

## Correlation of Benthic Mollusca with Substrate Composition in Lower Galveston Bay, Texas

BY

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(5 Text figures)

THE QUESTION of what role sediment composition plays in the distribution of benthic mollusks is a complex one, for which no brief answer may suffice. Among the increasing number of reports on this subject, its complexity may be demonstrated by comparing several which deal with diverse areas, such as PACKARD (1918, 1918a) on San Francisco Bay, JOHNSON (1965) and MAURER (1969) on Tomales Bay, California, RICE & KORNICKER (1965) on the Campeche Bank and EISMA (1966) on the Netherlands coast. PURDY (1964) has evaluated many other papers dealing with marine sediments as substrates.

The present paper is about benthic mollusks of a limited area wherein other environmental factors may be more uniform than the diversity of the substrate. The value of dead shells in determining the distribution of benthic mollusks is also considered. The area studied is one which is experiencing rapid change through human impact, so that the present data may be useful in detecting future biotic modifications there.

### THE GENERAL ENVIRONMENT

The Galveston Bay complex is a shallow body of brackish water of irregular outline. It extends about 50 km inland, and is divided into 5 parts. An inland eastern part, Trinity Bay, and a western one, Upper Galveston Bay, open southward into Lower Galveston Bay, which has 2 extensions as lagoons along the coast, East Bay behind Bolivar Peninsula and West Bay behind Galveston Island (Figure 1). These bays are less than 2 m deep over most of their area. The natural substrate is of fine sand and smaller particles, with occasional reefs of oyster shell. The Trinity and San Jacinto are major rivers entering the upper bays, and numerous smaller streams drain a more

limited area around the whole bay complex. The bays are connected to the Gulf of Mexico through Bolivar Pass at the east end of Galveston Island, and San Luis Pass at the western end; a small, artificial cut at the base of Bolivar Peninsula allows an interchange of water between East Bay and the Gulf.

The climate is temperate, with air temperatures of 25° to 30° C in summer and 10° to 20° C in winter. Air temperature of 0° C, usually lasting only a few hours, occurs nearly every winter. Cold fronts, called "northers", move in from the north at irregular intervals of 1 to 3 weeks. Their effect is most noticeable in the winter, when periods of sunny, warm days are suddenly terminated by an abrupt drop in temperature, often within an hour, and usually accompanied by rain and strong north winds. There follow a few days of clear skies, with temperature and cloudiness increasing as the next front approaches. Owing to the shallow depth, the water temperature throughout the bay complex responds quickly to that of the air.

A continually high turbidity is present in most of the bay complex, caused by the river-borne sediments and abundant phytoplankton. Objects below 0.3 m depth are scarcely visible. Macroscopic aquatic plants are rare in most of the region, except for a few permanent patches of sea grass and a few species of seasonal algae, mostly in West Bay.

There is a marked salinity zonation throughout the bays, difficult to characterize because of its frequent and irregular fluctuations (PULLEN & TRENT, 1969). At the upper ends of Upper Galveston Bay and Trinity Bay the salinity is about 5‰ most of the time. Lower Galveston Bay, and the Gulf of Mexico near shore, seldom exceed 30‰ and 20‰ is more characteristic. The salinity of West Bay is generally high, while that of East Bay corresponds to that of Upper Galveston and Trinity Bays. The molluscan faunas of East and West Bays reflect their anomalous salinity patterns (unpublished data).

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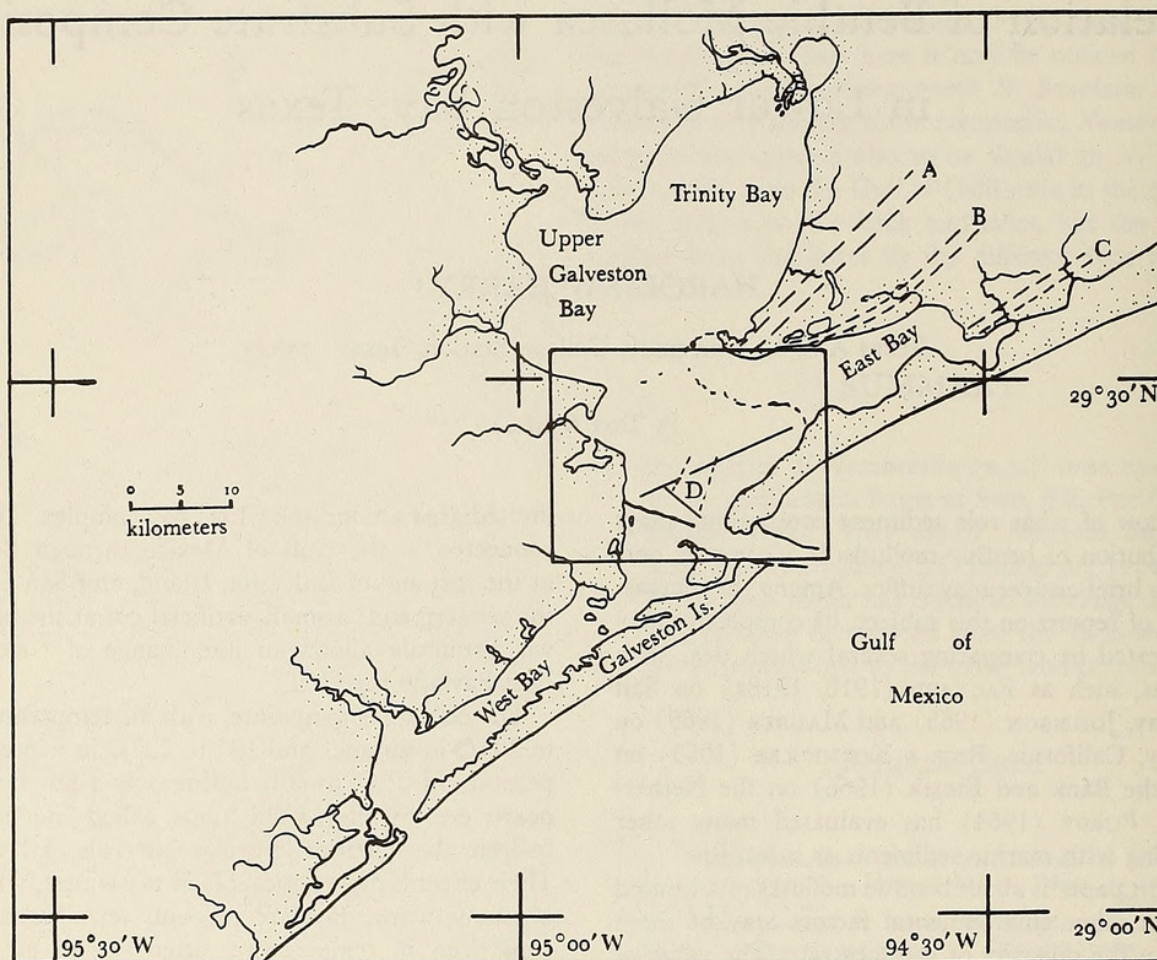


Figure 1

Map of the Galveston Bay Complex, Texas. The rectangular inset includes the part called Lower Galveston Bay, and indicates the 2 transects (see Figure 2). D is the sandy area of an ancient beach crossed by the transects, and the areas A, B and C, margined by dashed lines above East Bay, are thought also to represent ancient beaches

Major oyster reefs separate several of these bays. Lower Galveston Bay is separated from East Bay by Hanna's Reef (Figure 2), and from the upper bays by Redfish Reef (not shown on the map). Oyster reefs between Lower Galveston Bay and West Bay, just west of the causeway from the mainland to Galveston Island, are less symmetrically arranged and have not been named. REHKAMPER (1969: 28) has published a map of the oyster reefs of most of the bay complex.

The tides of this region have a mean range of 0.3m. The lower part of the intertidal zone around all of the bays consists of mudflats at its maximum exposure. But the winds of the more severe "northers" are often strong

enough to push the water mass offshore, so that considerably more than the normal amount of the intertidal zone is exposed at low tide. Around Lower Galveston Bay and East and West Bays, the upper intertidal zone is occupied by the lower zone of the salt marsh, with the cord grass, *Spartina alterniflora*, extending bayward along the water line. The marsh zone of Upper Galveston and Trinity Bays is considerably reduced by the presence of the cliff of a low Pleistocene terrace, and, where the marsh is present, it is transitional to a freshwater marsh. Windrows forming shell ridges about 1 m high, and several to many meters long, accumulate along the bay shore, where there are strong enough winds across a sufficient fetch of water.

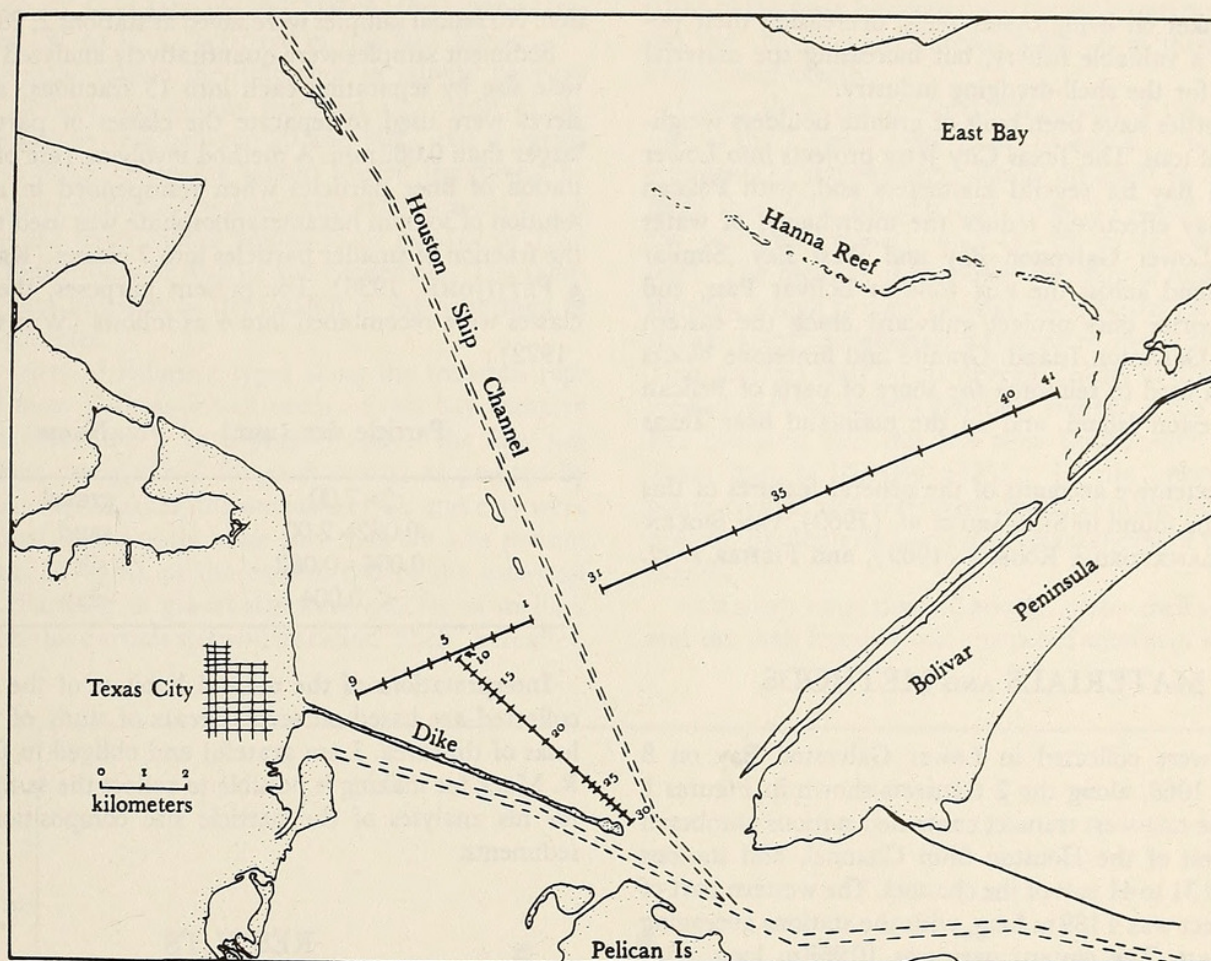


Figure 2

The position of the transects in Lower Galveston Bay, showing the station numbers

The shell mounds are chiefly of *Rangia cuneata* Gray, 1831 in Upper Galveston, Trinity and East Bays, but of oyster shell in Lower Galveston and West Bays. The gulfward shore of Bolivar Peninsula and Galveston Island has a broad beach of fine, siliceous sand, bounded by sand dunes about 1 - 3 m high shoreward, and a surf zone of several hundred meters width gulfward.

The human impact on the Galveston Bay complex has already been intense, diversified and largely detrimental from the environmental standpoint (CARTER, 1970). Most notable with respect to the present study are several artificial shipping channels, which are periodically dredged. The Houston Ship Channel, which is 12.8 m deep, passes across Lower and Upper Galveston Bays, with branches to

the City of Galveston and Texas City. The intracoastal canal is 4 m deep, and passes across Lower Galveston Bay. Sediments dredged from these channels are often piled near them, forming "spoil" islands which may considerably modify the natural movement of the water in the bays. Pelican Island (Figure 2) is almost entirely of dredged spoil.

Dredging of shell from old oyster reefs, which do not produce live oysters in commercial quantities, is an industrial exploitation which has caused much political controversy (ECKHARDT, 1968). The shell is washed free of mud when it is dredged, and the mud is flushed back into the bay, further increasing the turbidity load and redistributing sediments. The discarded mud may settle as a smoth-

ering blanket on living oyster reefs, decreasing their potential as a valuable fishery, but increasing the material available for the shell-dredging industry.

Long jetties have been built of granite boulders weighing several tons. The Texas City Jetty projects into Lower Galveston Bay for several kilometers and, with Pelican Island, may effectively reduce the interchange of water between Lower Galveston Bay and West Bay. Similar jetties extend across the surf zone at Bolivar Pass, and several shorter ones project gulfward along the eastern fourth of Galveston Island. Granite and limestone blocks have been used to reinforce the shore of parts of Pelican and Galveston Island, and on the mainland near Texas City.

More extensive accounts of the general features of this area will be found in SHEPARD *et al.* (1960), VAN SICLEN (1961), LANKFORD & ROGERS (1969), and FISHER *et al.* (1972).

## MATERIALS AND METHODS

Samples were collected in Lower Galveston Bay on 8 February 1968, along the 2 transects shown in Figures 1 and 2. The east-west transect contained stations numbered 1 to 9 west of the Houston Ship Channel, and stations numbered 31 to 41 east of the channel. The western part of this transect was 4 189 m long, with the stations averaging 524 m apart. The eastern part was 10 968 m long, with stations about 1 097 m apart. A north-south transect between the Texas City Jetty and the Houston Ship Channel was 5 179 m long, with stations numbered 10 to 30 spaced about 259 m apart.

All samples were taken with a small orange-peel grab sampler, which circumscribed a circle of 22.5 cm diameter when open and potentially held about 6 l of material when closed. Orange-peel samplers sink deeper into soft sediments than into firm ones and cannot be used for exact quantitative samples (SUMNER *et al.*, 1914; HOPKINS, 1964).

Half a liter of each sample was saved for analysis of the particle size composition of the sediment. The rest was prepared for faunal analysis by washing it through a screen of 1 mm mesh opening; the concentrate remaining on the screen was placed with appropriate labels in plastic bags. At the end of the day the faunal samples were placed in a refrigerator at 4° C. During the next 10 days each sample was examined by placing it in a shallow, white enamel pan (or Petri dish in the case of smaller samples), covering the sample with fresh sea water and picking out representatives of each species. Living specimens all revived and showed activity, even after 10 days of refrigera-

tion. No faunal samples were saved at stations 2, 28 and 40.

Sediment samples were quantitatively analyzed for particle size by separating each into 13 fractions; sediment sieves were used to separate the classes of particle size larger than 0.062 mm. A method involving rate of precipitation of finer particles when resuspended in a 0.18% solution of sodium hexametaphosphate was used to divide the fraction of smaller particles into 7 classes (KRUMBEIN & PETTIJOHN, 1938). For present purposes, the 13 size classes were recombined into 4 as follows (WENTWORTH, 1922):

Particle size (mm)	Name
> 2.00	gravel
0.062 - 2.00	sand
0.004 - 0.062	silt
< 0.004	clay

Interpretations of the natural habitats of the mollusks collected are based on several years of study of the mollusks of this area. I am grateful and obliged to Cornelius R. Mock for making it possible to collect the samples, and for his analyses of the particle size composition of the sediments.

## RESULTS

Station depths varied between 2.1 and 2.4 m along most of the east-west transect, and 2.4 and 3.0 m along the north-south one. Two stations were on oyster reefs (Nos. 10 and 41), at which the depth was only 1 m. Stations 8 and 9 at the extreme western end of the east-west transect had depths of 1.2 and 1 m respectively. The depths are those of "mean low water" as recorded on the U. S. Coast and Geodetic Survey Map of Galveston Bay, No. 1282 (second edition, 1967, converted from feet). No correlation of species and depth was detected along the transects. All of the stations were subtidal, even at the extremes of mud-flat exposure produced by the more severe "northers".

The extensive hydrographic data of the Galveston Bay complex reported by PULLEN & TRENT (1969) contain surface and bottom temperatures and salinities at weekly to monthly intervals, extending over several years at selected stations. Their station 24 was slightly west of the midpoint of the north-south transect of the present study, at a place where the water is 8 feet (2.4 m) deep at mean low tide. At that station, surface and bottom temperatures were usually within 1° C of each other. From January 1963 through November 1967 the bottom temperature ranged

from 8° to 10° C in January and March; the highest temperatures, 29° to 32° C, occurred in July and August.

At the same station the difference in salinity between top and bottom was usually less than 1‰. Most of the time the salinity was between 20 and 30‰, but it varied from 5 to 35‰. Often the salinity varied irregularly by 10‰ or more within a few days, and at all seasons of the year. But the lower values tended to be in May or June and the higher ones in August and September. The salinity fluctuates inversely as the rainfall in the watershed of the bay complex.

The variety of sediment types along the transects represented most of those which occur in this bay complex (REHKEMPER, 1969). In Figures 3 and 4, the four size components are graphed for each station as percent by weight. At most stations the amounts of silt and clay were about equal, but slightly more clay than silt was present at stations 36 to 40, at the eastern end of the east-west transect. Particles of gravel size were entirely of mollusk shells, and this particle size will be called "shell" hereafter.

Most of the finer fractions were non-calcareous sediments, but the amount of calcareous material in them was not determined exactly.

Oyster shell was the chief component of the shell fraction at the 2 oyster reefs (Nos. 10 and 41), whereas the sediments at stations immediately adjacent to them were more than 50% silt plus clay (Nos. 3 - 7 and 34 - 40 on the east-west transect, and 11 - 13 on the north-south one). The method of graphing the data is misleading in showing a high percent of sand interpolated for the interstation areas immediately adjacent to the 2 oyster reefs. That subtidal oyster reefs develop chiefly in areas of sediments finer than sand is generally evident in the Galveston Bay complex, and this has been documented for other Texas bays by NORRIS (1953). In the intertidal zone oyster clumps and reefs may develop where more sand is present, particularly along the lagoon shores of the barrier islands.

At stations other than 10 and 41, oyster shell was sparse, and the shell fraction was composed mostly of other mol-

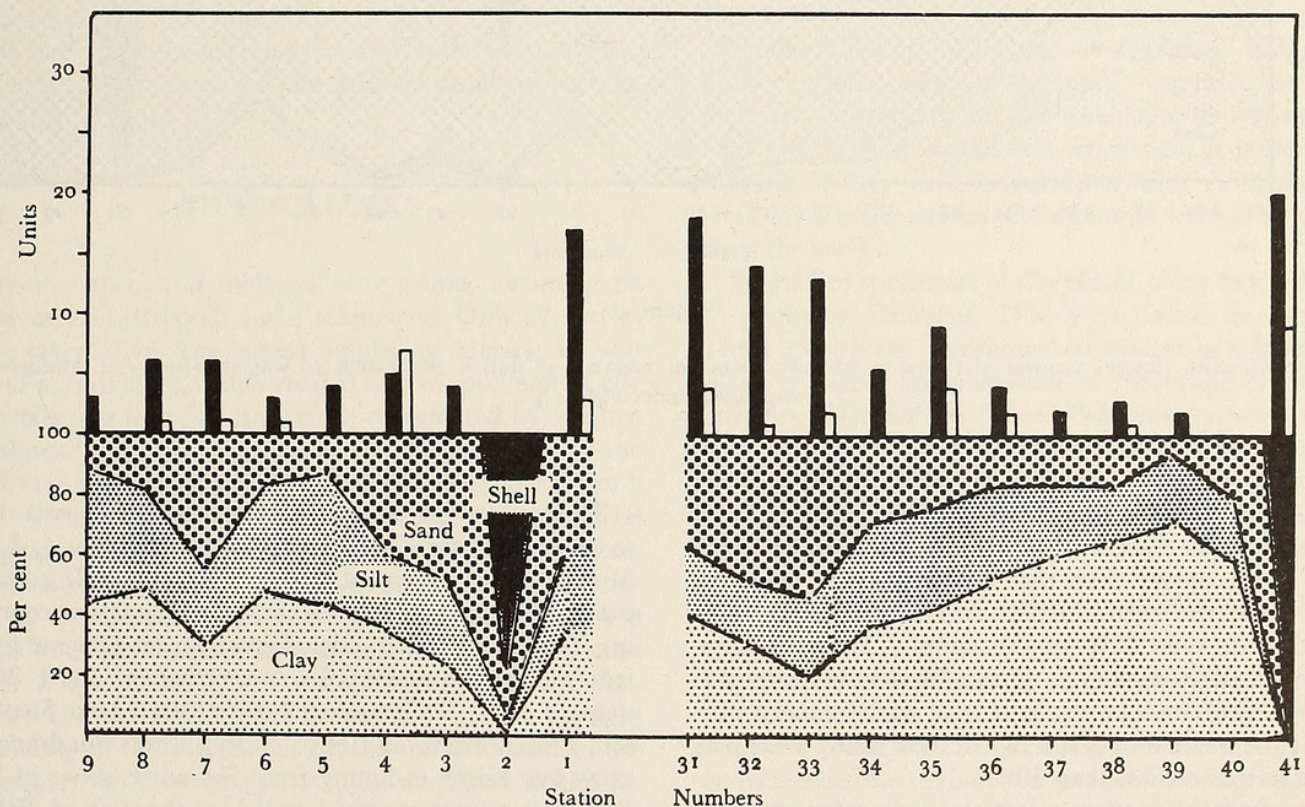


Figure 3

The east-west (upper) transect of Figure 2. The black bars in the histogram represent the number of species of mollusks, alive and dead. The white bars represent the number of live individuals of one or more species. Mollusks were not analyzed at stations 2 and 40. Station 41 was an oyster reef

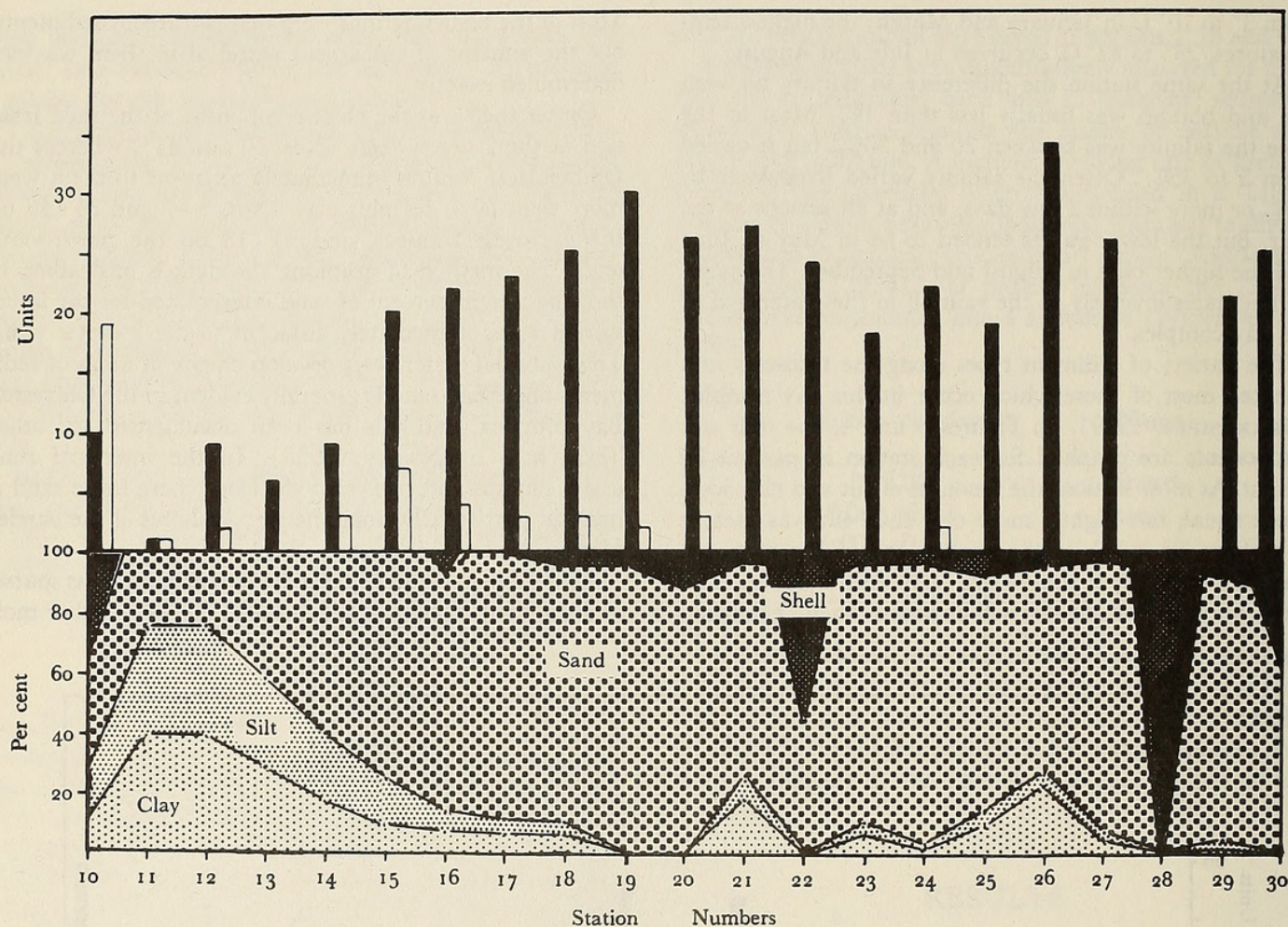


Figure 4

The north-south (lower) transect of Figure 2. Mollusks were not analyzed at station 28. Station 10 was an oyster reef. Histograms explained under Figure 3.

lusks. A shell fraction of less than 1% was present at 18 stations, but that fraction is only shown in Figures 3 and 4 where it was larger than that amount. Away from the oyster reefs, the shell fraction was larger where sand formed more than 50% of the sample. The very large shell fractions at stations 2, 22 and 28 may indicate patches of shell of small areas, the sizes of which are exaggerated by the method of graphing. In most sandy areas, the shell fraction was less than 10%.

Apart from the exceptions just noted, the substrate composition varied gradually from one station to the next along the transects. Owing to the method of graphing, the amount of silt plus clay, hereafter collectively called mud, varied inversely with the amount of sand and shell.

The major sandy areas are those included in stations 14 to 30 on the north-south transect, and stations 1, 2 and 31 to 33 on the east-west transect (Figure 4). If a line be drawn connecting stations 2 and 14, and another connecting 30 and 33 (dashed lines, Figure 1), an elongate figure is formed which suggests an ancient beach. The 1:24000 maps of the U. S. Geological Survey (1961, Lake Stephenson, Frozen Point, and High Island, Texas quadrangles) show low ridges radiating from the north shore of East Bay, and approximately parallel to the axis of Bolivar Peninsula (Figure 1, lines A, B, and C). These may also be ancient beaches. REHKEMPER (1969) noted that sand beaches were developed in this area about 7000 years ago: "they have been encountered in several borings and are

Table 1

Average, maximum and minimum (in parentheses) of species and live specimens of molluscs per station, correlated with the per cent of sand-shell in the substrate. The two oyster reef stations (Nos. 10 and 41) are not included.

Per cent sand-shell in substrate	Number of stations	Average number of species (and range)	Average number of live specimens (and range)
0-25	9	4.0 (2-9)	1.0 (0-4)
26-50	10	8.5 (1-18)	1.9 (0-7)
51-75	4	17.3 (9-27)	3.0 (0-7)
76-100	13	24.2 (18-34)	1.3 (0-4)

reflected in the seismic records as a low-relief system of ridges and troughs." That his data indicated only buried beaches, not exposed at the substrate surface, I think is due to the few borings he took in the area, and the shortness and position of the seismic profile which he published (*l. c.*, p. 36).

### THE MOLLUSKS

Sixty-nine species of mollusks were found, including 42 bivalves, 26 gastropods and 1 scaphopod. Only 22 species were taken alive. The largest number of species, 34, was found at station 26, which yielded no live specimens. Only 1 species was found at station 11, represented by one live specimen. Station 26 had sand-shell forming 83% of the substrate, whereas station 11 was 75% mud. In Figures 3 and 4, the number of species, represented by material ranging from recognizable fragments to living specimens, is indicated by the dark bar above each station. The number of living specimens of all species is shown by the blank bar. The stations are arranged in locality sequence in the 2 figures. In Figure 5 the species are listed systematically and the stations are arranged from left to right according to the increase in percent of sand-shell in the substrate; the 2 oyster reef stations are listed at the far right.

### THE OYSTER REEFS

The mollusks found on the oyster reefs constitute a distinct assemblage which contrasts strikingly with the assemblages

of the other stations. But the 17 species found on the reefs did not represent the total mollusk fauna of this type of habitat in these bays. Six species were found only on the oyster reefs, and 4 others there were found only at single stations away from the reefs. Shells of *Crassostrea virginica* (Gmelin 1791) formed the bulk of shell material at both reefs, but no live oysters were found. This may have been due to the small size of the samples. Although *Ostrea equestris* Say, 1832 was not found at either reef, it probably occurs there, as does *Ischadium recurvus* Rafinesque, 1820, which is chiefly an oyster reef inhabitant in these bays. The total number of species found at these 2 stations was small, 11 and 9 respectively, when compared to other stations. The number of live individuals was relatively large, 19 and 20 respectively, but most of them were the small pholad *Diplothyra smithii* Tryon, 1862. It has been found in the shells of large *Thais haemastoma* Linnaeus, 1758, in calcareous nodules ("caliche," in Brazos River deltaic clays) in West Bay, and even in limestone boulders along the jetties on the beach. *Trachycardium muricatum* (Linnaeus, 1758), *Cyclinella tenuis* (Récluz, 1852), *Seila adamsi* (H. C. Lea, 1845), *Lyonsia* cf. *L. floridana* Conrad, 1849 and *Amygdalum arborescens* Dillwyn, 1817 seem to be more common on oyster reefs than elsewhere in this area. *Odostomia impressa* (Say, 1822) is semi-parasitic on oysters; it is significant that this species was not found elsewhere along the transects, but 2 other species of *Odostomia* were present away from the reefs.

Single live specimens of *Crepidula plana* Say, 1822 and *C. fornicata* Linnaeus, 1758 were found on the reefs. These species are uncommon on oysters in this area; *C. plana* is chiefly an inhabitant of the inside of the shell aperture of large shells (*Thais*, *Polinices*, *Busycon*) carried by hermit crabs within the bays and in the Gulf. *Crepidula fornicata* lives chiefly on the outside of such shells in the Gulf; in the bays it is infrequent.

### STATIONS AWAY FROM THE OYSTER REEFS

The diversity of mollusks at the stations other than those of the oyster reefs seems to be at least partly correlated with the particle size composition of the substrate. For convenience, the variation in particle size is grouped into quartiles, shown by the vertical lines in Figure 5. The number of species of mollusks was low where mud predominated, and high where sand-shell formed the most abundant component. In most samples, the number of species of mollusks was less than 10 where shell-sand was less than half of the total substrate, and more than 10 where sand-shell was present in larger amounts. There are

**Figure 5**

Station Number →	39	9	5	6	37	38	8	36	35	12		11	34	31	4	1	13	7	3	32
Species	% Sand Shell →	6	11	13	16	17	17	18	23	25		26	28	37	39	39	42	43	47	47
BIVALVIA																				
1 <i>Nuculana concentrica</i>				F										R		F				1
2 <i>Noetia ponderosa</i>														Rj						
3 <i>Lunarca ovalis</i>														Fj	R					R
4 <i>Anadara transversa</i>									F					lj		F				
5 <i>Anadara brasiliiana</i>																				
6 <i>Ischadium recurvus</i>																				
7 <i>Amygdalum aborescens</i>																				
8 <i>Crassostrea virginica</i>						Fc		Fc		Fc				Fc					Fc	
9 <i>Ostrea equestris</i>				F					F				Rc						F	
10 <i>Anomia simplex</i>																				
11 <i>Aligena texasiana</i>														Rc		F		R		R
12 <i>Mysella planulata</i>								1	1				F							
13 <i>Lepton?</i> sp.																				
14 <i>Crassinella lunulata</i>														F						
15 <i>Lucina amiantus</i>																				
16 <i>Diplodonta</i> sp.																				
17 <i>Tellina alternata</i>																				
18 <i>Tellina versicolor</i>														F		1				
19 <i>Tellina texana</i>																				
20 <i>Macoma mitchelli</i>																				
21 <i>Macoma tenta</i>							R									R	R			
22 <i>Macoma constricta</i>														R						
23 <i>Donax variabilis</i>							R													R
24 <i>Semele proficua</i>																				
25 <i>Abra aequalis</i>										F						F				M
26 <i>Cumingia tellinoides</i>																				
27 <i>Tagelus divisus</i>																1				
28 <i>Ensis minor</i>																				
29 <i>Dinocardium robustum</i>														Rc						
30 <i>Trachycardium muricatum</i>																				
31 <i>Dosinia discus</i>							Rj													
32 <i>Cyclinella tenuis</i>																				
33 <i>Chione cancellata</i>																				
34 <i>Mercenaria mercenaria</i>														Fj		lj				
35 <i>Petricola pholadiformis</i>																				
36 <i>Mulinia lateralis</i>	F	F	F	F	F	F	R	F	F	F			F			M	F	1F	F	M
37 <i>Corbula caribaea</i>										F				2	5F	F				
38 <i>Diplothyra smithii</i>																				
39 <i>Cyrtopleura costata</i>																				Rc
40 <i>Pandora trilineata</i>																				R
41 <i>Lyonsia</i> cf. <i>floridana</i>																				
42 <i>Periploma orbicularis</i>				1					1											
SCAPHOPODA																				
43 <i>Dentalium texasianum</i>																				
GASTROPODA																				
44 <i>Acteocina canaliculata</i>								R						R		R		R		R
45 <i>Odostomia acutidens</i>																				
46 <i>Odostomia impressa</i>																				
47 <i>Odostomia teres</i>																				
48 <i>Turbonilla aequalis</i>																				
49 <i>Turbonilla interrupta</i>							1		R	R			R	F				R	R	F
50 <i>Pyramidella crenulata</i>																				

Figure 5

Station Number →	33	14	21	15	26	16	25	17	18	23	27	24	29	22	19	20	30	10	41	
% Sand Shell →	53	60	74	74	83	86	87	88	89	90	94	98	99	100	100	100	100			
BIVALVIA																				
1 <i>Nuculana concentrica</i>			F		F			F		F	R	F	R	F	F	F	F			
2 <i>Noetia ponderosa</i>					R	Rj					F	R	R	R	Rj	Rj	F			
3 <i>Lunarca ovalis</i>	F		F	F	Fj		F	F	F	F	F	F	F	F	Fj	Rj	F			
4 <i>Anadara transversa</i>			M	F	M	F	F	F	F	F	M	M	M	F	M	M	F		R	
5 <i>Anadara brasiliiana</i>			F							F						F	Fj			
6 <i>Ischadium recurvus</i>			Fc								R	Rc				Rc	Fc			
7 <i>Amygdalum aborescens</i>																				
8 <i>Crassostrea virginica</i>			Fc		Fc	Fc	Fc	Fc	Fc			Fc				Fc	Fc	M	R	
9 <i>Ostrea equestris</i>		R	F	F	F		F	F		F	F	F	F	F	F	F	R		M	
10 <i>Anomia simplex</i>			R													R				
11 <i>Aligena texasiana</i>	F		R	1	R	F		R	F		F				R	F				
12 <i>Mysella planulata</i>	1																			
13 <i>Lepton?</i> sp.															R					
14 <i>Crassinella lunulata</i>			R		F		F			F	F	F	F	F	F	F	F			
15 <i>Lucina amiantus</i>									R											
16 <i>Diplodonta</i> sp.							R		F				R							
17 <i>Tellina alternata</i>		1j			R			1j							Rj					
18 <i>Tellina versicolor</i>	1		F	1F	F	1F	F	F	1F	R	F	R	R		F	F				
19 <i>Tellina texana</i>											R									
20 <i>Macoma mitchelli</i>			R																	
21 <i>Macoma tenta</i>				1F	F			R	F		F									
22 <i>Macoma constricta</i>						R											R			
23 <i>Donax variabilis</i>	R		F	F	F		F		F	F	F	M	M	F	M	M	M			
24 <i>Semele proficua</i>			R		R						R		R		F	F	F			
25 <i>Abra aequalis</i>	M	F	M	F	M	M	M	M	M	M	M	M	M	M	M	M	M	F		
26 <i>Cumingia tellinoides</i>																		R		
27 <i>Tagelus divisus</i>		1		F				R	F				F	R		R	F			
28 <i>Ensis minor</i>														R					R	
29 <i>Dinocardium robustum</i>																				
30 <i>Trachycardium muricatum</i>	Rj				Rj		Rj				Rj				Rj	Rj	Fj	R		
31 <i>Dosinia discus</i>				1j	Rj	1j			Fj				Rj		Rj					
32 <i>Cyclinella tenuis</i>												Rj							1	
33 <i>Chione cancellata</i>					Rc															
34 <i>Mercenaria mercenaria</i>			F	Rj	F					Fc	Fj			Rj	F	R				
35 <i>Petricola pholadiformis</i>			R				R		R	R		R	R				R			
36 <i>Mulinia lateralis</i>	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M		F	
37 <i>Corbula caribaea</i>				F	F	1F	F	F	1F		F	F	R	F	2F	2F		18	17	
38 <i>Diplothyra smithii</i>																				
39 <i>Cyrtopleura costata</i>																				
40 <i>Pandora trilineata</i>						R		F	F		F		R		R	F				
41 <i>Lyonsia</i> cf. <i>floridana</i>																			1	
42 <i>Periploma orbicularis</i>																				
SCAPHOPODA																				
43 <i>Dentalium texasianum</i>			R		R						F	R	R		F	R	F			
GASTROPODA																				
44 <i>Acteocina canaliculata</i>			R	F	R		R		R		F		R	R	R		R			
45 <i>Odostomia acutidens</i>								R				R			R					
46 <i>Odostomia impressa</i>																		R		
47 <i>Odostomia teres</i>												R								
48 <i>Turbonilla aequalis</i>					F	R		F	F			F			F	R				
49 <i>Turbonilla interrupta</i>	R		R	1	F	F	R	F		R	F			F	F		R			
50 <i>Pyramidella crenulata</i>			F						R											

Figure 5 [continued]

Station Number →	39	9	5	6	37	38	8	36	35	12	11	34	31	4	1	13	7	03	32
Species % Sand Shell →	6	11	13	16	17	17	17	18	23	25	26	28	37	39	39	42	43	47	47
51 <i>Cyclostremiscus pentagonus</i>																			
52 <i>Litiopa melanostoma</i>																			
53 <i>Seila adamsii</i>																			
54 <i>Epitonium angulatum</i>																			
55 <i>Epitonium rupicolum</i>																R	Rc	Rc	
56 <i>Crepidula plana</i>										F			F	F					
57 <i>Crepidula fornicata</i>																			
58 <i>Polinices duplicata</i>		Rj								lj		R	R		Fj				
59 <i>Natica pusilla</i>										1			R	1	F	R			
60 <i>Thais hemostoma</i>																			
61 <i>Anachis obesa</i>										1	1		1	1		R			F
62 <i>Anachis cf. avara</i>																			
63 <i>Mitrella lunata</i>										Rc									
64 <i>Nassarius acutus</i>	R	F	F	R		1	F	1	F	1		F				F	F	F	F
65 <i>Busycon perversum</i>																			
66 <i>Cantharus cancellaria</i>																			
67 <i>Olivella mutica</i>																			
68 <i>Mangilia sp.</i>																			
69 <i>Succinea luteola</i>																			

only 3 exceptions to this generalisation, at stations 1, 14 and 31, among the remaining 36 stations at which both fauna and substrate analyses were made. Those 3 stations were in transition zones between the areas of sand-shell and mud.

The number of species was directly proportional to the amount of sand-shell present as indicated by Table 1. Live mollusks, of one to several species, were found at only 21 or 60% of the 36 stations. They seemed to be more frequent where sand-shell and mud were present in sub-equal amounts, and less frequent at stations having extremes (over 75%) of either of these 2 components (Table 1, Figures 3 and 4).

A few species were so rare in this and other explorations of the area that little can be deduced about their characteristic occurrence. Two other small groups do not represent established, reproducing populations along the transects: one group is of fossil shells, and the other consists of adventitious specimens from adjacent habitats. The vast majority of the species found are established in the area, and of these we may seek to determine those which are limited to or prefer the extremes of substrate type, and those which inhabit a broad substrate diversity.

The species of which little is known regarding their general occurrence are:

Figure 5

The mollusks found along the transects shown in Figure 2, listed in systematic sequence. The per cent of sand-shells is in the 2<sup>nd</sup> row from the top, in increasing sequence from left to right. The vertical lines separate the sediments into quartile classes on the basis of per cent sand-shell. Capital letters refer to dead shells: F: few; M: many; R: one; small letters refer to condition: c: fragments only; j: juvenile; numerals indicate the number of living specimens

*Lepton ? sp.*

*Lucina amiantus* (Dall, 1901)

*Diplodonta sp.*

*Odostomia acutidens* Dall, 1884

*Odostomia teres* Bush, 1885

*Mitrella lunata* (Say, 1826)

*Mangelia sp.*

Found at 1 to 3 stations in limited numbers, these species were about as infrequent in other surveys which I have done in the bays (see also HARPER, 1970 and PETERSON, 1972). None were found alive during this study; most were found only in substrates of more than 50% sand-shell, but *Mitrella* was found at one station of only 25% sand

Figure 5 [continued]

Station Number →	33	14	21	15	26	16	25	17	18	23	27	24	29	22	19	20	30	10	41
% Sand Shell →	53	60	74	74	83	86	87	88	89	90	94	98	99	100	100	100	100		
51 <i>Cyclostremiscus pentagonus</i>	R	R		R		R													
52 <i>Litiopa melanostoma</i>					R												R		
53 <i>Seila adamsii</i>					R													R	
54 <i>Epitonium angulatum</i>					R										R				
55 <i>Epitonium rupicolum</i>		Rc	Rc	1	R	Rc		1									Fc		
56 <i>Crepidula plana</i>	F				F	F	F	R	F		F	F		F	F	F	F	1j	
57 <i>Crepidula fornicata</i>														R					1
58 <i>Polinices duplicata</i>		1j		R		Fj	Fj	Rj		Rj	Rj				F	F	F		
59 <i>Natica pusilla</i>			F	1	R	F		F			R	R		F	F	R	F		
60 <i>Thais hemostoma</i>									Rc					Rc		Rc	Fc	R	
61 <i>Anachis obesa</i>			F		F	F		F	1R			F	F	F	F	F		F	
62 <i>Anachis cf. avara</i>					R						R								
63 <i>Mitrella lunata</i>																			
64 <i>Nassarius acutus</i>	1F	F	F	F	F	1F	F	1F	F	F	F	F	F	F	1F	1	F		
65 <i>Busycon perversum</i>										Rc									
66 <i>Cantharus cancellaria</i>						R													
67 <i>Olivella mutica</i>			R						R										
68 <i>Mangilia sp.</i>						R													
69 <i>Succinea luteola</i>										R									

(carried there by hermit crabs?). *Lucina amiantus* has been found infrequently in Lower Galveston Bay; *Mitrella* is abundant in the western part of West Bay; *Mangelia* has been found on oyster reefs of West Bay, where its shells are sometimes so eroded, even while the animal is alive, that sculptural features are obliterated.

Six species are represented by fossil specimens, mostly of species which do not live as regularly established populations along these transects:

*Anomia simplex* d'Orbigny, 1842

*Chione cancellata* (Linnaeus, 1767)

*Donax variabilis* Say, 1822

*Noetia ponderosa* (Say, 1822)

*Anadara brasiliensis* (Lamarck, 1819)

*Lunarca ovalis* (Bruguière, 1797)

Most of the presumed fossil shells of the above list were opaque, grey, somewhat chalky, and eroded in a peculiar way which suggested the deterioration of the organic matrix in them. *Anomia* was an exception: fresh shells are white and only slightly opaque, but weathered shells become light tan or jet black, yet retain their translucency. *Anomia* valves are common on the beach, and the species has been found alive on oysters in West Bay, as well as on various other shells at several meters depth offshore. Live specimens are rare in this area. Its abundance as shell is

out of all proportion to the live population which seems to occur here.

Only a single valve of *Chione* was found. I have never found it alive, or even as empty shells in dredged samples in the Galveston Bay area, before the present survey. Empty shells, all worn, are common on the beach at the western end of Galveston Island, and they become progressively abundant on the beaches farther south; at Port Isabel they sometimes pave the mainland shore of Laguna Madre. All specimens in the Galveston area are probably fossil, representing a time when the climate was warmer here. That occasional adventitious specimens may occur alive cannot be discounted.

Most species of the above group are characteristic of the nearshore fauna along the beach, where their shells are often washed in abundantly. That they were limited (except *Lunarca*) to the sandy stations on the 2 transects is further evidence that these stations may represent an ancient beach which was washed by the surf of the open Gulf in prehistoric time.

*Donax variabilis* lives at the shoreward edge of the surf zone on the sandy beach. It is occasionally found alive in the bays as small, adventitious juveniles. On the beaches it does not seem to live seaward of the surf zone, yet occasional bottom samples from well offshore have specimens

of large size which are probably fossil, indicating ancient beaches. I have examined *Donax* shells from 42 m [18 fathoms] offshore from Galveston.

*Noetia* and *Anadara brasiliiana* are characteristic species of the outer surf zone along the beach. I have not found large, live specimens of them in the bays. The abundance of *Lunarca ovalis* shells of medium to large size was again disproportionate to the frequency with which live specimens, some large, are found in the bays. It is another characteristic species of the outer surf zone and beyond in the Gulf to depths of several meters.

Adventitious species may be subdivided into 2 groups according to the methods whereby they arrived at their unusual situation: (1) species adventitious by active vagility are those which came in by their own locomotor abilities, either as larvae or adults; (2) species adventitious by passive vagility are those which arrived by some other agency than their own ability to move about. Both groups seem to be well represented along the transects. Those adventitious here by active vagility are:

*Anadara brasiliiana* (Lamarck, 1819)

*Noetia ponderosa* (Say, 1822)

*Dosinia discus* (Reeve, 1850)

*Tellina alternata* Say, 1822

*Macoma mitchelli* Dall, 1895

*Tellina texana* Dall, 1900

The first 4 species are characteristic of the outer surf zone, and they extend to varying depths gulfward. Except for one large, fresh shell with attached valves of *Tellina alternata* (at station 26), the adventitious specimens of these 4 species were only represented by small specimens, alive or as fresh but empty shells. They were only found at stations of high sand-shell content in those parts of the transects which may represent an ancient beach. Probably their veligers were carried by flooding tides into the bay; those which settled on sandy substrate were able to survive and grow, rarely even to adult size, but conditions were not suitable for maintaining a permanent population.

The adventitious juveniles of *Noetia* and *Anadara brasiliiana* at stations where there were also presumed fossils of those species admittedly cast doubt on the hypothesis that the larger shells may be fossil at these stations. Yet the fossil shells were more abundant and frequent from station to station than the adventitious juveniles.

*Macoma mitchelli* is a species of Upper Galveston, Trinity and East Bays, thus of areas of low salinity, generally, than that prevailing along the transects. *Tellina texana* is characteristic of West Bay, which usually has higher salinity than Lower Galveston Bay. These species were represented by single specimens of adult size.

Species	Probable agent of dispersal
<i>Dinocardium robustum</i> [Lightfoot, 1786]	man ?
<i>Cyclostremiscus pentagonus</i> (Gabb, 1873)	hermit crabs
<i>Pyramidella crenulata</i> (Holmes, 1859)	hermit crabs
<i>Busycon perversum</i> (Linnaeus, 1758)	hermit crabs
<i>Epitonium angulatum</i> (Say, 1830)	hermit crabs
<i>Cantharus cancellarius</i> (Conrad, 1846)	hermit crabs
<i>Olivella mutica</i> (Say, 1822)	hermit crabs
<i>Crepidula plana</i> Say, 1822	hermit crabs
<i>Crepidula fornicata</i> (Linnaeus, 1767)	hermit crabs
<i>Litiopa melanostoma</i> Rang, 1829	<i>Sargassum</i>
<i>Succinea luteola</i> Gould, 1848	drift wood

The only bivalve of this list, *Dinocardium*, was represented by a small fragment of a large shell. This species lives beyond the surf zone of the open beach and gulfward to several meters. I have never found it alive or as dead shell in the bay complex before the present survey. The fragment may have been discarded by man; it is a popular collector's item, but large specimens are not easily obtained by dredging in this area (HARPER, 1970).

The other species of the list are all snails, most of which are assumed to have been brought in by hermit crabs (Paguridae). These crabs have a well known propensity for exchanging a smaller shell for a larger one as they grow, with little regard for the species of the shell. *Cantharus cancellarius* and *Busycon perversum* live only in the Gulf beyond the surf zone in the Galveston area, although *Busycon*, at least, invades the bays at Corpus Christi. I have never found these 2 species alive in the Galveston Bay complex, but hermit crabs are often found carrying shells of both species there. That the smaller species of snails of the above list are also brought in by hermit crabs is more speculative: they are known to live beyond the surf zone in the Gulf, but I have not found them alive in the bays. *Olivella*, *Pyramidella*, *Cyclostremiscus* and *Epitonium angulatum* seem to live just beyond the surf zone in the Gulf.

Probably several other species of snails should be added to the list of those having their shells dispersed by hermit crabs, even within the limits where they normally live: *Thais haemastoma* is chiefly found on oyster reefs, jetties, pilings and other surfaces on which barnacles are abundant. *Anachis avara* (Say, 1822) lives chiefly intertidally, on the jetties and in the bay on oysters. Even the shells of *Dentalium* harbor hermit crabs in West Bay (PETERSEN, 1972). The 2 species of *Crepidula* were almost certainly distributed along the transects by hermit crabs, although the crabs never seem to inhabit the *Crepidula* shells themselves.

The pelagic sea weed, *Sargassum* spp. is not infrequently carried into the bays by flooding tides on the occasions when it appears along the beach, one to several times per year. *Litiopa* is a frequent inhabitant of *Sargassum* while the latter is well offshore, and the snail is not known to live elsewhere. The shells are very rare in offshore sediments, where they might be expected to accumulate on substrates over which the sea weed frequently floats; perhaps the shells are not very durable in substrates. Most *Litiopa* seem to drop off before the *Sargassum* is washed upon the beach.

*Succinea luteola* is a common land snail which frequently seals itself to wood along the Texas coast. Great quantities of drift wood and many species of land snails, most with narrow, toothed apertures and many-whorled shells often float across the bays at times of heavy rains in the hinterland; the drift wood and land snails are thrown upon the beach after they enter the Gulf. *Succinea* shells are rare among such stranded specimens, perhaps because their shape allows them to be easily filled with water, so that they sink soon after entering the bays.

Besides the species segregated above, there remain those which have established reproducing populations along the transects. Of these, the great majority occurs throughout a wide variety of substrate composition, from mud to sand-shell (Figure 5), but a few species seem to be limited to the sandy and others to the muddy ends of the range.

Only *Mysella planulata* (Stimpson, 1857) and *Periploma orbiculare* Guppy, 1878 seem to be restricted to substrates of more than 50% mud. One of the 4 stations at which *Mysella* was found had slightly more sand-shell than mud (No. 33, 53% sand-shell), but this may be considered essentially a species of muddy substrate. Both species were found at stations of more than 75% mud. Nearly all specimens of these species were alive, the exception being *Mysella*, which was represented at station 34 only by 2 fresh valves.

*Periploma orbiculare* is a new addition to the list of Mollusca of the Northwest Gulf of Mexico. It is common in the middle of West Bay, where it occurs in soft mud below low tide level. I have recently found it in Matagorda Bay, farther south on the Texas coast. This species has been tentatively identified by Dr. Joseph Rosewater, a specialist on the Periplomatidae (ROSEWATER, 1968).

The only other species limited to mud environment was *Cyrtopleura costata* (Linnaeus, 1758), which was found at only one station, represented by fragments of a large valve. The sampler would probably not collect live *Cyrtopleura*, which burrow over 30 cm deep even when fairly small. It

is common in the intertidal zone of the more saline bays, chiefly in the winter.

The list of species which were found only in substrates of more than 50% sand-shell is considerably longer:

- Ischadium recurvum* (Rafinesque, 1820)
- Semele proficua* (Pulteney, 1799)
- Trachycardium muricatum* (Linnaeus, 1758)
- Petricola pholadiformis* (Lamarck, 1818)
- Dentalium texasianum* Philippi, 1848
- Turbonilla aequalis* (Say, 1827)
- Thais haemastoma* (Linnaeus, 1758)

These species have all been found alive in Lower Galveston Bay or West Bay, but none were found alive during the present study. *Ischadium* is chiefly limited to oyster reefs and the concrete rubble often used to buttress the bay shores; *Petricola* is a deep burrower, often found with *Cyrtopleura* in the intertidal zone, but characteristically in clay. *Dentalium* has been found alive in West Bay, but it may only occur alive in the more saline bays at irregular periods of several years (PETERSEN, 1972), perhaps being adventitious there from populations established offshore.

The species indigenous to substrates of both more and less than 50% sand-shell are the following. The number of stations at which each was found is indicated for the mud and sand-shell substrates, and the numbers in parentheses indicate the number of live specimens found in each bottom type.

Species	mud	Sand-shell
<i>Nuculana concentrica</i> (Say, 1824)	4(1)	11(0)
<i>Lunarca ovalis</i> (Bruguière, 1792)	4(1)	15(0)
<i>Anadara transversa</i> (Say, 1822)	3(1)	15(0)
<i>Crassostrea virginica</i> (Gmelin, 1791)	5(0)	9(0)
<i>Ostrea equestris</i> Say, 1834	4(0)	13(0)
<i>Aligena texasiana</i> Harry, 1969	4(0)	10(1)
<i>Crassinella lunulata</i> (Conrad, 1834)	1(0)	11(0)
<i>Tellina versicolor</i> DeKay, 1843	2(1)	14(4)
<i>Macoma tenta</i> Say, 1834	3(0)	5(1)
<i>Abra aequalis</i> (Say, 1822)	3(0)	17(0)
<i>Tagelus divisus</i> (Spengler, 1794)	1(1)	8(1)
<i>Mercenaria mercenaria</i> (Linn., 1758)	2(1)	8(0)
<i>Mulinia lateralis</i> (Say, 1822)	16(1)	17(0)
<i>Corbula caribaea</i> d'Orbigny, 1842	4(7)	12(6)
<i>Pandora trilineata</i> Say, 1822	1(0)	7(0)
<i>Acteocina canaliculata</i> (Say, 1822)	5(0)	10(0)
<i>Turbonilla interrupta</i> (Totten, 1835)	8(1)	12(1)
<i>Epitonium rupicolum</i> (Kurtz, 1860)	3(0)	7(2)
<i>Polinices duplicatus</i> (Say, 1822)	5(1)	9(1)
<i>Natica pusilla</i> Say, 1822	5(2)	10(1)
<i>Anachis obesa</i> (C. B. Adams, 1845)	6(4)	10(1)
<i>Nassarius acutus</i> (Say, 1822)	14(3)	17(5)

The wide occurrence of the 2 oysters, *Ostrea* and *Crassostrea*, may result from their propensity to attach to any firm object, often very small, throughout this bay; they do not survive more than a year or so in areas unfavorable to the growth of oyster reefs. *Crassinella* may be adventitious from a neighboring colony known to persist in the Houston Ship Channel (HARRY, 1966).

Probably the absence of live individuals of those species represented only by dead shells was a matter of sampling, or it may indicate irregular periodicity or patchiness in their distribution. Even a cursory examination of the relative abundance of live individuals to dead shells, as detailed in Figure 5 and summarized above, indicates the ratios are larger on the muddy side of the midway point of particle size array. Or, if a species is found in muddy substrate it is more likely to be alive, whereas if it is found in a substrate predominantly of sand, the converse is true. The shells of most species which live in a broad array of substrate composition are more durable in sand than they are in mud.

Some species of the above list live as established populations both in the surf zone and gulfward, as well as in the subtidal parts of the more saline bays. They present special problems in determining their optimal and limiting environments. An example is *Anadara transversa*: small, live specimens less than 1 cm long are regularly abundant in the more saline bays and beyond the surf to 7 m [4 fathoms]. But in aquaria these specimens will grow to twice that size, or slightly more, and such large specimens are characteristic of the zone from 9 to 18 m [5 - 10 fathoms] in the Gulf. Whether the specimens less than 1 cm long reproduce is unknown, but it is possible that this species is regularly adventitious near shore and in the bays, where it may not reach maturity. HARPER (1970) also noted the abundant but small live specimens of this species along the Gulf shore.

The data of the above list and Figure 5 demonstrate another interesting point which has not been reported: the overwhelming abundance of 3 species of shells in most subtidal samples. The species are *Mulinia*, *Abra*, and *Nassarius acutus*. Shells of these species are so abundant that they obscure other species in a sample, making the sample difficult to analyze. This assemblage is characteristic of offshore samples from 6 to 36 m at Galveston, that is, from the outer surf zone to as far offshore as I have reliable data. It extends eastward to Alabama, and southward at least to Corpus Christi, thus covering an area of thousands of square kilometers. But live individuals of these 3 species are about as uncommon in the offshore area as they are in the present samples.

## DISCUSSION

Ecologists term the living biota of a given area a biocoenosis, defined by a uniformity of species composition, to emphasize the interaction of the organisms as a dynamic community. To the neoecologists, who limit their interest to the living phenomena of Recent geological time, the cycling of materials and transfer of energy brought about by the death of members of the community may be the most important aspect of the biocoenosis, particularly in constructing food chains and other ecological "models". The paleoecologists also recognize a necrocoenosis (a population of dead organisms not yet fossilized), a thanatocoenosis (dead organisms derived from one or more biocoenoses which did not live in the environment in which they were entombed) and other concepts which subtly differentiate various assemblages of organic remains (HECKER, 1965).

These concepts are particularly useful in studying the distribution of benthic marine mollusks. The question of whether empty shells should be included in such studies is a vexing one which has been a major impediment to doing detailed synecological work on these animals. Fresh shells, showing little wear, are particularly troublesome, especially when no live ones are found. To preserve the samples in alcohol or formalin causes extreme retraction in some snails, so that one can not be sure, without crushing the shell, whether they were alive when collected. Drying the samples is equally poor, no less for small bivalves than for many snails. Refrigerating the samples and reviving the live specimens in sea water, as was done in this study, is a satisfactory method; but it requires much tedious work soon after the samples are collected, if it is to be reasonably accurate.

The reports of some benthic surveys have ignored the problem, with the assumption that if the area of the survey was sufficiently large, and some species were limited in their distribution within it, they lived in the part of the area where they were found, whether or not live specimens were taken during the survey (PACKARD, 1918, 1918a). Some studies do not mention whether or not their data were based solely on living material (RICE & KORNICKER, 1965; HARPER, 1970). A notable exception is an unpublished thesis by KENNEDY (1959), which reports the percent of each species of mollusk shell found at 18 stations along an offshore transect east of Galveston, and furthermore notes the number and identity of live individuals. The number of live individuals in each sample was usually very low in comparison with the number of empty shells. He gave generalized analyses of the sub-

strate type of each sample, but these may not be characteristic of the whole of each station because the samples were taken by a dredge, hauled over a considerable distance at each station. The large range of other factors along his transect precludes a close comparison with the data of this study.

EISMA (1966) studied several hundred bottom samples from the North Sea along 19 transects normal to the Dutch coast, and correlated the benthic mollusks with substrate type, shore proximity and other factors. He relied chiefly on live specimens, but also recorded empty shells. The relative distribution of living specimens and their dead shells is mapped for several of the species. In all cases, the area of the dead shells was somewhat larger than the area in which he found living specimens, and the latter was usually included in the former. He noted that the snail, *Buccinum undatum*, was not found even as dead shells in his samples, and that one bivalve, *Macra corallina*, was found only a few times (evidently alive). However, shells of both species are abundant on the beach along the Dutch coast. Of other species which he did not find living, *Spisula solida* and *Mya truncata* were "regarded as rather common", and 2 others, *Cardium crassum* and *C. echinatum*, "lived at least once in a rather dense population not far offshore, as their mass-strandings indicate, but [they] have disappeared completely since then" (EISMA, 1966: 120).

If we consider only the living mollusks away from the oyster reefs, the data of the present study support the view that a certain amount of mud is favorable to abundance, and that too little or too much results in depauperate molluscan faunas. Probably each species has a broad, if limited range of preference of particle size array. EISMA (1966: 142 - 144) emphasized this, and summarized the extensive literature which has already appeared on the mollusks of his area.

The ecological importance of silt and clay in the distribution of benthic marine organisms, particularly filter and detritus feeders, is being increasingly recognized (PURDY, 1964). Organic material dissolved in sea water, where it is poorly available as food, may be concentrated by a factor of thousands by being adsorbed on the finer particles in suspension and on the bottom, and thus more available as food for filter and detritus feeders. Silt and clay in small amounts give a certain rigidity to sandy substrates, so that tunnels of burrowers would tend to stay open. But in filling the interstices between larger particles, the finer sediments may inhibit movement of capillary water, producing anaerobic conditions and an acid environment which is detrimental to the preservation of shell.

That mollusk shells are durable objects which may last for a long time after the death of the animal, and the possibility of their being moved about by various agents, have been reasons sufficient to render them suspect in charting the distribution of benthic mollusks. Yet if all shells were equally durable and easily moved about, one could expect to find a large number of species and many specimens of molluscan shells in every benthic sample. Such is obviously not the case. Probably the shells of some species are more durable than others, remaining for years in the environment, and easily fossilized, whereas the shells of other species persist in recognizable form for brief periods only. The shells of a given species might last longer in one environment than in another.

An early attempt to note the differential durability of shells in general in contrasting environments was reported by HAMACKER (1930). He noted that Long Island Sound was populated by numerous species of mollusks, the individuals of which lived no more than a few years; and he wondered why that body of water had not been completely filled up with mollusk shells since the last glacial period. Analyses of the calcium carbonate content of particles of sand size and smaller from 84 beach stations between upper New Jersey and the Florida Keys demonstrated the gradual increase of calcium carbonate southward, from an average of  $\frac{1}{2}\%$  in the northern samples to 100% in the Keys. Oddly, he did not expressly note the direct correlation of calcium carbonate persistence with increasing average temperature. But he also noted that samples of substrate from the lagoon side of the coastal barrier islands had less carbonate than those from the ocean side. "Why the waters of the New Jersey coast should dissolve the shells more rapidly than those of the Florida coast I can not say, nor yet why the enclosed salt waters are more active in this respect than the water of the open sea" (HAMACKER, 1930: 13).

The shells which seem to have the greatest durability in their natural habitat in the Galveston area are those of the following species: *Anadara transversa*, *A. brasiliensis*, *Lunarcia ovalis* and *Noetia ponderosa* of the Arcidae; *Ostrea equestris* and *Crassostrea virginica* of the Ostreidae; *Anomia simplex* of the Anomiidae; *Rangia cuneata* and *Mulinia lateralis* of the Mactridae; *Donax variabilis* of the Donacidae; and *Abra aequalis* of the Semelidae. These species have been singled out as the most durable because their shells are the most abundant throughout the Galveston area. It would be difficult at present to propose a more precise ranking of the relative durability among them. Other species can be cited as somewhat less durable than these, and such a list would include some Pectinidae

and Veneridae. In coastal marine environments (*i. e.*, discounting deep sea pteropod oozes), snail shells are rarely as persistent as a group as are the shells of bivalves.

The 12 species thought to be most durable represent only 6 families, and this suggests that some intrinsic characteristic of these shells may be different from that of other, less durable species even within the families to which they belong. The thinness and delicacy of *Anomia*, *Mulinia* and *Abra* shells suggest that the thickness of the shell is not the only factor responsible for the shells of some species being more durable.

There are considerable numbers of *Rangia* and oyster shells at localized places offshore of Galveston, at 27 to 32½ m [15 to 18 fathoms] and beyond, which are generally interpreted as representing fossil oyster reefs; these were probably reefs of a mid-bay environment, where *Rangia* and *Crassostrea* overlap, for the 2 usually occur together. That there are fossil beach deposits in the same offshore area is not as well known. The beach deposits contain *Donax*, *Anomia* and 4 species of Arcidae; some of the *Mulinia* and *Abra* shells may be fossil there also. PARKER (1960: 330) mapped the distribution of fossil *Donax variabilis* at 2 general zones, at 27 and 54 m [15 and 30 fathoms] off the coast of Texas and Louisiana. These presumably represent ancient beaches, formed during "still-stands", as the water level fluctuated coordinately with the formation and destruction of the Pleistocene ice caps. His maps also indicate in a general way the presence of *Crassostrea* and *Rangia* assemblages in those areas. Although a few other species of the beach and bay assemblages are mentioned as fossils associated with the above (PARKER, *op. cit.*, 328 - 329), including some snails, the list of fossilized species is still far short of the species known to live in those assemblages along the Texas coast today.

The expense and other factors involved in determining the age of shells in marine substrate material by their radioactive isotope content (carbon-14 dating) has possibly impeded the use of this technique. In any event, shells so used are usually preselected on the basis of their general appearance before analysis is made; species of the thanatocoenosis are used for the analyses and those of the necrocoenosis at the same place are rejected. In a report on the age of fossil shells offshore from Texas the species cited above as most durable constitute more than half of those used for isotope studies (CURRAY, 1969: 254 - 255). Unfortunately, the analyses of several species are often combined in that study and so it sheds little light on the question of ranking species according to the relative durability of their shells. But many reports on determining the age of shells by using isotope analysis do not even list the species which were used (numerous references in the index of the symposium edited by SHEPARD *et al.*, 1960).

The conflicting accounts of the mineral composition of bivalve shells, that is, whether the shells of a family are of aragonite or calcite or both, and the relative durability of these major mineral species, merely confuse the issue. One need only compare the accounts of BØGGILD (1930), and the earlier papers cited by him (which he mostly contradicted) with the more recent studies by TAYLOR & KENNEDY (1969) and TAYLOR, KENNEDY & HALL (1969). The mineral composition of the shells of the Galveston area is not known.

Important factors affecting the abundance of shells of a given species are the rates of production and destruction of the shell. If the shells normally decompose in their natural environment in a shorter time than the life span of the individual there may be few or no dead shells present, and the species would be represented chiefly by living individuals. Recalling that shells in general seem to last longer in sandy than in muddy substrates, we may find some support for the above hypothesis from the data of Figure 5. *Periploma orbiculare* and *Mysella lunulata* were represented only by living specimens, with the exception of one fresh, dead shell of *Mysella*. These species are mud dwellers, and their empty shells probably decompose in a shorter time than the length of life of the average individual. *Anachis obesa* was found only as live individuals at the muddier stations; but it was also found alive once, and abundantly represented by dead shells in the sandy samples. The durability of this shell in mud may be shorter, and in sand longer, than the life span of this species. The same may be true of shells of *Natica pusilla*.

If the shells of a species were very durable relative to the life span, and if the living population was sparse, only dead shells might be found in a survey of the present kind. This is probably true of *Abra* in the present study, and it may also account for EISMA's (1966) finding only dead shells of some common species in the North Sea.

The role of vagility in the distribution of mollusk shells, particularly beyond the area in which reproducing populations are permanently established, may be somewhat more difficult to determine than that of their durability. Five agents were postulated as responsible for moving shells about in the present study area. In contrast to their relative durability, gastropod shells have a greater vagility than those of bivalves, chiefly because of hermit crabs, but also because there are several pelagic species, and snail shells may be more easily rolled about by currents.

With the exception of a fragment of *Dinocardium*, adventitious bivalves in the present study are thought to have reached their present station through chance settling of the larvae. They grew only to a small size, or very rarely to a size which is assumed to be adult. *Tellina alternata*

is an example of the "small adults" adventitious on the transects studied. Such adventitious adults are usually isolated. In Lower Galveston Bay I have also seen small, isolated live adults of *Dosinia discus*, another bivalve of the surf zone and seaward thereof, and on one occasion there were found single small live adults of *Raeta plicatella* (Lamarck, 1818) and *Pitar texasiana* (Dall, 1892) (HARRY, 1969; see also BOYER, 1967 for the distribution of the latter species as *Callocardia*). But in the samples of the present study, *Dosinia* was represented only by small juveniles; the absence of this species as fossil adults in the ancient beach may indicate that it is less durable than the other beach shells.

Some species may be regularly adventitious in areas where they are not established, as juvenile *Dosinia* and *Anadara transversa*; but other species, as *Raeta* and *Pitar*, may be adventitious only at irregular intervals of several years. A remarkable instance of a species being regularly adventitious over an extended area has been reported by CHANLEY (1969), who persuasively argued that the *Donax fossor* Say, 1822, found from Connecticut to North Carolina, is in reality only environmentally modified populations of *Donax variabilis* Say, 1822 found from Virginia southward along the Atlantic coast of North America. He proposed that the *D. fossor* populations might grow to maturity and reproduce during the warmer part of the year, thus extending the population farther northward during that season, but he concluded that *Donax* does not regularly survive the winter in its northernmost range. There is a growing body of evidence that live specimens are not necessarily reliable indicators of established populations in a given area.

The vagility potential, both of live and dead individuals, may vary among species. The adventitious species of the present study were all from adjacent environments, but the species found were only a few of those from whence they came. Most conspicuous by their absence were *Littorina irrorata* (Say, 1822) and *Cerithidea pliculosa* (Menke, 1829), both of the salt marshes; their shells are often used by hermit crabs on the mudflats. Perhaps those shells are less durable than *Cantharus*, which lives much farther away from the present transects than the 2 marsh species.

The 5 agents postulated as responsible for the vagility of adventitious species of the present study area do not exhaust the possible ones. Transportation of shells by water movement is an additional and plausible factor. JOHNSON (1965) studied the relation of the bivalves of the biocoenosis and necrocoenosis in Tomales Bay, California. He concluded that "There are a few places in the bay with accumulations consisting primarily of transported shell remains, and in each of these accumulations

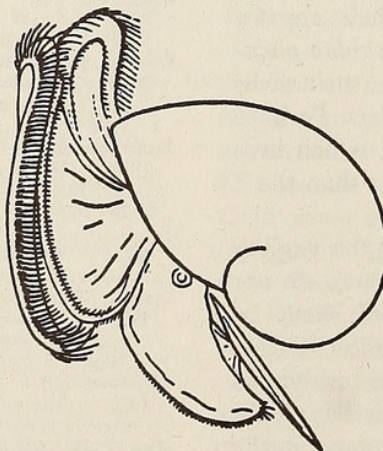
the shells are badly worn and fragmented. From the nature of these deposits it seems likely that the paleontologist would recognize them when encountered in a fossil record." The fragmentation of specimens along the Galveston transects might have been due to agents other than currents, such as a combination of chemical and biotic ones. No assemblage of dead shells was found in this study area which could be attributed to wave or current action. This difference may be due to varying conditions in Tomales and Galveston Bays, particularly the range of the tides and the accompanying force of the tidal currents; the tidal range in Tomales Bay is several times that of the Galveston Bay complex.

The currents of Galveston Bay may play a role in molluscan distribution, in maintaining a particular substrate type at a particular place. Thus, the areas with high sand content probably have stronger prevailing currents than those where silt accumulates. If the ancient beach crossed by the transects was not washed free of mud, it would soon be covered by sediments finer than sand. The winter stranding of surf zone mollusks on the beach and the shell ridges on the bay shore marshes attest to wave transport of benthic mollusks in this area, but there is no evidence that this regularly occurs in any but the shallowest subtidal area.

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## Aggregation and Trail-Following in Juvenile *Bursatella leachii pleii*

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(1 Plate; 1 Text figure)

### INTRODUCTION

*Bursatella leachii pleii* Rang, 1828, the ragged sea hare, is a common member of the shallow-water fauna of the Florida Gulf Coast. During mating and spawning seasons *Bursatella* may be locally abundant. *Bursatella* exhibits common gastropod behavior patterns such as trail-following (queuing), formation of copulatory chains, and aggregation. Little else is known of its behavior. Information concerning the ecology and physiology of *Bursatella* is equally rudimentary. The few studies in the literature have focused on distribution, development, anatomy, histology and systematics (e. g., EALES & ENGEL, 1935; HENRY, 1952; DAVIS, 1967; BEBBINGTON, 1969; KRUCZYNSKI & PORTER, 1969).

Aggregation and trail-following in *Bursatella* are generally associated with copulation and oviposition, which occur during winter and spring in Florida (HENRY, 1952; personal observation). In January 1974, however, we found dense aggregations and queues of immature *Bursatella*. In this paper we describe the aggregations and queues and discuss the physical and biological factors which might have promoted them.

### OBSERVATIONS

Aggregations and queues of *Bursatella leachii pleii* were found along a beach on 11 and 12 January 1974 at Passa-Grille Channel, Tierra Verde, St. Petersburg, Florida (27°39'N; 82°45'W). Similar aggregations occurred several kilometers south at Fort De Soto Park (J. Moss, personal communication). The aggregations were charac-

terized by extremely high densities of very small individuals. Subtidally the distribution was markedly clumped with the density in one aggregation being 6600/m<sup>2</sup>. Aggregations formed at less than 1 m depth by the convergence of queues of sea hares coming in from deeper water (Figure 1). Onshore aggregations appeared to be formed by stranded individuals from queues proceeding shoreward from the subtidal aggregations. A shoreline density of 24300/m<sup>2</sup> was obtained. The trail-following behavior exhibited by many individuals resulted in the formation of long queues. The queues, oriented perpendicularly to the wave fronts (Figure 2), were not copulatory chains because most of the individuals were not in physical contact (Figure 3), and were sexually immature (see below). Mucous trails were apparent on the sandy bottom.

On 14 January, densities were greatly reduced (J. Lawrence, personal communication), and no *Bursatella* were found on 7 February. Neither copulatory chains nor egg strings were observed at these times or on 11 and 12 January. A red tide occurred shortly after 7 February, and *Bursatella* were not observed in the area in the subsequent spring and summer.

In a sample of 602 individuals collected on 11 January 1974 from a subtidal aggregation, 95% of the specimens were between 1 and 22 mg dry body wall weight (DBWW) (Figure 4), corresponding to body lengths of about 3 - 15 mm. The median size was 7.5 mg DBWW. Of the 602 specimens collected, only one exceeded 100 mg. Two larger specimens are included in Figure 4 for comparison. Body walls of 35 adults collected in January 1975, however, had a range of dry weight of 1000 - 3200 mg and a mean of 2200 mg. A 500 mg specimen is approximately 100 mm in body length.

Examination of individuals in the laboratory indicated that few were sexually mature. Although gonads, hermaphroditic ducts, and copulatory bursae were present in all 604 specimens, gonads in specimens below 55 mg DB

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