the length of the minor cheliped. The two middle specimens, males, have major chelipeds at least one-and-one-half times the length of the minor cheliped.

low color, and females bearing these lack ovarian eggs. Large males of *C. islagrande* have a slender major cheliped which is one-and-one-half times the length of the minor cheliped (Fig. 4). Females of *C. islagrande* have a major cheliped which is less than one-and-one-half times the length of the minor cheliped. There is little sexual dimorphism in cheliped shape of *C. j. louisianensis* and, in both sexes, the major cheliped is less than one-and-one-half times the length of the minor cheliped. Female callianassids may also be recognized by the opening of the oviduct on the coxa of the third pereiopod. These openings are larger and more easily distinguished in *C. j. louisianensis* than in *C. islagrande*. Specimens which could not be sexed were classified as juveniles. Mudshrimp were fixed in 20% formalin for 7 days and then transferred to 70% ethanol.

Table 2: Frequency Distribution of Carapace Lengths of Mississippi Sound Callianassids Studied

	Juveniles		Juveniles		Juveniles	
Carapace Length (mm)	C.j.louisianensis	C.islagrande	C.j.louisianensis	C.islagrande	C.j.louisianensis	C.islagrande
2	1					
3	6	1				
4	48	5				
5	40		1		1	
6	12	12	4	3		
7	12	9	6	5	2	1
8		6	3	8	5	2
9		1	4	8	2	4
10		1	6	9	8	9
11		1	5	6	8	11
12			3	8	3	9
13				9		5
14			6	11	1	8
15				11	2	2
16			2	4	4	
17			1	4	3	
18						
19				1		
Totals	99	44	41	87	39	51
Mean Carapace Length (mm)	5.0	5.7	11.8	12.1	12.3	11.3
Variance (sq mm) (±)	2.3	16.1	14.8	11.4	11.7	34.1
Standard Deviation (±)	1.5	4.0	3.8	3.4	3.4	5.8

Carapace lengths and apparent sex ratios of all study material, including specimens from the Gulf Coast Research Laboratory Museum are given in Table 2. Carapace length is the straight line distance from the tip of the rostrum to the posterior margin of the carapace. All measurements of mudshrimp were made with dividers or calipers and recorded to the nearest one-half mm. Measurements were made of the propodus of the second and third right pereiopods and merus and ischium of the right third maxillipeds (Table 3). Certain parameters derived from these data are used in the discussion of the behavior of these callianassids.

Table 3: Proportional Measurements (mm) and Surface Area Indices* of **C. islagrande** and **C. j. louisianensis** in Mississippi Sound

A: **C. islagrande**

Carapace Length	Third Maxilliped h	b	Index	Second Pereiopod h	b	Index	Third Pereiopod h	b	Index
8	3.0	4.5	1.70	2.0	2.0	0.50	2.5	4.0	1.25
8	3.0	4.0	1.66	2.0	2.0	0.50	2.0	4.0	1.00
10	4.0	5.0	2.00	2.5	3.0	0.75	2.0	5.0	1.00
10	4.0	6.5	2.60	3.0	3.0	0.90	3.0	6.0	1.80
11	4.0	6.0	2.09	2.0	2.5	0.45	2.5	5.5	1.25
13	4.0	7.0	2.15	4.0	4.0	1.23	3.0	6.0	1.38
15	6.0	9.0	3.60	3.5	4.0	0.93	3.0	8.0	1.60
15	5.0	8.0	2.66	3.5	4.0	0.93	3.0	8.0	1.60
15	5.0	7.0	2.33	3.5	4.0	0.93	4.0	7.0	1.87
17	6.0	9.0	3.18	4.0	4.0	0.94	4.0	8.0	1.87
Mean indices			2.40			0.81			1.46

B: **C. j. louisianensis**

Carapace Length	Third Maxilliped h	b	Index	Second Pereiopod h	b	Index	Third Pereiopod h	b	Index
8	1.5	3.5	0.66	2.0	1.0	0.25	1.5	2.5	0.47
8	1.5	3.0	0.56	2.0	1.5	0.38	1.5	2.5	0.47
10	2.0	4.0	0.80	2.5	2.0	0.50	2.0	4.0	0.80
11	2.0	5.0	0.91	2.5	2.0	0.46	2.0	4.0	0.73
12	2.0	5.0	0.83	2.0	1.5	0.25	2.0	4.0	0.66
14	3.0	7.0	1.50	4.0	2.5	0.71	3.0	6.0	1.29
15	3.0	7.5	1.50	4.0	2.5	0.66	2.5	5.0	1.25
15	3.0	8.0	1.60	5.0	3.0	1.00	3.0	7.0	1.40
16	3.0	8.0	1.50	5.0	3.0	0.94	3.0	7.0	1.30
16	3.0	9.0	1.69	4.0	3.0	0.75	3.0	5.5	1.03
Mean Indices			1.12			0.59			0.94

$$\frac{^{*}\text{Length (h) x Breadth (b)}}{\text{Carapace Length}} = \text{Index of Surface Area (mm) (Fig. 3).}$$

Substrate Analysis:

Bottom samples from inshore and offshore collecting sites were analyzed for their relative sand and silt contents by elutriation, the gravimetric fractionation of an unstable suspension

(Priddy *et al.* 1955). Approximately 200 ml samples of fresh bottom material were homogenized for 15 min in a blender and then decanted into 1-liter graduated cylinders. Volumes were adjusted to 1 liter with sea water and the cylinders were shaken vigorously to resuspend the sediments. The samples were allowed to stand for 72 hrs. and then examined to determine the relative proportions of sand and silt by recording the volumetric percentages of the sand and silt layers. The volumetric compositions of bottom samples are given in Table 4.

Table 4: Volumetric Analysis of Selected Mississippi Sound Substrates

Substrate	Occurrence	Percentage Composition by Volume Sand	 Silt
Sand	Offshore littoral and neritic zones	98	2
Sand	Inshore littoral zone	80	20
Hard Mud	Inshore littoral and neritic zones	50	50
Clay	Inshore littoral and neritic zones	10	90
Soft Mud	Inshore littoral and neritic zones	traces	100-

Aquarium Studies:

The objective of these studies was to determine the ability of these mudshrimps to burrow and survive in various substrates from Mississippi Sound and to determine if these callianassids are selective when given a choice of substrates. Aquarium studies of both species were divided into the following categories: (1) tests on individual substrates, (2) tests on stratified substrate columns, (3) tests of superimposing substrate on burrowed specimens and (4) substrate preference tests. Half-liter beakers, graduated cylinders (250 ml, 500 ml, and 1000 ml), shallow pans (26 x 23 x 5 cm and 32 x 26 x 8 cm), mason jars (1 qt), test tubes and 5 and 10 gal tanks served as aquarium vessels. All were aerated by means of an airstone suspended just below the water surface. Except where noted to the contrary, Mississippi Sound water from the habitat of each species was used in these experiments and water depth was never less than 2.5 cm. Specimens were released at the water surface.

In all of the columnar experiments the depth of the upper layer was 8-15 cm and that of the lower was 12-15 cm. In cases where substrate was superimposed on an established mudshrimp colony the depth of the superimposed substrate was 8-9 cm and that of the original substrate layer was about 14 cm. In the substrate preference tests two substrates were placed in apposition in shallow pans. Mudshrimps were released above the interface of the two substrates. The arrangements of substrates in the substrate preference tests are shown in Fig. 5. The sub-

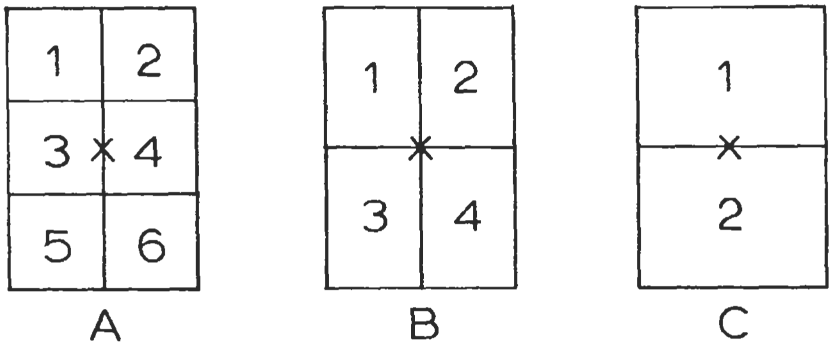

Figure 5

Substrate Arrangements in Preference Tests

A: Test 5. Sectors 1, 4, 5 contain hard mud whereas sectors 2, 3 and 6 contain inshore sand.

B: Test 6. Sectors 1 and 4 contain hard mud, whereas sectors 2 and 3 contain inshore sand.

C: Arrangement of All Other Tests: Sector 1 contains one substrate and Sector 2 the other.

In all instances "X" indicates the site at which mudshrimps were released.

strate preference tests, summarized in Table 5, are discussed according to the following categories: (1) sand inshore *versus* sand offshore, (2) sand, either type, *versus* hard mud, (3) sand, either type, *versus* clay and (4) hard mud *versus* clay.

Table 5. Summary of Behavior in Substrate Preference Tests of **Callianassa** of Mississippi Sound

	Preference	
Substrate Combination	**C. j. louisianensis**	**C. islagrande**
Sand, inshore **versus** Sand, offshore	No Preference	Equally Preferred
Sand **versus** Hard Mud	Hard Mud	Sand
Sand **versus** Clay	Clay	Sand
Hard Mud **versus** Clay	Equally Preferred	Hard Mud

Salinity tolerance tests were conducted to determine whether salinity affects the gross behavior of callianassids in the tests involving substrate. The tests (Table 6) show the responses of burrowed and free specimens to the same salinity changes. These experiments were conducted at room temperature (21.1-23.9°C). Salinity tests on free shrimp were conducted by placing the animals in waters of varying salinity. For burrowed shrimp, salinity was adjusted by decanting supernatant water and adding water of the desired salinity.

Table 6: Salinity Tolerance Tests on **C. j. louisianensis** and **C. islagrande**

Salinity (g/kg)				No. of	Observations		
From	To	Change	Species	Specimens	One Hour	Two Days	Five Days
A: **Free-swimming Mudshrimps**							
20	20	0	**C. j. louisianensis**	6	All active	All active	All dead
29	29	0	**C. islagrande**	6	All active	All active	All dead
20	29	+9	**C. j. louisianensis**	6	All active	All active	All dead
29	20	-9	**C. j. louisianensis**	6	All active	All active	All dead
29	20	-9	**C. islagrande**	6	4 dead	2 torpid	All dead
29	tap water	-29	**C. j. louisianensis**	7	All active	All active	All dead
29	tap water	-29	**C. islagrande**	4	All dead		
B: **Burrowed Mudshrimps**							
20	20	0	**C. j. louisianensis**	10	All active	All active	All active
29	29	0	**C. islagrande**	6	All active	All active	All active
20	29	+9	**C. j. louisianensis**	7	All active	All active	All active
29	20	-9	**C. j. louisianensis**	6	All active	All active	All active
29	20	-9	**C. islagrande**	6	All active	All active	All active
20	tap water	-20	**C. j. louisianensis**	7	All active	All active	All active
29	tap water	-29	**C. j. louisianensis**	6	All active	All active	All active
29	tap water		**C. islagrande**	4	Two dead	All dead	

Stomach Content Analyses:

The stomach contents or recently collected specimens of both taxa and of animals used in the aquarium studies were analyzed. The stomachs were removed and opened. Aliquots of the contents were placed on a slide and examined with a compound miscroscope fitted with an ocular micrometer. These analyses were performed to determine the nature and size range of particulate stomach contents.

FIELD OBSERVATIONS

The bottoms of the inshore Mississippi Sound stations, predominantly muddy, vary from sand to extremely soft mud, whereas those of the offshore stations are uniformly sandy. The compositions of representative bottom samples from the two environments are given in Table 4.

The presence of mudshrimps in a beach can be recognized by their characteristic burrow openings (Fig. 6). There is no apparent species-related difference in the shape or structure

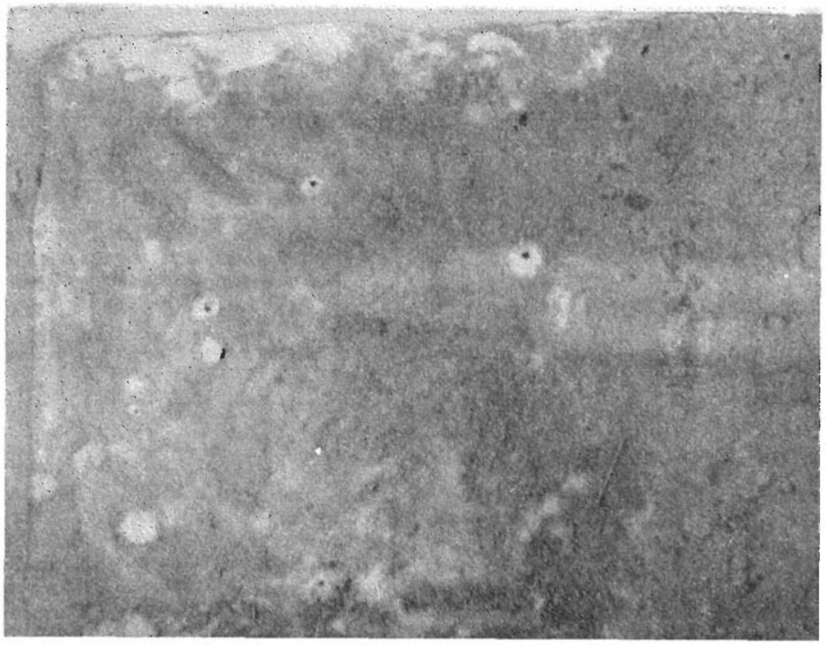

Figure 6

Openings of *C. j. louisianensis* Burrows

Callianassid burrow openings in the natural habitat resemble those produced in the laboratory. This figure shows the surface of Substrate Preference Test 12, 24 hr after the start of the experiment.

Although 10 out of 13 *C. j. louisianensis* were recovered from clay, numerous burrow openings appeared in sand.

of burrow openings. The openings, resembling those reported for other callianasids (Hailstone and Stephenson 1961, Lunz 1937, Pearse *et al.* 1942, Pohl 1946, Weimer and Hoyt 1964), are raised mounds (0.5-2 cm high) with an opening, 0.5-1 cm in diameter, in the center. Openings, often surrounded by fecal pellets, are most abundant in the intertidal bottoms below the belt of surf action and in the shallow neritic zone. On several occasions burrow openings in the inshore and offshore habitats were seen through a maximum water depth of 1.2 m.

The incidence of burrow openings is quite variable in the offshore habitat. At Station 7, the west end of Horn Island (2 December 1966), there was a low tide count of 100+ openings per sq m. During the spring months at the same station there were less than 5 openings per sq m. At Station 9, Ship Island Quarantine Station, during April 1967, there were 100+ openings per sq m. There were no burrow openings at this station on 11 June 1967. No such drastic fluctuations in number of burrow openings were observed in the inshore habitat. It is possible that the fluctuation in number of *C. islagrande* burrow openings results from wind and surf action and does not necessarily represent variations in population density. Certain structural features of the *C. j. louisianensis* burrow wall, discussed later, may also serve to establish a situation wherein the burrow remains long after the mudshrimp has died or otherwise departed. The persistent burrow walls of *C. j. louisianensis* may at times be left protruding as much as 5 cm above the bottom following the displacement of surrounding substrate by strong surf action.

The *in situ* depth of 20 *C. j. louisianensis* burrows, measured by the insertion of flexible plastic tubing, ranged from 32-137 cm (mean, 77 cm). The extreme fragility of burrows of *C. islagrande* prevented similar measurements for that species. Pohl (1946), using this method, found that burrows of *C. major* Say reached a depth of 210 cm.

Burrow walls of both forms vary from 5-15 mm in thickness, but show significant differences in composition. Walls of *C. j. louisianensis* burrows are of very cohesive clay-like mud with a smooth mucilaginous lining, whereas those of *C. islagrande* are composed of loosely cemented sand with no apparent lining. Wall texture of *C. j. louisianensis* burrows is the same, regardless of the composition of the surrounding substrate.

BURROWING BEHAVIOR ON SUITABLE SUBSTRATES

Although Willis (1942) reported an ovigerous *C. islagrande* swimming near the water surface, free-swimming mudshrimps were never encountered in this study. Both taxa treated here are certainly capable of at least short term swimming activities. Forward propulsion is achieved by pleopod motions and backward motion is achieved by rapid and repeated flexure of the abdomen. Mudshrimps will swim for a short period, usually for less than 1 min and for a distance of less than 1 m, when first released in an aquarium. They will then invariably cease swimming and burrow headfirst into any acceptable substrate and will be completely hidden within 1 min.

All observations of burrowing behavior and burrow construction were made in the laboratory. Fortunately burrows were frequently constructed against the aquarium wall (Figs. 7 and 8) and direct observation could be made of subsurface activities. In initiating a burrow a mudshrimp usually backs out of the burrow one or more times, depositing displaced substrate near the burrow opening. Excavated material is carried in a basket formed by the third maxillipeds. The burrow ex-

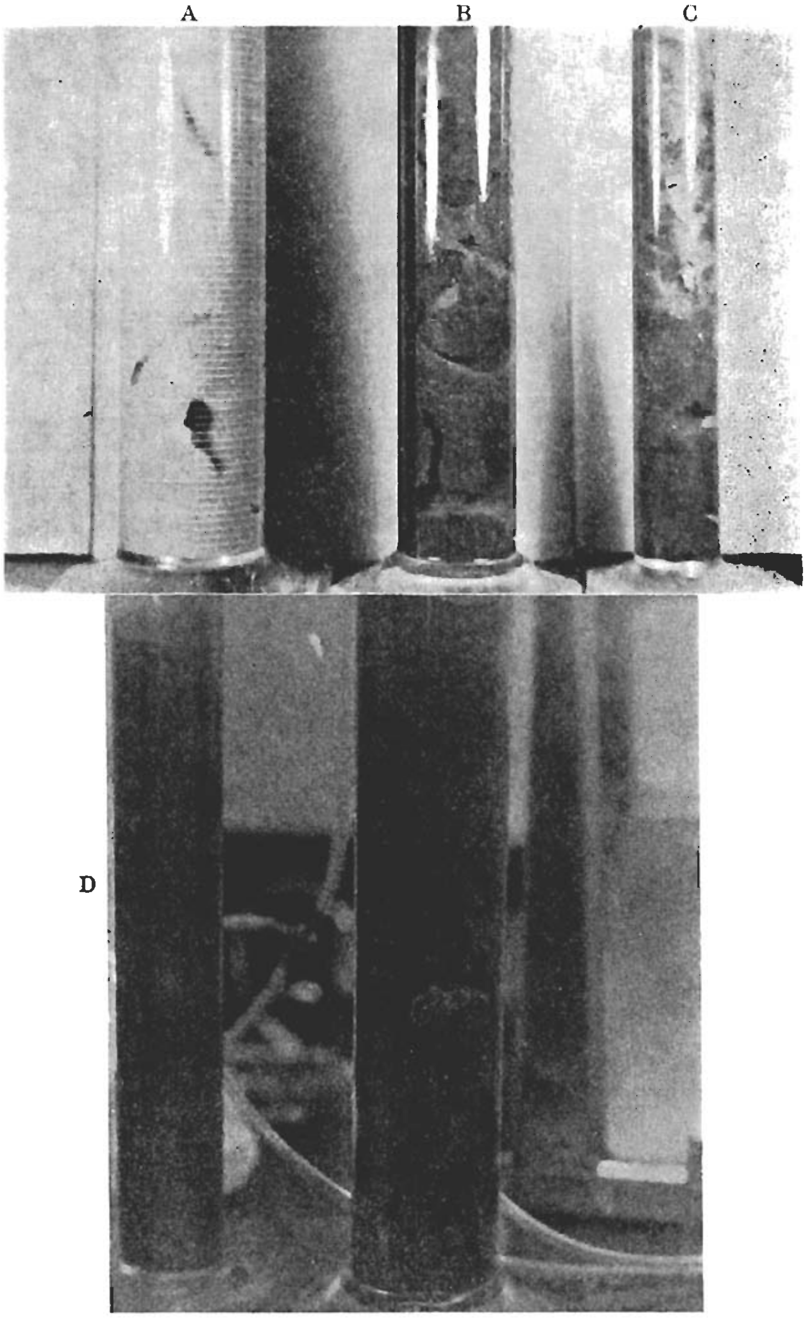

Figure 7

C. j. louisianensis and *C. islagrande* Burrows in Suitable Substrates

A: Burrows of 2 *C. islagrande* after 2 days in offshore sand.

B and C: Burrows of *C. j. louisianensis*, 2 animals in each column, after 5 days in mud.

D: *C. j. louisianensis* in burrow in habitat substrate.

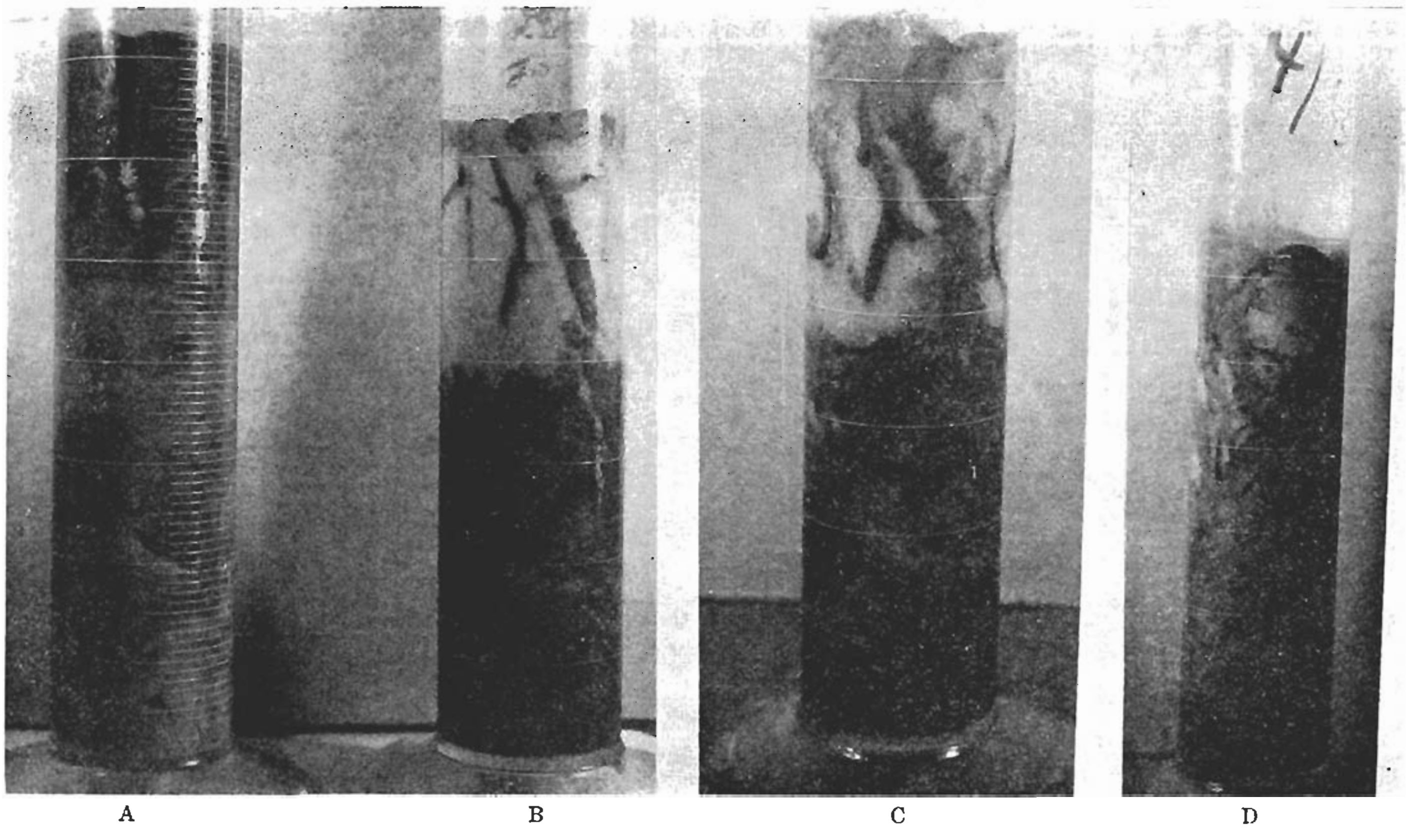

Figure 8 Responses of Burrowed Mudshrimps to Superimposed Substrates

A shows that within 3 days one *C. islagrande* extended its burrow through superimposed mud. B, C and D show progressive thickening of *C. j. louisianensis* mud-lined burrow walls in superimposed sand at 3, 14 and 21 days, respectively. Disturbance of the sand (upper)—mud (lower) interface by the burrowing activities of *C. j. louisianensis* is also evident (B, C, D).

tends downwards vertically or at a slight angle to the vertical axis (a maximum of 30°). When the burrow is 3-4 times the carapace length of the burrowing animal, an expanded chamber (about twice the diameter of the rest of the burrow) is constructed. This chamber enables the animal to turn around. When these soft bodied animals turn around there is flexure of almost 180° at the junction of the cephalothorax and first abdominal segment. Laboratory observations indicate that mudshrimp only rarely leave the burrows after the construction of the first turning chamber. Additional turning chambers are constructed periodically throughout the burrow. Substrate displaced by further burrowing operations is usually tamped into the burrow walls and, less often, pushed out of the burrow opening.

The complexity of individual burrows increases with time and the aquarium substrate may eventually resemble a maze (Fig. 7). Burrows within aquaria may be deepened at a considerable pace. It was not unusual for both forms, given suitable substrate, to burrow 36 cm, the maximum depth available, within 24 hrs (Fig. 7). This represents a minimum burrow construction rate of the order of 1.5 cm per hr. There is no apparent difference in burrowing rate with respect to size. The diameter of the burrow is usually about twice the breadth of the animal but may vary from 1-5 times this dimension.

Present observations suggest that, under natural conditions, each burrow is occupied by a single callianassid. On one occasion when 20 specimens were held in an aquarium containing 500 ml of substrate, two individuals were seen in the same burrow. The possibility of similarly crowded conditions ever occurring in the natural habitats of local mudshrimp is difficult to conceive.

In both forms, the chelipeds, third maxillipeds and second and third pairs of pereiopods are used in burrowing. The chelipeds and third maxillipeds are essential for burrowing. If both chelipeds or both third maxillipeds are missing burrowing does not occur. The chelipeds and third maxillipeds are used to displace substrate in front of the mudshrimp. The third maxillipeds and, to a lesser extent, the second and third pereiopods are employed to tamp displaced substrate into the burrow wall. The third maxillipeds are also used to carry substrate from one portion of the burrow to another. The second and third pereiopods also function in displacing substrate, but to a considerably lesser extent than the chelipeds. The dactyls of the fourth pair of pereiopods are brushlike and are used in cleaning the body surfaces, branchiae and, in the case of ovigerous females, attached ova. The fifth pair of pereiopods function in balancing the mudshrimp against the burrow walls.

Callianassids produce a cementing substance used in construction of the burrow wall. Weimer and Hoyt (1964) stated that *C. major* produces a cementing substance over the entire body surface and that this cementing material is collophonite, an amorphous calcium phosphate. In the case of *C. j. louisianensis* and *C. islagrande,* sand grains and other particulate matter are often embedded in mucoidal strands originating in the vicinity of the third maxillipeds. Possibly secretion of the cementing substance is localized in the vicinity of the third maxillipeds in the taxa included in this study.

Within their burrows, callianassids generate currents which may be involved in respiration with their pleopods (MacGinitie and MacGinitie 1949). Respiratory currents are produced in the branchial chambers by rapid beating of the scaphognaths of the second pair of maxillae and by occasional flushing of the branchial chambers by lateral contraction of the carapace. The epipodites of the first pair of maxillipeds form a shield over the anterior opening of the branchial cavity and possibly function as a barrier to the entry of foreign particles.

FEEDING

Feeding behavior appears to be variable in *Callianassa.* Pohl (1946) stated that *C. major* feeds primarily by sifting the substrate for useable organic material, whereas MacGinitie and MacGinitie (1949) considered *Callianassa affinis* Holmes to be a filter feeder. Stomach content analyses of five recently collected specimens of both *C. j. louisianensis* and *C. islagrande* indicate that these taxa feed, at least in part, by sifting through the substrate. In both cases recognizable stomach contents consisted of about 50% sand grains by particle count. Grain diameter ranged from 10-800u and averaged about 107u. The remaining particulate matter consisted of diatoms of the genera *Navicula, Pleurosigma, Tabellaria, Synedra* and *Pinnularia,* bacteria (cocci and bacilli), and significant quantities of shredded brown material which was probably of vegetable origin. Similar stomach contents have been reported for *C. major* (Pohl 1946).

COMMENSALS AND PARASITES

About ten percent of the *C. islagrande* collected were infested with the copepod ectoparasite *Clausidium* sp. These were found on all portions of the exoskeleton and not confined to any specific anatomical region. Pohl (*op. cit.*) reported finding a similar parasite of the genus *Clausidium* infesting *C. major* on the Atlantic coast. No ectoparasites were found on *C. j. louisianensis.* Burrows of both Mississippi Sound mudshrimps harbored pinnixid crabs (*Pinnixia cristata* Rathbun), about one to five crabs per burrow. The *Pinnixia* inhabiting *islagrande* burrows exhibited considerable polymorphism with respect to coloration. Those infesting *jamaicense* burrows were uniformly black and were covered with a dense hydroid growth. The significance of the pinnixid polymorphism is unclear, but it is probably related to substrate.

AQUARIUM STUDIES

Responses to Selected Bottom Types:

a. *Sand (inshore and offshore types).*

C. j. louisianensis does not burrow readily. Only one specimen of 15 reached the bottom of a 10 cm sand column within 4 days. Remaining specimens constructed only shallow burrows, up to 3 cm deep, and were observed to leave these burrows and swim more or less continuously for periods of up to 8 hours. As much as 15 min. was required to construct a 3 cm burrow, whereas a similar burrow may be constructed within 1 min. in a mud substrate. The single deep burrowing individual survived for 6 weeks, at which time it died of unknown causes outside its burrow. All other specimens exposed to sand died within 5 days. Examination of the burrow wall of the deep burrowing specimen revealed no conspicuous lining. Stomach contents of 10 specimens, five exposed to each sand type (including the sole deep burrowing individual) consisted of a few bacteria only. There was no difference in response to either offshore or inshore sand; both sand types were equally unsuitable.

C. islagrande burrows readily in sand of either source. Shallow burrows were usually constructed within 1 minute. Burrows were deep and extensive (Fig. 7). Five specimens were kept in aquaria containing either inshore sand or offshore sand for as long as 2 months, at which time the experiment was terminated. Among five specimens exposed to each sand type, stomach contents consisted of a few bachteria only. Evidently the feeding behavior of *C. islagrande,* in suitable substrates, is altered in the laboratory environment.

b. *Hard Mud.*

C. j. louisianensis burrow very readily and burrows 3 cm deep are constructed within 1 minute. Burrows in hard mud were deep and very extensive (Fig. 7). The burrow walls were very similar to those in the natural habitat. Mortality over a 2-month period was low, being 3 out of 35 specimens (8.6%). Stomach contents of five specimens kept in aquaria 2 months were very similar to those of recently collected specimens.

C. islagrande does not burrow readily in hard mud. Only 22% (4 of 18) burrowed and survived in mud for 5 days. *C. islagrande* which did construct burrows in hard mud did so just as rapidly as in sand. This species evidently has the ability to burrow into mud, although it seldom does so. Death is preceded by blackening of the margins and articulating borders of the exoskeleton and occlusion of the branchial chambers with silt.

c.*Clay.*

C. j. louisianensis burrowing behavior was the same as on hard mud.

C. islangrande did not survive on clay for more than 5 days. Specimens swam constantly and seldom attempted burrowing. One specimen of the 10 tested constructed a shallow burrow but died in the burrow within 1 hr. As was the case on hard mud, death was preceded by blackening of the exoskeleton and occlusion of the branchial chambers with silt.

d. *Soft Mud.*

C. j. louisianensis exhibited the same behavior as on hard mud or clay.

C. islagrande exhibited the same behavior on soft mud as on clay with the exception that none of the 15 tested specimens burrowed or attempted to burrow.

Table 7: Burrowing Responses and Survival of **Callianassa** on Selected Mississippi Sound Substrates*

Substrate	Survival		Construction of Burrows at Least 10 cm Deep	
	C.j. louisianensis	C. islagrande	C.j. louisianensis	C. islagrande
Sand, inshore	Poor	Good	Rare	Frequent
Sand, offshore	Poor	Good	Rare	Frequent
Hard Mud	Good	Poor	Normal	Rare
Soft Mud	Good	Poor	Frequent	Never
Clay	Good	Poor	Frequent	Never

*A minimum of 15 specimens of each taxon was tested on each substrate.

Behavior in this series of tests is summarized in Table 7 with respect to survival and the relative number that constructed burrows deeper than 3 cm. *C. islagrande* survives well and burrows deeply only in sand, whereas *C. j. louisianensis* shows optimal survival and burrowing activity in mud or clay environments.

Effects of Columns Composed of Two Substrate Layers on Burrowing Behavior

a. *Offshore Sand Above Hard Mud.*

C. j. louisianensis showed essentially the same behavior pattern in this test as when tested on said previously. Of six specimens, only two had constructed shallow burrows by the second day. After 4 days one of the two specimens that had constructed a shallow burrow reached the lower mud layer and the five remaining specimens were dead on the sand surface. The mudshrimp reaching the lower mud layer immediately began to line the upper sand burrow with mud. After 2 weeks the entire burrow had a thick mud wall similar to that found in the natural habitat.

C. islagrande burrowed readily into the sand, and all four specimens, in two separate trials, reached the bottom of the sand layer within 6 hrs. One burrow was continued into the mud layer 5 days after the start of the experiment, but no additional mud burrows were seen during the 2-week test. All specimens were recovered alive from the sand layer at the termination of the experiment.

b. *Hard Mud Above Offshore Sand.*

C. j. louisianensis all burrowed into the mud within 1 min. and reached the bottom of the sand layer within 24 hrs. Within 2 weeks the layering between the sand and mud was sufficiently disturbed by burrowing activities to partially obliterate the previously distinct substrate interface. Burrow walls were similar to those found in the natural habitat.

C. islagrande reacted to the hard mud as they did in previous tests. Only one of the four specimens succeeded in burrowing through the mud into the sand layer during a 4-day period. The remaining specimens repeatedly constructed shallow burrows, then left them and spent most of the time swimming. Within 4 days all free specimens were dead. The burrowed individual died within 8 days. In each case the branchial chamber was occluded with silt and the margins and articulating surfaces of the exoskeleton were blackened.

Evidently *C. j. louisianensis* can burrow through sand if there is mud available for burrow wall construction. Availability of sand does not facilitate burrowing or survival of *C. islagrande* in mud.

Behavior of Colonies to Superimposed Substrate:

In this series of tests approximately 250 ml of hard mud or offshore sand were superimposed on established colonies of 10 *C. j. louisianensis* in approximately 400 ml of hard mud or 4 *C. islagrande* in the same volume of offshore sand. Depth of the superimposed layer was approximately 8.5 cm and the depth of the base layer was approximately 14 cm.

C. j. louisianensis extended their burrows through superimposed mud or sand within 6 hrs. Burrows extending through sand were lined with mud layers which were thickened throughout the course of the test (Fig. 8). Mud linings of the burrows in sand resembled those found in the natural habitat and some disturbance of the sand-mud interface was noted (Fig. 8).

C. islagrande burrows were extended through superimposed sand within 6 hours and all four specimens were recovered alive after 4 weeks. One burrow was extended through the superimposed mud layer by the third day (Fig. 8) and all four animals were found dead in the sand layer at the end of 4 days. Portions of the exoskeletons of the dead test animals were blackened and in each case the branchial chambers were occluded by silt. *C. islagrande,* even when established in a suitable substrate,cannot tolerate silt in the environment.

Substrate Preference Tests:

The results of these tests, detailed in the Appendix, are summarized in Table 6, and discussed according to each category. Observations were made of the numbers of test animals burrowing into each substrate, speed of burrowing (rapid or slow) into each substrate and the number of test animals recovered from each substrate after a minimum period of 24 hrs.

Category 1: Sand offshore versus sand inshore (see Appendix Tests 1-4).

C. j. louisianensis exhibited the same behavior pattern as when tested on either substrate alone. Both sand types are equally unacceptable and no preference was shown.

C. islagrande showed the same response to each sand type. Approximately equal numbers of test animals burrowed into and were recovered from each substrate. Both substrates were equally suitable and burrowing was rapid (within 1 min) in each.

Category 2: Sand (inshore or offshore) versus hard mud (see Appendix Tests 5-11).

C. j. louisianensis overwhelmingly preferred mud. After one or two attempts to burrow into sand, test animals usually burrowed into mud upon coming into physical contact with it. Numerous burrow openings appeared in sand although most mudshrimps were recovered from the mud.

C. islagrande preferred sand. Although a significant number (27%) burrowed rapidly into the hard mud and almost all left their mud burrows within 1 hr and burrowed into the sand upon coming into contact with it. The majority were recovered from the sand. Those specimens recovered from mud had occluded branchial chambers and partially blackened exoskeletons.

Category 3: Sand (inshore or offshore) versus clay (see Appendix Tests 12-14).

C. j. louisianensis exhibited the same behavior as in Category 2. The muddy substrate was preferred.

C. islagrande never initiated burrows in clay. All test animals were recovered from the sand.

Category 4: Hard mud versus clay (see Appendix Tests 15, 16).

C. j. louisianensis did not favor either substrate. Both clay and mud were equally suitable.

C. islagrande did not burrow into clay. Mud was favored, although it was an unsuitable substrate. Behavior on mud approximated that of previous tests, wherein specimens would repeatedly construct shallow burrows, leave them and swim for varying periods of time. Despite the fact that it is a lethal choice, *C. islagrande* favors mud rather than clay when forced to choose between these substrates. The lower silt content of hard mud makes it more acceptable than clay.

These substrate preference tests showed that *C. j. louisianensis* favors the muddy substrate as opposed to sand and did not show any favoritism between clay or mud. *C. islagrande* selected sand as opposed to mud or clay and did not show any favoritism between inshore and offshore sands. When it comes into contact with a substrate in which it can burrow and survive, the callianassid stays there.

Salinity Tolerance Tests:

On two occasions (substrate preference tests 4, 11 Appendix) 10 out of 25 (40%) and 13 out of 25 (52%) *C. islagrande* died within 1 hr. To determine if this mortality was the result of osmotic shock, salinity tolerance tests were conducted. The results (Table 6) show that free *C. Islagrande* cannot withstand salinity changes from 29 g/kg to 20 g/kg or lower and that the same salinity variations have no apparent effect on *C. j. louisianensis*. As burrowed *C. islagrande* did not show any apparent response to a change from 29 g/kg to 20 g/kg, the substrate probably acts as a buffer against rapid *in situ* salinity changes within the burrow. These tests have shown that, although extreme salinity change may cause mortality in *C. islagrande*, less drastic changes have no apparent effects on the gross behavior of these callianassids.

DISCUSSION

The habitat isolation, within Mississippi Sound, of *C. j. louisianensis* and *C. islagrande* is apparently a function of species- related differences in ability to burrow and survive in substrates of each habitat. *C. j. louisianensis*, because of poor burrowing efficiency and poor survival in sand is incapable of inhabiting the *C. islagrande* habitat. *C. islagrande*, conversely, as a result of an inability to survive in a silty environment, is incapable of inhabiting the muddy inshore waters. The condition that enables *C. j. louisianensis* to burrow and survive in the sandy littoral zone of some inshore beaches is the availability of mud with which to construct burrow walls.

Although the mean salinity of the offshore environment is higher than inshore (Christmas *et al.* 1966), both environments are subject to drastic short term salinity fluctuations (Christmas *et al.* 1966, Dawson 1965). The salinity tolerance tests (Table 6) were insufficient to determine whether salinity has any influence on the distribution of these callianassids. Although the salinity records (Table 1) show a lower salinity for the inshore stations than for the offshore stations, there is considerable overlap during the spring months. Drastic salinity change may be responsible for population variations in the natural habitat but apparently has little or no influence on the apparent habitat isolation of these species.

Survival is dependent upon burrowing. MacGinitie (1934) stated that *C. californiensis* Dana soon die if their body surfaces are not in contact with either glass tubing or burrow walls. Pohl (1946) stated that free *C. major* die as a result of starvation. With respect to the forms considered here, starvation is not the cause of death. Both free and burrowed mudshrimps (*C. islagrande* survived 2 months in sand, and the sole *C. j. louisianensis* survived 6 weeks in sand) had stomach contents consisting only of a few bacteria. Evidently feeding is not crucial for short term survival providing the animal can burrow into the substrate. There is at present no adequate explanation for the apparent necessity of burrowing *per se* for survival.

These forms were never observed to leave burrows in suitable substrates during the course of the aquarium studies. Gunter (1945) reported *C. j. louisianensis* from the stomach contents of the sea catfish, *Galeichthys felis* (Linneaus) and Darnell (1958) reported *Callianassa* sp. from the stomach contents of the blue channel catfish, *Ictalurus furcatus* (Le Sueur). Therefore, callianassids probably leave their burrows on occasion and are subject to predation by these and other bottom feeders.

Although *C. islagrande* has the ability to burrow into hard mud, this form seldom does so and exhibits poor survival in such bottoms even when burrowed. The mortality of *C. islagrande* on muddy substrates is not exclusively a result of an inability to burrow but also of an inability to tolerate silt. The poor survival of *C. j. louisianensis* on sand can only be correlated with an inability to burrow, which is possibly due to a mechanical inability to handle sand, a considerably less cohesive material than mud.

MacGinitie (1934) stated that *C. californiensis* could only live in sand-mud bottoms tenacious enough for the construction of burrow walls. *C. j. louisianensis* evidently requires a more cohesive substrate than sand. The greater surface areas of both the third maxillipeds and the second and third pereiopods in *C. islagrande* (Fig. 3, Table 3) are probably adaptations for living in a sandy bottom. The relatively smaller surface areas of the corresponding appendages of *C. j. louisianensis* limit this form to the effective handling of only muddy substrates. If the product of the length and breadth (b and h, Fig. 3) for the digging surface of each appendage, divided by the carapace length, is taken as an index of surface area, *C. islagrande* has a considerably greater indexed area than *C. j. louisianensis* (Table 3). The merus-ischium surface area of the third maxilliped (Fig. 3) is strikingly different in these species. The pediform third maxilliped of *C. j. louisianensis* has a mean index of 1.12, whereas the foliaceous third maxilliped of *C. islagrande* has a mean index of 2.40. The other two appendages show less striking differences in gross morphology (Fig. 3), but the mean propodal indices of the second and third pereiopods are considerably greater in *C. islagrande* (Table 3).

The fact that the sand inhabiting *C. major* also has foliaceous third maxillipeds (Pohl 1946) lends support to the conclusion that a foliaceous third maxilliped is an adaptation to a sandy environment. Since the cementing substance may, in large part, be localized in the vicinity of the third maxillipeds, a greater merus-ischium surface area could also serve to enhance the efficient use of the cementing substance. Greater surface area would likewise be advantageous in feeding, enabling the organism to sift through larger quantities of substrate per unit of effort. This would be especially important in the *C. islagrande* habitat where sand grains account for 98% of the volumetric composition of the substrate (Table 4). Sand grains, however, only account for 50% of the recognizable stomach contents of *C. Islagrande*. Evidently this species selectively rejects large quantities of sand. Additional evidence supporting this is shown by the fact that sand grains in the stomach contents were considerably smaller than those of the substrate. Of five specimens examined, the size of ingested sand ranged from 10-800 u with a mean of 107u, whereas that of the substrate ranged from 10-1000u, with a mean of about 400u.

The pediform third maxillipeds of *C. j. louisianensis* are apparently inadequate for feeding in sandy bottom. This is supported by the fact that the sole specimen that burrowed and survived 6 weeks in sand had only a few bacteria in its stomach.

There are no gross anatomical differences in the remaining oral appendages of these two forms. This indicates that the major anatomical differences related to feeding activities are the size and shape of the third maxillipeds.

Pearse (1935) noted that there was a habitat isolation of *C. major* and the burrowing thalassinid, *Upogebia affinis* (Say), at Beaufort, North Carolina. *U. affinis* was found only in muddy bottom and *C. major* was found exclusively in sand. This parallels the situation in the present study. *Upogebia*, however, is not comparable to *C. j. louisianensis* because it is a filter feeder (Pearse 1935, MacGinitie 1930, MacGinitie and MacGinitie 1949) and because adult *Upogebia*, when moved from their burrows, are incapable of constructing new burrows (Pearse 1935, MacGinitie 1930). Pearse (1935) states that *U. affinis* is well adapted for inhabiting a muddy bottom but did not attempt to explain its apparent absence from sand.

From an ecological viewpoint, one group of organisms comparable with callianassids are those polycheates which feed by the ingestion or sifting of substrates. Both groups are responsible for sediment overturn. MacGinitie (1934) and MacGinitie and MacGinitie (1949) compared *Callianassa* with terrestrial earthworms, stating that both perform the same role in their respective environments. The concept that mudshrimps are responsible for sediment overturn is supported by the fact that *C. j. louisianensis*, over a relatively short period of time, partially obliterated the originally distinct substrate interface in columnar studies (Fig. 8).

Gordon (1966) demonstrated that the deposit feeding polychaete *Pectinaria gouldii* (Verrill) was responsible for considerable substrate overturn (10 worms per sq m overturning a 6 cm thick surface layer every 15 years). MacGinitie (1934) stated that an average size *C. californiensis* is responsible for complete turnover of 1 sq in. of substrate to a depth of 30 in. in a period of 240 days. There are no quantitative data on the populations of burrowing Mississippi Sound animals and one cannot estimate the relative importance of callianassid populations in the turnover of Mississippi Sound sediments.

Hailstone and Stephenson (1961) reported that *C. australiensis* carry attached ova for 6 weeks, at which time hatching occurs and planktonic larvae invade the bottom within 9 months. The settling larvae resemble small juveniles and have a carapace length of 1-6 mm. In the case of Mississippi Sound callianassids, ovigerous females were taken in the spring and summer months (Table 1). If a similar growth rate can be projected in Mississippi waters, planktonic juveniles apparently enter the substrate during winter and spring months. Most juveniles collected had a carapace length of 4-7 mm (Table 2) and this suggests that entry into the substrate occurred in smaller size classes.

There were no detectable differences in the tested behavior patterns of juveniles and adults. Therefore, settling juveniles are presumed to have the same behavior patterns as the test animals, survival being dependent upon fortuitous contact with a suitable substrate.

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APPENDIX

Results of Substrate Preference Tests

Except where otherwise noted, substrate arrangement consisted of two equal rectangular sectors (Fig. 5).

Category 1: Sand, inshore *versus* sand, offshore

C. j. louisianensis:

Test 1:

Number of Test Animals: 6

Salinity: 10 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	3	Slow	2
(2) Sand, offshore	3	Slow	2

Additional Observations: Test animals repeatedly constructed shallow burrows, left them and swam continuously for as long as 8 hrs.

Burrowing time ranged from 10 min. to 1 hr. Two free specimens were found after 24 hrs.

C. islagrande:

Test 2:

Number of Test Animals: 20
Salinity: 25 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	11	Rapid	9
(2) Sand, offshore	9	Rapid	11

Test 3:

Number of Test Animals: 20
Salinity: 25 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	8	Rapid	10
(2) Sand, offshore	12	Rapid	10

C. j. louisianensis and *C. islagrande:*

Test 4:

Number of Test Animals: 25 *C. islagrande*
12 *C. j. louisianensis*
Salinity of Test: 20 g/kg
Salinity of *C. islagrande* Colony: 29 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	5 *C. j. louisianensis*	Slow	3 *C. j. louisianensis*
	8 *C. islagrande*	Rapid	8 *C. islagrande*
(2) Sand, offshore	7 *C. j. louisianensis*	Slow	3 *C. j. louisianensis*
	7 *C. islagrande*	Rapid	7 *C. islagrande*

Additional Observations: The behavior of *C. j. louisianensis* was similar to that in Test 1. Three free *C. j. louisianensis* were recovered after 24 hrs. Ten free *C. islagrande* died within 1 hr., death apparently due to osmotic shock (Table 6).

Category 2: Sand (inshore or offshore) *versus* Hard Mud
C. j. louisianensis:

Test 5:

Number of Test Animals: 4
Salinity: 8 g/kg
Arrangement of Substrates: Six juxtaposed sectors, 3 of mud and 3 of sand (Fig. 5).

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	0		0
(2) Hard Mud	4	Rapid	4
	(2 in sector 4, 1 each in sectors 1 and 5) (Fig. 5A)		(Same number recovered from sectors of initial burrowing)

Test 6:

Number of Test Animals: 4
Salinity: 8 g/kg
Substrate Arrangements: Four juxtaposed sectors, 2 of mud and 2 of sand.

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	0		0
(2) Hard Mud	4	Rapid	4
	(2 in sector 1, 2 in sector 4) (Fig. 5)		(Same number recovered from sectors of initial burrowing)

Test 7:

Number of Test Animals: 7
Salinity: 15 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, offshore	1	Slow	1
(2) Hard Mud	6	Rapid	6

C. islagrande:

Test 8:

Number of Test Animals: 12
Salinity: 26 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	9	Rapid	6
(2) Hard Mud	3	Rapid	2

Additional Observations: All test animals recovered from mud had occluded branchial chambers and exhibited blackening of the margins and articulating surfaces of the exoskeleton. Four free specimens were dead after 24 hrs., their branchial chambers occluded and exoskeletons blackened.

Test 9:

Number of Test Animals: 8
Salinity: 27 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	7	Rapid	7
(2) Hard Mud	1	Rapid	1

Additional Observations: All specimens recovered from mud had blackened exoskeletons.

Test 10:

Number of Test Animals: 20

Salinity: 27 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, offshore	14	Rapid	14
(2) Hard Mud	6	Rapid	1

Additional Observations: Five free specimens were found dead, their branchial chambers occluded with silt and margins of the exoskeleton blackened. The specimen recovered from mud exhibited only blackening of the exoskeleton.

C. j. louisianensis and *C. islagrande:*

Test 11:

Number of Test Animals: 25 *C. islagrande*
10 *C. j. louisianensis*
Salinity of Test: 20 g/kg
Salinity of C. islagrande Colony: 29 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, offshore	8 *C. islagrande*	Rapid	8 *C. islagrande*
	2 *C. j. louisianensis*	Slow	1 *C. j. louisianensis*
(2) Hard Mud	4 *C. islagrande*	Rapid	4 *C. islagrande*
	8 *C. j. louisianensis*	Rapid	8 *C. j. louisianensis*

Additional Observations: Thirteen free *C. islagrande* died within 1 hr. due to osmotic shock (Table 6). All *C. islagrande* recovered from mud were dead, their branchial cavities occluded with silt and the margins and articulating surfaces of the exoskeleton blackened.

Category 3: Sand, (inshore or offshore) *versus* Clay

C. j. louisianensis:

Test 12:

Number of Test Animals: 13
Salinity: 20 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, inshore	2	Slow	3
(2) Clay	11	Rapid	10

Additional Observations: Numerous burrow openings appeared in sand and clay sectors (Fig. 6).

Test 13:

Number of Test Animals: 8
Salinity: 20 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, offshore	0	—	2
(2) Clay	8	Rapid	6

C. islagrande:

Test 14:

Number of Test Animals: 18
Salinity: 29 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Sand, offshore	18	Rapid	18
(2) Clay	0	—	0

Category 4: Hard Mud *versus* Clay

C. j. louisianensis:

Test 15:

Number of Test Animals: 16
Salinity: 15 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Hard Mud	8	Rapid	8
(2) Clay	8	Rapid	8

C. islagrande:

Test 16:

Number of Test Animals: 9
Salinity: 29 g/kg

Substrate	No. Burrowing Within 1 hr.	Burrowing Speed	No. Recovered After 24 hrs.
(1) Hard Mud	9	Rapid	8
(2) Clay	0	—	0

Additional Observations: All specimens had their branchial chambers occluded with silt and the margins and articulating surfaces of the exoskeleton blackened.

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