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BIODEMOGRAPHIC STUDIES OF THE CLAM
RANGIA CUNEATA GRAY

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PROXIMAL RETINAL PIGMENT RESPONSES AND THEIR RELATIONSHIP
TO TOTAL PHOTOMECHANICAL ADAPTATION IN THE DWARF
CRAYFISH, *CAMBARELLUS SHUFELDTI*

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GEOGRAPHIC VARIATION IN THE CRAWFISH *FAXONELLA CLYPEATA*
(HAY) WITH THE DEFINITION AND DEFENSE OF THE GENUS
FAXONELLA CREASER (DECAPODA, ASTACIDAE)

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I. INTRODUCTION

Rangia cuneata Gray, 1831, a pelecypod mollusk of the Family Mactridae, is commonly found in brackish water regions of the northern coast of the Gulf of Mexico. Synonyms of this species are given by Dall (1894), Maury (1920), and Abbott (1956). Its range according to Abbott is northwest Florida to Texas. Dall (1894) described it as "living in Mobile Bay, Alabama, and westward on the north shore of the Gulf to Vera Cruz, Mexico, in shallow water, either brackish or perfectly salt". The geological distribution of *Rangia cuneata* includes the Pliocene of the Carolinas and Florida. It is also known from Pleistocene deposits along the Atlantic coast of North America, ranging from Chesapeake Bay southward to cover the entire northern Gulf coast, as well as the northern coast of South America (Dall, 1894; Richards, 1939). The abundance of *Rangia* in Neocene fossiliferous deposits of the Mississippi embayment, particularly in the prairie regions of southern Louisiana, indicates the importance of this animal in the stratigraphic formation of this part of the country (Harris, G. D., 1902: 32, 36, 265-266). References to *R. cuneata* in the literature are generally limited to mention only in species checklists (Johnson, 1934; Behre, 1950; Pulley, 1952; Moore, 1961) and ecological reports (Strecker, 1935; Hedgpeth, 1950, 1953; Ladd, 1951; Gunter and Shell, 1958). *R. cuneata* apparently is restricted to waters of low salinity, occurring landward of the oysters (Hedgpeth, 1953; Ladd, 1951) and its abundant occurrence in the extensive brackish water regions of Louisiana and Texas are well known to biologists familiar with this part of the Gulf coast (Gunter, 1952; Hedgpeth, 1953; Gunter and Shell, 1958). The biology of *Rangia*, other than a cursory knowledge of its limits of salinity, appears poorly understood.

Quantitative or semi-quantitative studies of the abundance of pelecypods are few in the literature. In the absence of precise methods in the study of population density of animals, investigators seeking quantitative estimates of clams have used various methods. According to Moore (1958: 303) Peter-

sen defined ecological bottom communities on the basis of "relatively small grab samples" from the shallow waters of the Danish coasts where the communities were made up generally of echinoderms or mollusks of species that were present in large numbers. Pratt (1953) and Bader (1954) used tow-type dredges for set periods of time and at set speeds of the towing vessel. Since their interests were in comparative abundance on bottom types the results were not expressed in terms of population density per unit area. Petersen's results, as represented by Moore, were expressed in number per one-fourth square meter. Manning and Pfitzenmeyer (1958) used a hydraulically operated "20 square foot sampler"; taking one to 30 samples at a location and seven samples at any one location were not uncommon. Their results were expressed in number of individuals per acre. Among the variety of mechanisms that have been used in quantitative bottom sampling the Petersen and Ekman dredges, of the "clam shell" type, have probably been most extensively employed on all types of bottom (Welch, 1948; Sverdrup *et al.*, 1942).

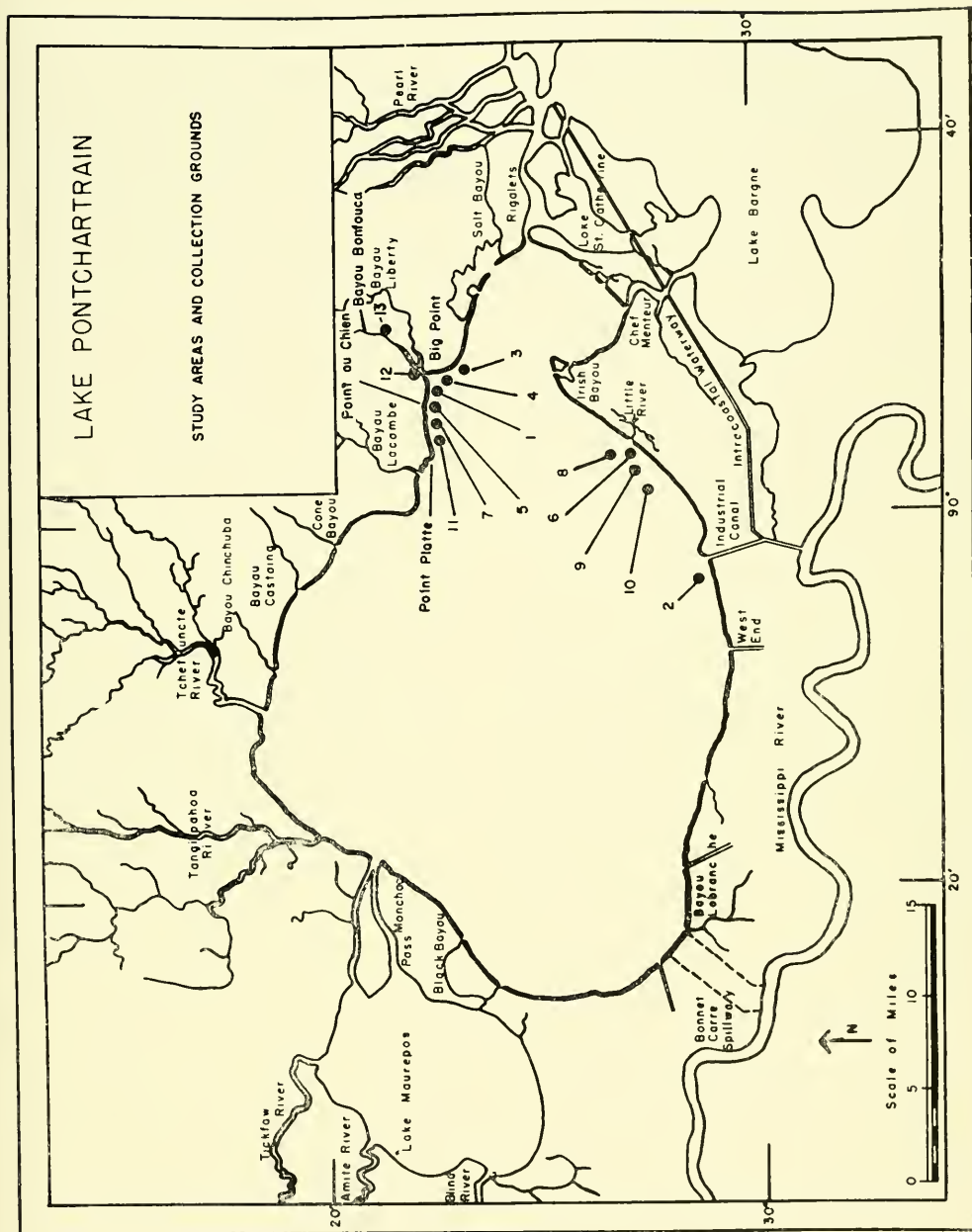
Complexities involved in a study of populations and difficulties encountered in mathematical treatment of biological data are well known to ecologists (*cf.* Hutchinson, 1948: 221, 222; Allee *et al.*, 1949: 386).

The principal objectives of the present investigation concerning *Rangia cuneata* were: (1) to describe the habitat in terms of some of the pertinent physical and biological factors; (2) to ascertain environmental factors correlated with population density and sizes of individuals; and, (3) to describe reproduction in terms of seasonal events concerning the breeding cycle.

II. MATERIALS AND METHODS

A. Study Areas

Two limited localities in Lake Pontchartrain were chosen for habitat and population study areas because of the abundance of *Rangia* and accessibility to the writer. Many of the physical features of Lake Pontchartrain were described by G. D. Harris (1902), R. A. Harris (1902), and Steinmayer (1939). Some of its flora and fauna



were described by Suttkus, Darnell and Darnell (1953-54). Because of potentially variable and heterogeneous conditions in Gulf coast brackish water environments (Ladd, 1951: 135; Gunter, 1952: 138; Gunter and Shell, 1958: 19-28) and a possible wide range of tolerance of *Rangia* to changing conditions, two areas were selected that were

expected to be different throughout any one year. Consistent or conclusive biological differences found between two parts of the population were considered likely attributable to certain local and consistent differences in environment.

One of the two areas chosen extends along the northeast shore of the lake from Point

Platte eastward to Big Point (fig. 1) including the mouth of Bayou Bonfouca, a distance of approximately 3.5 nautical miles. Bayou Bonfouca is navigable to small industrial barges up to Slidell, Louisiana and a permanently marked channel from deeper water in the lake is kept open to the mouth of the bayou. The other area extends along the southeast shore of the lake from the mouth of Little River westward to the lake-shore "camps" at the junction of Hayne Boulevard and Paris Road, a distance of about one nautical mile (fig. 1), (U. S. War Dept., 1936, 1939 maps, and U. S. Dept. Commerce, 1956 chart 1269).

For the most part the water and bottom samples were taken within an estimated one thousand yards offshore in these two areas. The area identified along the north shore will be referred to hereafter as the "north shore area" while "south shore area" will refer to the identified area along the southeast shore.

A broad band of marshland averaging about one and one-fourth miles in width extends landward from the north shore area which receives considerable drainage from Bayous Liberty and Bonfouca from the north and east and Bayou Lacombe from the north and west, as well as directly from the marsh itself. When the water level in the lake is high, the marsh is flooded by flow across low points along the shore. There may be a rapid reciprocal influx of water from the marshland into the lake when the latter is low. This is somewhat in contrast with the south shore area which receives only slight drainage in comparison, although likewise joined landward by natural marshland. The shore in this area is modified and interrupted by a railroad embankment extending along the shore several miles in both directions so that exchange between the lake and marsh is greatly limited or even prevented. The flow across the inlet of Little River has been confined to a shallow channel little more than three feet deep and about thirty feet wide. The direction of flow has depended chiefly on the level of the lake: landward when the lake is high and *vice versa* when the latter is low. Natural flow through this channel was terminated in the spring of 1958 by the installation of a control valve. Much of the south shore in other areas has been separated from the lake by a protective levee, and communication with water out-

side the lake is controlled by valves, pumps, or locks.

In the north shore area the bottom consists of irregular reefs, flat or sloping alluvial deposits, and to some extent of a compact base of clay soil. The reefs, probably of quaternary origin, and alluvial deposits are composed of a mixture of sand, highly eroded shell, and copious proportions of dark mud apparently high in organic material (G. D. Harris, 1902; Steinmayer, 1939). The bottom is overlain by a thin cover of shifting sand generally less than half an inch thick. In the south shore area the bottom is typified by ridges approximately 30 to 40 feet wide and two to three feet high. These ridges are composed essentially of sand and shell, probably thrown up by wave action, and are situated more or less parallel to the shore. Depth appears to increase more rapidly with distance from the shore in the south shore area than in the north shore area. Few bottom samples were taken from a depth greater than eight feet in either area.

B. Collection of Bottom Samples

Field work was carried out between February 10, 1957 and September 15, 1958, except investigations done in 1960 and 1961 to be explained later. Trips to the north and south shores were made at least once monthly to one or both areas with the exceptions of March, May, and December of 1957 and August of 1958. More attention was given to the north shore area chiefly because the population in this area seemed likely to yield more information concerning the general biology of the species.

A fourteen foot fishing skiff equipped with a small outboard motor, and an anchor, was used in transporting equipment and samples to and from the areas where collections were made. The benthic population of *Rangia* was sampled quantitatively and qualitatively as regularly as practicable to better estimate population densities of the various sizes and to collect material for observation of the gonadal condition. Seasonal information concerning changes in density of the smaller individuals together with the changes accompanying gametogenesis were expected to indicate the time and duration of spawning. Also, higher densities of similar size classes were expected to indicate the spawnings of previous seasons and permit an estimate of growth rate and age, at least for

the younger clams. This essentially follows the method used by Coe (1947) on the Pismo clam. Many unsuccessful attempts were made to collect pelagic larvae. The early embryonic development to a veliger stage was, however, observed in the laboratory after artificial fertilization of eggs taken from mature females.

Water and air temperatures were recorded regularly in °F. Water samples were taken as regularly as possible and later analyzed in the laboratory for salinity, total phosphorus, organic matter, and phytoplankton pigment. These particular environmental measurements were made with the hope of contributing to a more precise description of the habitat of *Rangia* and to ascertain if these factors or combinations of them were limiting or conducive to biological productivity. The organic matter and phytoplankton pigment determinations were carried out to give a rough estimate of available food and the effect of seasonal change on available food. Field notes were kept concerning the weather, water level in the lake, air and water temperatures, approximate location and depth from which bottom samples were taken, type of dredge used, locations from which water samples were taken, observations concerning the behavior of animals, and quantity of water used in sampling for larvae.

Quantitative samples.—Two Ekman dredges, six and nine inches in size, were used in collecting quantitative bottom samples. For convenience in handling when loaded, the nine inch dredge was suspended by a small plastic coated steel cable and was lowered and raised by a portable hand-operated hoist for small boats, similar to that described by Welch (1948: 179). From six to twenty samples were taken on each collecting trip. Difficulty was sometimes experienced in obtaining large numbers of samples because of rough water, inefficient anchoring, the rather slow procedure in operating the hoist, and tripping and setting the nine-inch dredge. Since few samples were taken from depths greater than eight feet, and the majority were taken from depths of three to six feet, depth was not consistently recorded. In most situations the nine inch dredge proved to be more effective because of its deeper "bite". In bottom predominantly of shell or submerged vegetation neither dredge could pick up samples be-

cause of incomplete closure of the jaws. A bottom of shell and sand was troublesome only occasionally. Fortunately there were few places within the two areas that were difficult to sample. However, the quantitative samples are somewhat biased. In case of incomplete closure of the jaws the sample was discarded and another taken at a new location. Thus difficult areas were avoided. Each sample was dumped from the dredge onto several thicknesses of newspaper in the bottom of the boat.

The samples were allowed to remain in storage in freely circulating air until thoroughly dry, a period of three to five weeks. At the end of this time the samples frequently were found congealed into a single mass depending upon the proportion of sand to organic matter in the sample. For analysis, each dry sample was removed from the paper, pulverized by hand and passed through a screen having meshes one millimeter in diameter. The fine material passing through the screen was collected, poured into a gallon-size glass jar and thoroughly homogenized by mixing with a paddle or shaking and turning. It was then measured volumetrically in a 500 cc graduate cylinder and the total volume recorded on an analysis sheet together with the number, date and location of the collection and individual sample. From 50 to 300 cc, depending on the total screened volume, were poured in single portions of 10 cc each into a shallow flat-bottomed petri dish. The petri dish was shaken and rotated to spread the fine material out uniformly to a depth of about one to two mm. The shaking and rotating action rapidly worked the lighter dried whole or half shells of young clams to the surface of the material. At the surface of the sand the clam shells could be noticed and identified easily under the low power of a stereoscopic microscope and often without the aid of a microscope if a bright light was used and the correct angle of reflection was caught by the eye, depending for contrast upon the color of the background material. The probability existed that certain shells may have represented clams dead at the time of collection and these were not counted if possible. Only intact, (*i. e.* whole shells, having the valves tightly closed but with tiny particles of sand stuck to the ventral edges) were counted. The sticky material indicated dried body fluid from the dying clam after

being out of water (death after collection). The ventral edge of the shell (opposite the hinge) is the natural course for escaping fluids from dying clams undergoing cytolysis. Half shells soiled on the inside, indicating death before collection, had no sand particles clinging to the ventral edges. Half shells or gaping shells were not counted and were actually quite rare. All the small shells from each 10 cc portion, some as small as 0.35 mm, were identified and counted, using the 2X objective (20 diameters), and measured by an ocular micrometer. The greatest length, (*i. e.*, anterior to posterior), was used in all size measurements of *Rangia* in this study. The number of 100 cc portions from each sample was not consistent but depended on the size of the screen sample and number of small clams (shells) found. The total volume actually inspected was recorded and the ratio of volume inspected to the total volume of screened sample was used to obtain the density estimate per area sampled by the dredge. A sample analysis sheet with a list of possible sizes was used; tally marks were made adjacent to the appropriate size thus automatically dividing the shells into size classes. Both measurement and counting were aided by first removing all the tiny shells with a moistened camel's hair brush from the surface of the sand to a small watch glass that was then placed on a black background. This was also helpful in distinguishing *Rangia* from other small shells such as that of *Polymesoda*, whose shell has distinct concentric rings about the protoconch and an external ligament, and *Macoma* which is thin and elongate. The shape and proportions of specimens of *Rangia* smaller than 4 mm are not greatly different from the adult; also the ligament is internal.

The material retained by the screen, eroded shell, compact chunks of mud and bits of partly decayed vegetation, together with intact shells, was spread out on a white enameled tray and placed under sufficient light for the detection of small clam shells about one mm and larger. All intact shells (valves closed tightly and with sand stuck tightly to the ventral edges, particularly the siphonal ends) were removed and measured by laying them on a millimeter rule. The size and count were tallied on the sample analysis sheet.

Some small shells may have been overlooked by being embedded in chunks of

compact dried mud; although small *Rangia* are generally confined to the thin layer of surface sand covering the bottom. The incidence of small *Rangia* in dried portions of mud was investigated by breaking many small and large portions in the samples under analysis. Only in one set of samples, having what appeared to be a considerable proportion of dried colloidal material, were small shells found embedded.

Size classes of three different intervals, increasing with size of the clams, were assigned to better differentiate the smaller sizes in which density was particularly high. For convenience in grouping from the recorded measurements the class intervals were limited fractionally. Sizes up to 1.75 mm were placed in classes with an interval of 0.25 mm. Sizes between 1.75 mm and 14.75 mm were classed in intervals of 1.0 mm. Sizes about 14.75 mm were classed in 2.0 mm intervals. Population density for each size class was converted from density per sampled area (depending on the size dredged used) to density per square foot by multiplying by the reciprocal of the ratio, square inches taken by the sampler to the number of square inches in a square foot. For each group of samples collected on any one date the mean density was calculated for each size class represented, giving the estimated density by size classes. The results were plotted on a histogram with density expressed logarithmically to differentiate small densities and to partly offset seasonal increases of high densities.

Qualitative Samples.—A long-handled rake-type dredge with a wire retaining-basket with meshes approximately 3 mm square was used for collecting living specimens to be inspected in the laboratory. The dredge was equipped with a thin sharp-edged steel plate for cutting into the bottom. However, because of the light weight of the dredge, the writer had to wade out into the water and exert a fair amount of pressure downward on the handle to obtain a section of bottom without disturbing the natural position of the clams. *Rangia* were not found to burrow deeply. Specimens were also collected directly by hand since their siphonal ends can be felt easily when the hand is passed lightly over the surface of the bottom. The clams were taken to the laboratory in a bucket of environmental water and opened the following day for in-

spection of the gonads. The anterior and posterior adductor muscles were cut separately by inserting a knife blade between the valves at the anterior and posterior ventral edges respectively and cutting toward the muscle. The mantle was pulled away from the right valve and the latter was removed. An incision was made with a razor blade in the right wall of the visceral mass thus laying open the gonad. A few drops of fluid were withdrawn from the incision and one drop was placed on a slide for microscopic observation at a magnification of 430X. The sex of each animal was determined and recorded only when mature gametes were present. Also, the presence of parasites and the color of the gonadal tissue of each animal were noted and recorded. Early in the period of the investigation, slides were made of the fixed and sectioned gonadal tissue of clams whose sex had been determined by inspection of gonadal fluid to establish the presence or absence of gametes. The slides satisfactorily confirmed this method of sex identification although the gonadal condition as revealed by the sections of clams at that particular time of the year could not be expected to be the same at other times of the year.

C. Analysis of Lines of Growth Interruption

Although the lines of growth interruption, or "growth lines", have been used to determine or indicate age, the method cannot be relied upon to determine conclusively the age of an individual, particularly in southern latitudes (cf., Coe, 1947: 9-13; Haskin, 1954). The record of past winters may be observed easily as narrow indented bands located in concentric rings on the shell. These bands apparently occur when seasonal low temperatures bring about near complete cessation of growth. The greatest objection to using these rings or bands for estimation of age is that factors other than cold temperatures may cause growth interruptions. Local disturbances such as storms, heavy sedimentation, or seasonal high concentrations of plankton may cause withdrawal of siphons and mantle and cessation of pumping, feeding, and growth. Consequent differences in size for any one age might result. Notwithstanding, 40 right valve specimens of *Rangia* from each study area were analyzed for frequency of growth

interruption lines. Since the temperature in Lake Pontchartrain during the winter recedes in reasonably close conformity with the air temperature (U. S. Weather Bureau, New Orleans Station, 1956-58) a somewhat consistent pattern of lines, or growth bands between the lines of growth interruption, might be expected, on the average, to occur in the shells of *Rangia*. At least three lines of growth interruption are consistently situated on the shell of *Rangia*; these are the three smallest and proximal to the umbone. The first is generally obliterated by erosion on older, *i.e.* larger specimens, since it is so closely associated with the umbone, the oldest part of the shell. In smaller and younger shell, nevertheless, the first line is quite distinct. The greatest diameter (corresponding to original length at the time of the formation) of each easily observable line of growth interruption on each shell was measured, including lines out to the periphery. These were recorded together with the length of the shell. The percent frequency distribution of the different sizes of growth interruption line diameters was plotted giving a polymodal curve facilitating the analysis.

D. Plankton Analysis

A Wisconsin plankton net was used in sampling for the pelagic larvae. Generally about forty liters of lake water were sampled. No particular station within either area was chosen for sampling. However, most samples were taken in the local area where bottom samples were also obtained. Since most depths concerned in the investigation were less than eight feet the water samples were taken consistently from two feet beneath the surface. On several occasions the net was towed at the surface behind the boat at a standard rate of speed for a standard time. The plankton concentrates were preserved in about 10 per cent formalin and analyzed three weeks to three months later. The method of analysis used was essentially that described by Welch (1948: 279-283) using a Sedgewick-Rafter counting cell and Whipple micrometer.

E. Observation of Early Embryonic Development

In October and November, 1957 adult clams bearing mature gametes were brought into the laboratory and specimens of eggs and active spermatozoa were isolated in sep-

arate containers of environmental water for 30 minutes, following the method of Awati and Rai (1931: 92-93), and then mixed. A small portion of the mixed fluid was placed in a watch glass where fertilization and early cleavages were observed at a magnification of 430X. The room temperature varied between 73° and 80° F. The times required for attainment of major developmental stages were recorded. Although many embryos developed abnormally, as Coe (1947) noted for other species, there were many individuals that appeared to be normal and the latter are reported.

F. Salinity

Owing to the shallowness of the study areas, which were relatively close to the shore, and subject to mixing by prevalent wind action, samples from the surface only were routinely analyzed for salinity. In February, 1957 several samples were taken in the south shore area from both the surface and the bottom in about 12 feet of water. The greatest difference found between surface and bottom was 0.5 ‰. The greatest difference between surface and bottom reported by Suttkus *et al.* was 0.3 ‰. Their samples on which bottom salinity determinations were made were taken from several stations in the eastern half of Lake Pontchartrain in February, 1954.

Glass-stoppered bottles (250 ml size) were used for collection, transport, and storage until the analyses could be made. The determinations were made by titration using silver nitrate (0.05 N solution periodically checked against a standard 0.08 N sodium chloride solution).

G. Total Phosphorus

That phosphorus concentration, particularly total phosphorus, is of primary importance in indicating fertility and productivity of natural waters appears to be universally recognized by both marine and freshwater biologists (*cf.*, Sverdrup *et al.*, 1942; Welch, 1952: 109; Ruttner, 1953: 79-81; Hutchinson, 1957: 727).

Water samples to be analyzed for total phosphorus were collected in four-liter size glass-stoppered carboys. Immediately after the samples were brought into the laboratory from the field each sample was thoroughly homogenized by stirring and inverting and one liter was poured into a liter-size tightly

stoppered bottle for storage. To minimize loss of phosphates to bacteria that adhere to the inside of the storage bottle (Harvey, 1948: 357; Stephenson, 1949: 378-379), about 2 ml of an aluminum hydroxide precipitate solution was added to each sample before storage. The precipitate provided extensive surface area for the development of the bacteria (Harvey, 1948) so that in running the determinations the aliquot poured off for analysis from a thoroughly homogenized stored sample would contain a reasonably correct proportion of the original phosphorus, even though tied up in bacteria. The determinations were made after all samples had been collected for the period of the investigation. The method used was that of Hansen and Robinson (1953) employing perchloric acid oxidation of organic phosphorus to phosphates and is described concisely by these authors. The quantitative determination depends upon the formation of a blue color by the reaction of ammonium molybdate with phosphates in the presence of stannous ions. The blue color produced by the sample phosphates was compared with that of a standard by the use of a spectrophotometer (Coleman Jr. Model No. 6 A) at a wave length of 410 mμ. Blank solutions of sodium chloride having the same chlorinity as the samples were treated throughout the oxidation process simultaneously with the samples; their readings were subtracted from the sample readings. In practice a curve was drawn on semilog paper from plotted readings, in percent transmission, corresponding to several dilutions of a standard made by using potassium dihydrogen phosphate and containing 0.0250 microgram atoms (μg at) phosphate phosphorus per ml. The sample concentration values were read directly from the curve. After some initial determinations were made, inconsistency of results made necessary the use of metallic tin freshly dissolved in 12 N hydrochloric acid in place of the reagent stannous chloride (dissolved in hydrochloric acid) as recommended by Hansen and Robinson. The difficulty apparently lay in the instability of the stannous chloride even though the solution was freshly made. Stannous chloride cannot be allowed to become oxidized to the stannic condition as it must act as a reductant (*cf.*, Deming, 1944: 681-682; Harvey, 1948: 356). The metallic tin (1.131 gm in 20 ml 12 N hydrochloric acid)

was allowed to dissolve overnight and used only during the next day; before use it was diluted 1:24 with freshly boiled distilled water. This modification of the method gave consistent results.

H. *Phytoplankton Pigment*

A variety of methods has been used in determining the concentration of phytoplankton pigment for the purpose of measuring phytoplankton concentration in natural waters as well as for the study of the kind and proportional relationships of the different pigments. These pigments include chlorophyll and some yellow substances which seem to be the most important (*cf.*, Kozminski, 1938; Manning and Juday, 1941; Creitz and Richards, 1955; Korringa, 1956). Pigment concentration alone is not intended to be regarded as an index of productivity. According to Ruttner (1953: 144-145) cultures of algae have demonstrated that chlorophyll content, quantity of substance, and cell multiplication are to a certain extent independent of one another. The analysis used here was carried out in a manner similar to that of Korringa (1956: 310).

Water samples to be analyzed for phytoplankton pigment were collected in two four-liter size glass carboys. The samples were obtained with a four-liter Kemmerer sampler from two feet beneath the surface immediately before leaving the field. The pigment extraction was begun approximately two hours later after arriving in the laboratory. From two to eight liters were filtered by suction through Aloe filter paper (No. 42700) 9 cm in diameter. The same type filter paper was used throughout the period of investigation as a standard for seasonal and regional comparison. The number of liters filtered depended chiefly upon the concentration of material in the water as determined by the time required to filter a certain quantity, although, within limits the number of liters used was not important. The time required was later found to be directly proportional to the amount of pigment extracted. The filter paper containing the phytoplankton as well as various particles of detritus was folded several times and inserted into a 30 ml test tube. The tube and filter paper were placed in a boiling water bath for about one minute to destroy the chlorophyllase. Then 8-9 ml of methyl alcohol was added covering the folded filter

paper; the tube was stoppered securely and placed in a covered container in absolute darkness for storage until the determinations could be made conveniently, from three weeks to six months later. For determination of the pigment the filter paper was removed carefully from each tube containing the extracted pigment in alcohol, the paper being pressed to the side of the tube to allow as much alcohol as possible to drain back. The extract was transferred to a 15 ml graduated tube and made up to 10 ml with additional methyl alcohol. The extracts were then centrifuged to settle the insoluble detritus and the supernatant carefully poured off into cuvettes for comparison with a standard using a spectrophotometer (Coleman Jr. Model 6 A) at 410 mu. The standard was prepared according to Korringa's method (1956: 310) using a solution of 25 mg potassium chromate and 430 mg nickel sulfate made up to one liter with distilled water. A curve was drawn through points established by readings in percent transmission corresponding to dilutions of the standard and the sample readings were converted to values of the corresponding concentration of the standard divided by the number of liters filtered.

I. *Organic Matter*

The method often employed in determinations of organic matter in natural waters has usually involved oxidation by potassium permanganate either under acid or alkaline conditions at 100° C for a stated arbitrary time. Oxalic acid is then added and the excess back-titrated with standard permanganate (American Public Health Association, 1936: 136-139; Hutchinson, 1957: 878-879). A modification is necessary, however, for samples of sea water (Atkins, 1923: 160-163; Korringa, 1956: 310). These methods give no direct measure of organic carbon since only partial oxidation occurs and this depends upon the state of oxidation of the matter in solution (*cf.*, Ruttner, 1953: 84). The permanganate test has been used to estimate the biologically oxidizable organic matter, approximating the biochemical oxygen demand method (*cf.*, Korringa, 1956: 310-311). According to Korringa (*loc. cit.*) the test is believed to give an estimate of the readily oxidizable organic matter that can be "mineralized by bacteria, or, without previous transformation, be used as food by

filter feeders and the like". Ruttner (*loc. cit.*), in referring to the work of Birge and Juday, stated that "pure" lake waters contain considerable amounts of dissolved organic matter "exceeding by several times that in particulate form (which is chiefly plankton)".

The method used here was that of Koringa (*loc. cit.*). The water samples were collected in four-liter carboys immediately before leaving the field. Upon arrival in the laboratory the collections were thoroughly homogenized and samples were stored in liter-size bottles. One hundred mg of mercuric chloride was added to each storage bottle to preserve the organic matter until the determinations could be made (from one to fifteen months later).

III. ENVIRONMENTAL FACTORS

The dates and locations of collections of water and bottom samples are given in Table 1 together with the associated air and water temperatures, estimates of salinity, total

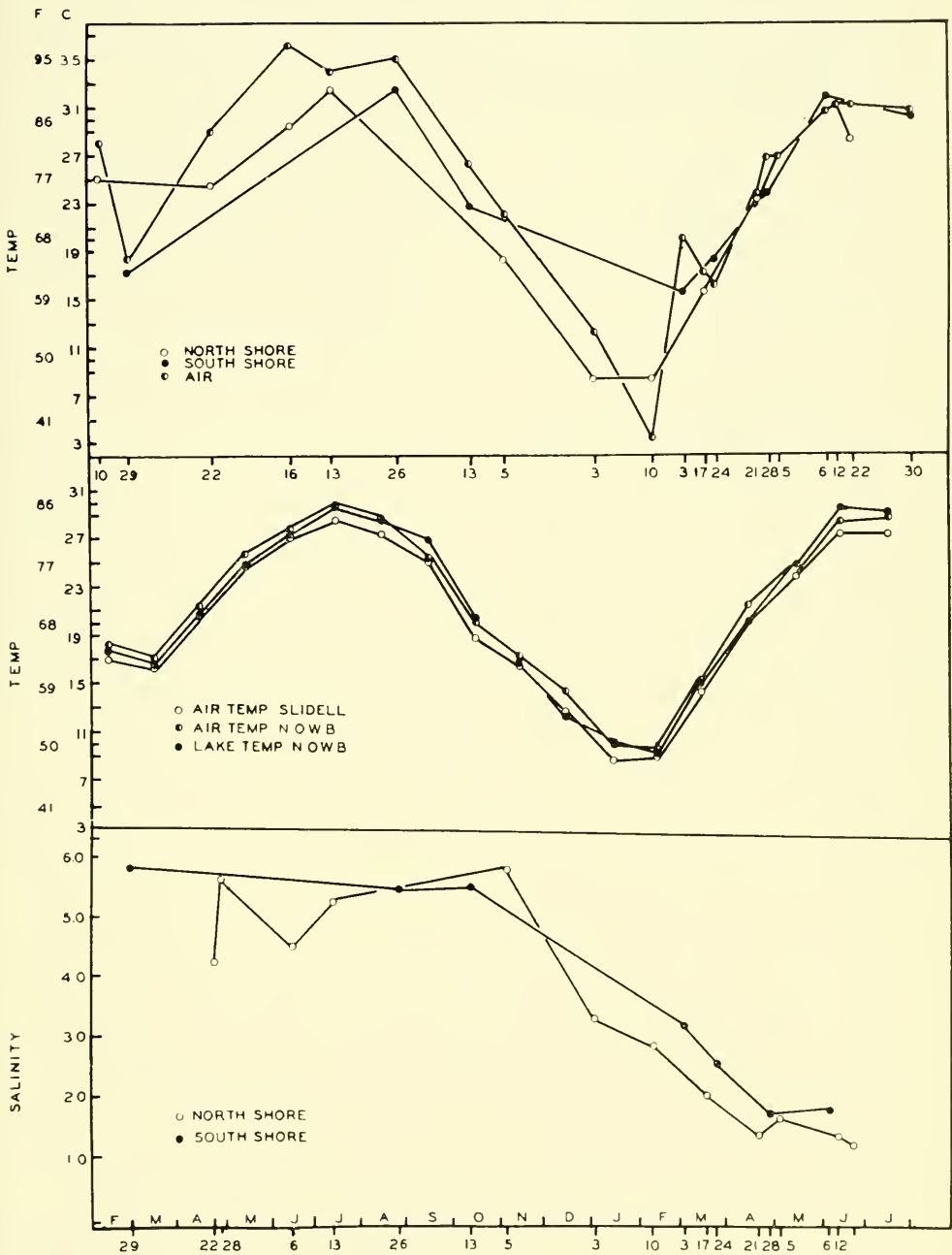
phosphorus, phytoplankton pigment concentrations, and organic matter. The locations are represented by numbers, in parentheses, referring to points on the map of the study areas (fig. 1).

A. Temperature

The distributions of air and water temperatures on collection dates are plotted in Figure 2. Monthly mean air temperatures as recorded by the U. S. Weather Bureau at stations nearest the study areas and monthly mean lake temperatures, recorded by the New Orleans Weather Bureau, are plotted in Figure 3. The influence of air temperature upon the lake is readily apparent. The range in monthly mean lake temperatures for the period of the investigation was 48.2° - 85.1° F while the ranges of monthly mean air temperatures were 47.3° - 83.1° for the north shore area (Slidell station) and 48.9° - 85.2° for the south shore area (NO WB station). The lake obviously has a low heat budget. This is understandable in con-

TABLE 1.
Physical and biological estimates at times and locations of collections.
(Bottom locations represented only in part).

Date	Location (nos. in parenthesis refer to fig. 1)		Bottom Sample Locations	Temp. °F air water		Salinity o/oo	P µg at/ml	Phyto- plankton Pigment Index	Organic Matter (mg. KMnO ₄ /L)
1957									
10 Feb.	NS	(1)		82	77				
29 Feb.	SS	(2)		65	62	5.77			
22 April	NS	(3)		84	76	4.20	.0064		22.9
		(1)					.0078	.105	23.7
28 April	NS	(3)				5.59		.075	23.3
		(1)				4.55	.0058	.071	
		(12)					.0062	.121	24.4
16 June	NS	(4)	X	97	85	4.43	.0084	.011	23.7
		(3)				4.44			
		(12)					.0091		26.9
13 July	NS	(5)	X	93	90	5.20	.0103	.236	22.6
26 Aug.	SS	(6)	X	95	90	4.72	.0088		
		(9)				4.99			
		(10)				5.07		.065	21.9
13 Oct.	SS	(6)	X	79	73	5.45	.0079	.209	20.8
5 Nov.	NS	(11)	X	72	65	5.63	.0105	.198	20.8
		(1)				5.56		.257	
1958									
3 Jan.	NS	(11) (7)	X	54	47	3.29	.0077		23.7
		(1)				3.19	.0064	.200	25.8
10 Feb.	NS	(11) (7)	X	38	47	2.82	.0053	.072	24.4
3 Mar.	SS	(8)	X	68	60	3.16	.0065	.227	23.3
17 Mar.	NS	(1)					.0091	.183	29.4
		(3)		63	60	2.01			
		(12)				1.60			
21 Mar.	SS	(8)		61	65				
		(9)				2.52			
21 April	NS	(1)	X	75	74	1.34	.0100	.485	26.5
		(12)				0.78	.0113		
		(13)				0.09			
28 April	SS	(8)		80	75				
		(6)				1.69	.0037	.385	24.8
5 May	NS	(11) (7)	X	80	80	1.47	.0060	.544	24.1
		(12)				1.62	.0045		25.8
6 June	SS	(6)		87	89	1.77	.0035	.160	23.7
12 June	NS	(1)		88	88	1.33	.0045	.112	23.7
22 June	NS	(7)	X	88	83	1.18	.0035	.268	23.7
		(11)						1.207	
30 July	SS	(6)	X	87	86	0.33		.763	



Figures 2-4. 2. (Top) Distributions of air and water temperatures at times of collection; F=°F., C=°C. 3. (Middle) Distributions of monthly mean air and lake temperatures computed from temperatures recorded by the U. S. Weather Bureau; N.O.W.B.=New Orleans City Weather Bureau station. 4. (Bottom) Distributions of salinity (o/oo) at times of collection from within the lake only.

sideration of its mean depth of about 14 feet. The range of lake temperatures recorded on collection dates (Table 1), 47°-90° F, represents extremes probably due to the relative shallowness of the areas and again reflects the immediate influence of air temperature.

B. Salinity

The distributions of salinity (fig. 4) within the lake itself (salinities in Bayou Bonfouca are not plotted) show a consistent decline between November 5, 1957 and April 21, 1958. A combination of several possible factors may be responsible for this. Precipitation in watershed areas that drain into the lake, mean tide level, and wind direction seem to be most important in determining salinity. Unpublished data recorded by The Corps of Engineers, U. S. Army, (New Orleans District) including total inflow to the lake based on combined monthly runoff in acre feet for the period, 1946 through 1956; chlorides (1946 through 1958), and mean monthly lake level (1940 through 1957) show annual cycles with peak chlorides occurring consistently in the fall and lows in early summer. The annual chloride peaks steadily increased, converted to terms of salinity, from 2.56 ‰ in 1949 to 9.78 ‰ in 1954. The greatest variation within any one year occurred in 1954 following a period of considerable runoff in December and January when the low in February was 1.47 ‰ and the high in October was 9.78 ‰ succeeding and accompanied by the lowest annual runoff of any year recorded in the data. The salinity lows succeeded periods of heavy runoff with a lag of about one month. As runoff is in the increasing phase, generally during the first few months of the year, salinity apparently decreases until mid-summer when the situation is reversed. Following the peak salinity in 1954 the yearly peaks decreased to 1958. The second highest peak was in November, 1956. The mean for August, 1957 was 4.63 ‰, and 1.20 ‰ for July, 1958 illustrating a stepwise decline from the peak in November, 1956.

The data indicate that monthly mean lake level is not primarily influenced by runoff. Annual peaks in mean lake level consistently occur in the fall, matching if not slightly preceding peaks of salinity concentration. One factor seemingly responsible for this is

tidal influence. Annual tidal peaks occur in the fall (U. S. Coast and Geodetic Survey, Tide Tables, 1957, 1958; Marmer, 1954: 115). Predicted monthly mean tide levels for Long Point in Lake Borgne are plotted in Figure 5. The average of the monthly means for February through July of 1957, 0.47 ft., is considerably higher than the average for the comparable period in 1958, 0.11 ft. Mean lake level was higher in September of 1957 than it had been since October of 1949. This suggests that mean tide level increased as did peak chlorides following 1949.

Variations in lake levels in relation to velocities and directions of winds associated with highs and lows (below and above mean sea level) for the period 1932 to 1947 inclusive also have been recorded for the south shore area of the lake by the Corps of Engineers. A cursory inspection of these data reveals that winds are of primary importance in determining temporary levels of a few days duration or perhaps longer. Average wind velocities and directions are recorded for only 24 hour periods preceding extreme fluctuations. Highs approaching three feet or more above mean sea level more often occur in the spring and fall (April, May, September, and October) with the peaks succeeding 24 hour periods of east wind variable by north or south having average velocities of 9 to 15 miles per hour. The peaks occurring in the fall are generally superimposed upon a rise of nearly one foot above mean sea level. The duration of the rise appears to be about three months, although this is highly variable. Mean tide level at this time of the year probably supports the rise. Lows approaching one foot below mean sea level are rare, occurring occasionally in December, January, March, and July. They succeed 24 hour periods of west wind variable by north or south having average velocities of 11 to 14 miles per hour. The data indicate a mean lake level somewhat above that of mean sea level which is not surprising in view of the large runoff areas draining into Lake Pontchartrain.

Salinity in the north shore area (fig. 4) was slightly lower and more variable than in the south shore area. In April, May, and June in the north shore area apparently this was more variable than at any other time during the entire period. The proximity of bayous draining into the area more heavily at this time of the year is probably responsi-

ble. However, currents from the Rigolets Pass, influenced by the Pearl River drainage, may have had some influence.

C. Total Phosphorus

All of the total phosphorus values are given in Table 1 while values for samples taken only from the lake itself are plotted in Figure 6. The lowest of these values, $0.0035 \mu\text{g at/ml}$, is higher than values reported by Harvey (1955: 8) for the north Atlantic below 600 M, $0.0013 \mu\text{g at/ml}$ (phosphorus as inorganic phosphate in solution), or below 150 M in the Antarctic, $0.0029 \mu\text{g at/ml}$. Total phosphorus values under the same conditions would have been higher. Concentrations of total phosphorus reported by Korringa (1956: 311-313, 340-343) for coastal and estuarine areas along the southeast coast of Africa ranged from 0.00025 to $0.00141 \mu\text{g at/ml}$. The higher value represented a sample from a bay entrance. An average total phosphorus value for western Lake Erie reported by Curl (1959: 68) was $93.0 \mu\text{g/L}$ ($0.0030 \mu\text{g at/ml}$). The values reported by Curl were positively and significantly correlated with turbidity originating in tributary streams of western Lake Erie. Hutchinson (1957: 728, 729) stated that total phosphorus varies greatly in lake waters, up to 78 g/M^3 ($2.51 \mu\text{g at/ml}$), or as much as 208 g/M^3 in saline lakes in closed basins. He quoted a mean value of 77 mg/M^3 ($0.00248 \mu\text{g at/ml}$) soluble phosphate phosphorus for lakes of Baltic Germany and stated that there was a clear tendency for the waters of brown lakes rich in peaty material to contain more phosphate than the clear-water lakes. The maximum value for these lakes was 600 mg/M^3 ($0.019 \mu\text{g at/ml}$).

If brownish coloration in the waters of bayous flowing into Lake Pontchartrain has any positive correlation with total phosphorus then the concentration of this element must be relatively high at times. The highest values obtained (Table 1) were from samples taken near the mouth of Bayou Bonfouca and within the bayou. However, the lake values show seasonal lows during the early summer months (fig. 6), probably resulting from dilution with the high runoff occurring at this time of the year. In general the pattern seems to follow that of salinity (fig. 4). That the south shore values are lower than those for the north shore area is

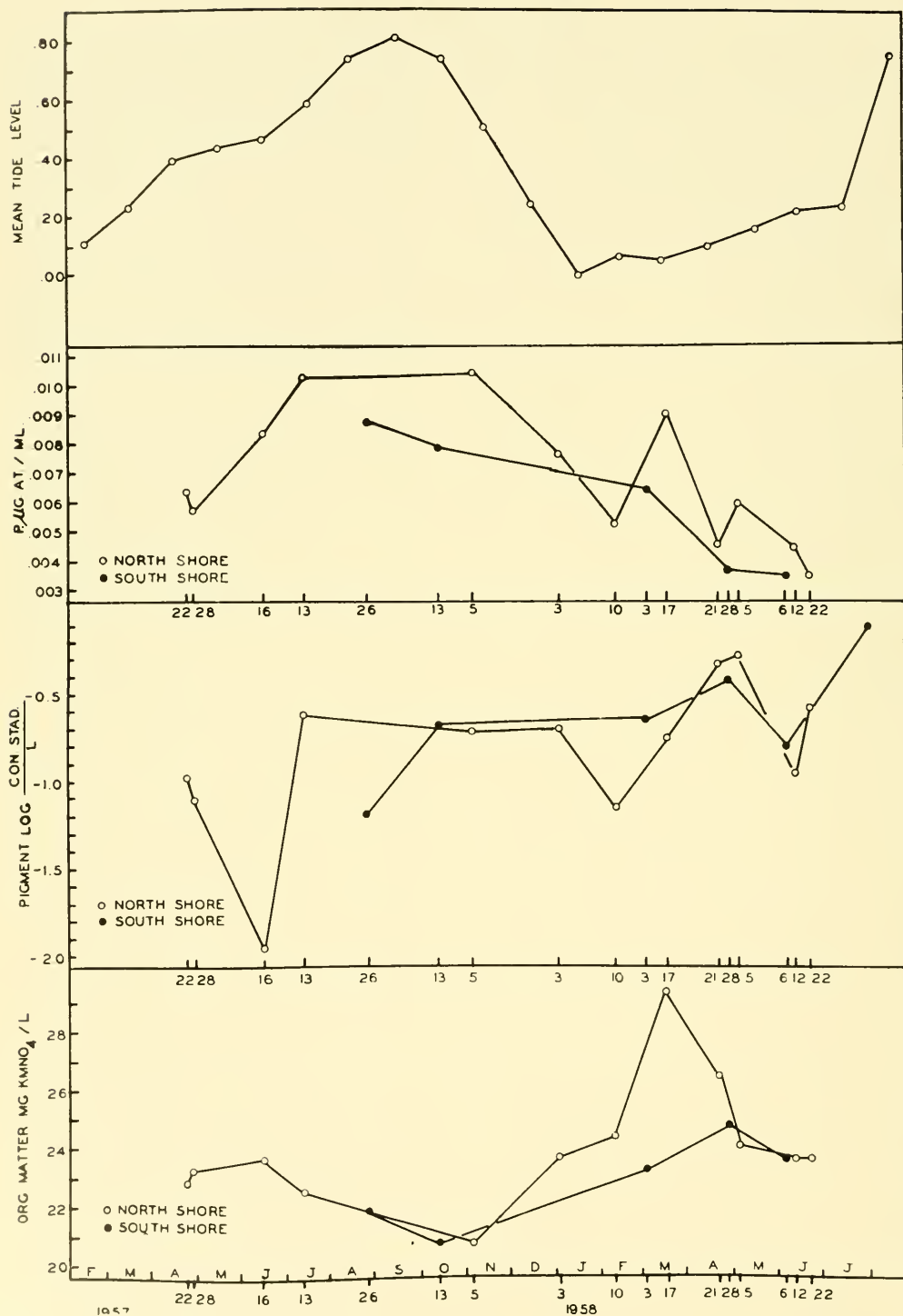
remarkable and may indicate that the lake is dependent upon its tributary streams (chiefly along the north and west shores) for phosphorus, although at times and in different areas it may be diluted by high influx of fresh water. The values for the south shore area were less variable than those for the north shore area. In view of the phosphorus concentrations reported for either the ocean or some freshwater lakes by the authors mentioned above, none of the values reported here can be regarded as an indication that phosphorus concentration in Lake Pontchartrain limits biological productivity.

D. Phytoplankton Pigment

All the values for phytoplankton pigment concentration are listed in Table 1 and only values for samples from the lake itself or parts of the areas farthest out into the lake away from the inlets are plotted in Figure 7. In general the production of phytoplankton may be inferred as having been greater in the spring and summer of 1958 than during the previous season in 1957. Decreasing salinity with the parallel seasonal influx of freshwater may have had some bearing on an increase in phytoplankton. Major increases in production during June and July of both years may have occurred as indicated, thus accompanying or immediately succeeding the period of high runoff. Suttkus, *et al.* (1953-54: 28-30) stated that "thick scums" of the alga *Anabaena* sp. were observed during late summer and early fall with the heaviest blooms occurring in the western half of the lake. *Anabaena* was referred to as one of the freshwater genera of the lake. Variability in concentration may have been no greater in one study area than the other (fig. 7) but the high value for the north shore area on June 22, 1958 from a sample at the mouth of Bayou Bonfouca and the relatively low value on the same date from a sample taken about two miles west of the mouth seem to indicate a greater variability for the north shore. Greater variability could be expected here if chiefly freshwater species of phytoplankton are involved.

E. Organic Matter

The estimates of oxidizable organic matter are listed in Table 1 and the lake values represented by samples taken farthest from inlets on collection dates are plotted in Figure 8. The latter figure shows summer highs for



Figures 5-8. 5. (Top) Distributions of predicted monthly mean tide levels (1957-1958) for Long Point, Lake Borgne (in feet above mean low water). 6. (Second) Distributions of estimates of total phosphorus from within the lake only. 7. (Third) Distributions of phytoplankton pigment concentration from within the lake only. 8. (Bottom) Distributions of organic matter from within the lake only.

both years with the highest values representing the spring and early summer of 1958. These high values do not seem to be necessarily dependent upon phytoplankton since the north shore peak values in 1958 slightly preceded peak pigment values for that year. The south shore peak values did, however, coincide. Concentration of organic matter reasonably could be expected to depend partly on phytoplankton. Perhaps a reasonable assumption concerning the origin of spring and summer highs is that they are more directly dependent upon allochthonous material carried in by yearly high runoff which precedes or coincides with high content of organic matter.

Estimates reported by Korringa (1956: 311-313, 340-343) for estuarine areas along the African shores of the Indian Ocean ranged from 6.5 to 70.4 mg potassium permanganate per liter (with the same method of analysis used in this investigation). Generally for areas having salinities of 33.0 ‰ or greater the estimates of organic matter were below 12.0 mg. The three highest values reported by Korringa were 31.8 mg representing an up-river sample (1.0 ‰ salinity) from "clear brown water", 50.6 mg and 70.4 mg representing samples from two different landlocked bodies of water with salinities of 1.0 ‰ and 17.0 ‰ respectively. In comparison to the majority of Korringa's estimates, the estimates for Lake Pontchartrain are high.

As far as the north shore area of the lake is concerned, high concentration of organic matter might be expected in view of the proximity of inlets from the marshland where organic matter, both in particulate form and in solution, must be high. The brownish coloration of bayou waters is undoubtedly associated with organic matter in one form or another.

IV. THE POPULATION STRUCTURE

In collecting qualitative bottom samples during the investigation several differences between the clams of the two areas soon became apparent.

A. Size and Abundance

Clams were found much more easily in the north shore area than in the south shore area. Near the mouth of Bayou Bonfouca as many as 100 could be dredged or picked up by hand in 30 minutes, whereas near the mouth of Little River dredging 60 clams

might have required as much as three hours or more. Specimens from the north shore area were always conspicuously smaller than those from the south shore.

B. Color

The periostracum of the north shore clams was generally charcoal or black in those near the bayou but lighter turning to chestnut brown streaked with green and black in specimens collected between Point Platte and Point au Chien west of the bayou. The gills of the dark specimens were often streaked dorso-ventrally with a deep-lying grayish substance. Streaking of the gills in chestnut colored specimens was rusty red. *Rangia* from the south shore area were of a chestnut brown to greenish yellow color with red streaking of the gills.

C. Shell Erosion

The umbones of the north shore specimens were conspicuously more eroded than those of the south shore. Erosion of the shell and black appearance of the periostracum may be due to high concentration of organic matter in the bottom sediments with consequent bacterial liberation of carbon dioxide, and immediate formation of carbonic acid responsible for erosion, although many other sources may contribute toward acidity in an environment such as that of the north shore (cf., Welch, 1952: 102, 118-119). A high residue of carbonaceous breakdown products of decay could be responsible for the black shell. The concentration of dead and decaying plant material, apparently in great part from the adjacent marsh areas along the north shore, is observable as black mud and gross particulate plant material mixed with sand in the bottom deposits, and as smaller black particulate plant matter in suspension in the water of the Bayou Bonfouca region and near Bayou Lacombe. Since the erosion is confined to the umbonal and anterior regions of the shell, acid formation could take place beneath the surface of the bottom and reach a considerable concentration before being removed by agitation of the water or by chemical combination.

D. Movement and Behavior

The apparent natural position of adult *Rangia* on the bottom is with the anterior end pointing directly downward, the siphonal end vertical with its tip just above the surface so that the umbones, lunule, and

greater part of the shell are completely buried. *Rangia* in aquaria with sand bottoms apparently move about rarely. Among several specimens kept for nearly a year in the laboratory the only movements observed were those for the ostensible purpose of burying themselves in the sand, movement of the shells allowing protrusion and withdrawal of the siphons, movement associated with pumping and pressure ejection of feces and pseudofeces from the mantle cavity, and movement toward the surface after being covered by the addition of sand to the aquaria. Many specimens collected from the lake had living barnacles and mussels as well as growths of algae adhering to different parts of the shell, chiefly on the siphonal end in which cases the lake bottom surface lines were obvious, indicating that the clams remain stationary for long periods. Also, such attached organisms have been found on the umbonal and anterior regions of the shell, particularly on those individuals from sand and shell bottoms in which "digging-in" may have been difficult. Frequently individuals of *Rangia* are found in groups of about 3-7, often with no more than a few inches of space between any two individuals. The clams within large groups, however, may be spread out more with perhaps 8-12 inches separating them. A more general aggrega-

tion of animals seems to occur with clumped areas of many small groups and relatively few isolated individuals. This was evident in parts of both study areas, but more obvious in the south shore area where some time was spent occasionally searching for places that would yield more clams per dredge haul in qualitative sampling.

E. Sizes of Adults

The distributions of sizes (antero-posterior shell lengths) of clams collected from the two study areas for gonadal analysis are shown in Figure 9. Since no clams below size class 25 (23.75 mm) were found whose gonads contained recognizable gametes, sizes larger than this were considered as representing potentially sexually mature adults. The distribution for the north shore area represents 651 right valve measurements with a mean length of 38.5 mm. The distribution for the south shore area represents 427 right valve measurements having a mean length of 42.4 mm. The individuals represented here were collected throughout the period of the investigation. From the appearance of the distributions the difference in mean length may be considered significant. The differences in shape and proportions of the distributions seem conclusive without the application of a statistical test.

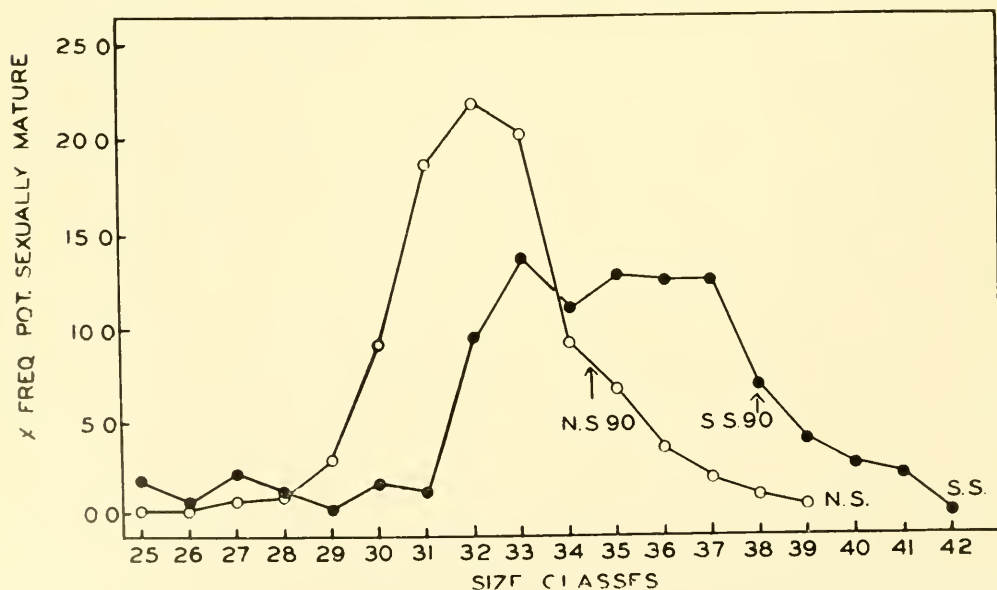


Figure 9. Distributions of size classes of adult clams; Pot.=potentially sexually mature adults, NS 90=90th percentile of the north shore distribution, SS 90=90th percentile of the south shore distribution (see Table 2 for actual sizes represented by size classes).

In regard to mean size and proportions of sizes, the adult population is different in one study area from the other.

F. *Relation of Shell Length to Shell Weight*

To determine whether or not differences existed in shell weight of the clams from the two areas the right valves of specimens collected from the north shore area on May 5, 1958 and from the south shore area on July 30, 1958 were cleaned and allowed to dry thoroughly and then weighed and measured. The north shore area was represented by 230 specimens and the south shore area by 216. The ratio of length to weight (L/W) for each shell was computed and the values grouped in classes according to shell size, with 2 mm intervals for each class. The mean ratio value for each class was computed and the means were plotted against size (fig. 10). From one to 56 specimens are represented for each size class from either of the two areas. The smaller numbers are represented only at the ends of the distributions.

The differences between mean ratio values of north and south shore clams for some of the matching size classes were tested for significance by application of the *t*-test. The

associated probabilities are listed opposite the size classes tested. The differences in intra-class means are conclusive up to 39 and 40 mm (size class 33) at the 0.01 level. Beyond this size where the differences are reversed with the north shore clams having higher ratio values, only the ratio difference for clams of 45 and 46 mm (size class 36) is conclusive (0.02 level). The reversal can be regarded as conclusive. The irregularity occurring in the distribution of the north shore ratios affects clams well above the average size for that area. Where size is constant a lower ratio value indicates greater weight in proportion to length. Evidently with increasing size the more horizontal deflection of the curve indicates a greater increment in shell length in proportion to increment in shell weight.

G. *Population Density, Growth, and Survival*

The size classes referred to concerning the data that follow are listed together with their intervals and mid-points in millimeters in Table 2. The estimates of population density of the different sizes of *Rangia* for each collection date are represented in Figure 11 (a-m). The densities of size classes 1-16

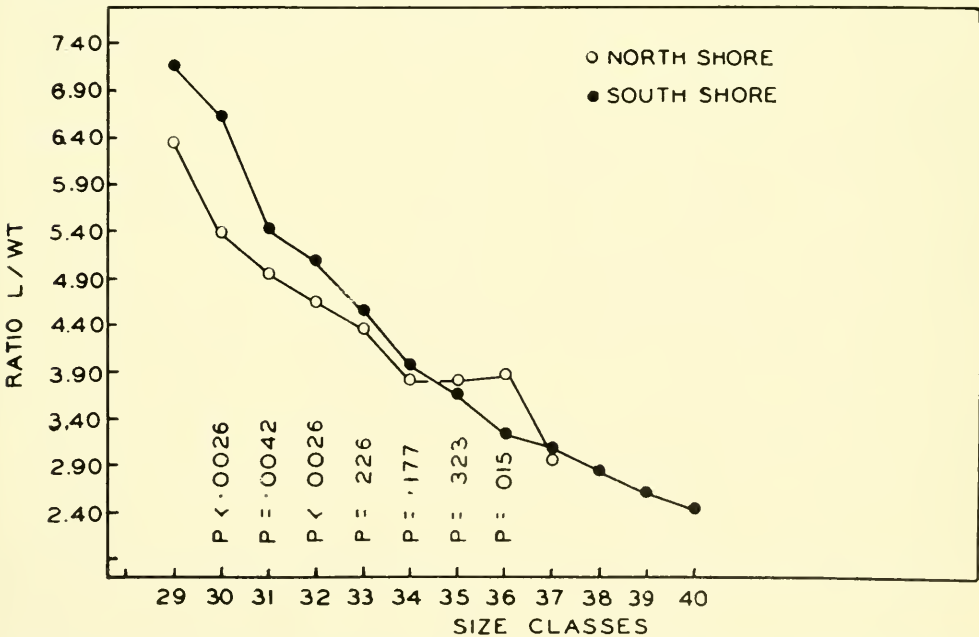


Figure 10. Distributions of length-weight relationship according to size class; P=probabilities derived from tests concerning the differences between the two mean ratio values for size classes indicated (see Table 2 for actual sizes represented by classes).

TABLE 2.
Size classes with intervals and mid-points
in millimeters.

Size Class	Interval	Mid-point
1	00.00-00.25	00.125
2	00.25-00.50	00.375
3	00.50-00.75	00.625
4	00.75-01.00	00.875
5	01.00-01.25	01.125
6	01.25-01.50	01.375
7	01.50-01.75	01.625
8	01.75-02.75	02.250
9	02.75-03.75	03.250
10	03.75-04.75	04.250
11	04.75-05.75	05.250
12	05.75-06.75	06.250
13	06.75-07.75	07.250
14	07.75-08.75	08.250
15	08.75-09.75	09.250
16	09.75-10.75	10.250
17	10.75-11.75	11.250
18	11.75-12.75	12.250
19	12.75-13.75	13.250
20	13.75-14.75	14.250
21	14.75-16.75	15.750
22	16.75-18.75	17.750
23	18.75-20.75	19.750
24	20.75-22.75	21.750
25	22.75-24.75	23.750
26	24.75-26.75	25.750
27	26.75-28.75	27.750
28	28.75-30.75	29.750
29	30.75-32.75	31.750
30	32.75-34.75	33.750
31	34.75-36.75	35.750
32	36.75-38.75	37.750
33	38.75-40.75	39.750
34	40.75-42.75	41.750
35	42.75-44.75	43.750
36	44.75-46.75	45.750
37	46.75-48.75	47.750
38	48.75-50.75	49.750
39	50.75-52.75	51.750
40	52.75-54.75	53.750
41	54.75-56.75	55.750
42	56.75-58.75	57.750
43	58.75-60.75	59.750

represented in Figure 11 and other figures based on the same data may be overestimated to some extent because of the inadvertent inclusion of an undescribed species of *Rangia* (*Rangianella*) unknown to the investigator during 1957 and 1958. Investigations pertinent to this species were made in 1960 and 1961 and are reported later in this paper. Density estimates for some of the associated mollusks are given in Figure 12 (a-o). Counts of the latter were not made for every collection.

The mean densities for each size class representing the entire investigational period are plotted in Figure 13. To elucidate the spawning period the seasonal densities of the three smallest size classes are replotted in Figures 14 and 15 for the north shore and south shore areas respectively.

The data represented in Figures 11, 14 and 15 indicate that spawning may occur almost continuously beginning sometime in late summer or fall and continuing through

the winter and spring into early summer. The actual beginning and end of spawning cannot be established from these data alone since duration of the larval period, size at metamorphosis, and growth rate of the "spat" or "set" after metamorphosis and settling are not known. These factors are variable and may depend chiefly on food and temperature. The latter two factors are thought to be most important in affecting the size of larvae and duration of their pelagic period in many mollusks (Thorson, 1946: 452; Loosanoff, 1954: 620-621). In January and February of 1958, the two coldest months, the smallest juveniles, 0.375 mm (size class 2), found during the investigation were more abundant in the samples than any other size. Juveniles of size class four (0.875 mm) were the least abundant of the three smallest size classes in the north shore collections (fig. 14).

Density estimates are conspicuously rare for clams between size classes 20 and 25 (14.25 - 23.75 mm). Specimens in this size range were found only with difficulty in the qualitative samples. Finding them only in the summer months is probably significant. A large qualitative sample of 314 individuals, both juvenile and adult, from the north shore area (fig. 16) was collected on September 15, 1958 to verify the results of quantitative sampling in regard to the scarcity of individuals of the sizes 14.25 to 23.75 mm. Only four specimens within this size range were found. Possibly they actually are few in number and their growth rate is probably high so far as annual increment in length is concerned. Growth rate for clams under size class 20 can be inferred by comparing the shift in position of modal peaks from one collection to the next [figs. 11 (j-m), 16]. As the shift proceeds to the right representing increase in size, density decreases sharply. The modal peak at size class 13 (midpoint, 7.25 mm) in September [fig. 16 (frequency is not plotted logarithmically)] most likely represents juveniles spawned in March or April, about six months of age. The small group at the right of the modal peak may be a few months older. Since growth rate declines with age, individuals of size class 13 could not reasonably be expected to reach size class 25 (midpoint 23.75 mm) during the six months following September 15th and probably not before the end of another year because of

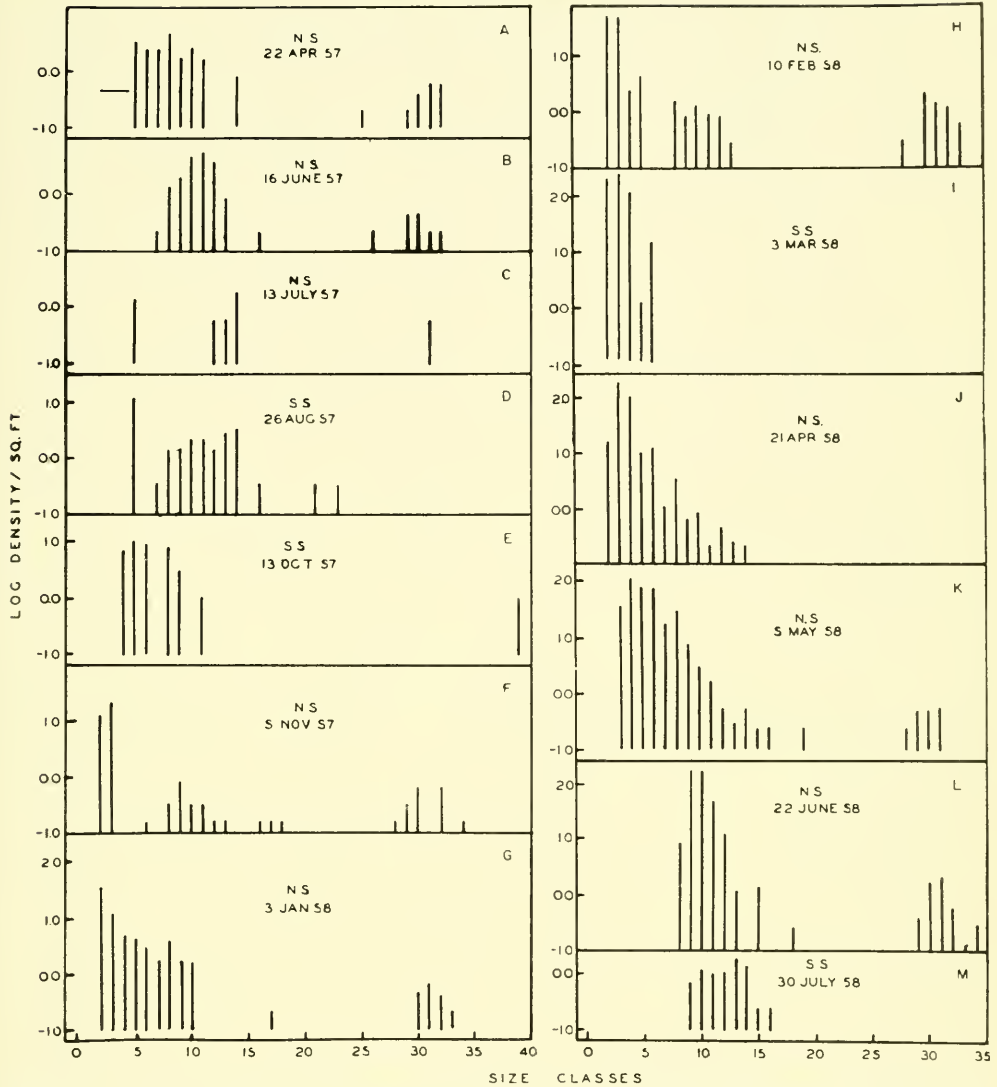


Figure 11. Distributions of population density by size classes; NS=north shore area, SS=south shore area, horizontal line in A indicates no estimates were made for size classes below size class 5 (see Table 2 for actual sizes).

the intervening period of storms, low temperature, and scarcity of food. If average growth rate remained nearly the same for the next six months they might be expected to have attained a length of 15 mm (size class 20) in one year depending upon environmental conditions. In the meantime the numbers of individuals (density) of this age would have declined greatly as is indicated by Figure 11. Any survivors of this size (15 mm) would have had seven months of warm growing season ahead in which pos-

sible rapid growth could effect an increase from approximately 15 mm (size class 20) to 24 mm (size class 25). The chances of picking up juveniles in this size range (14.25 - 23.75 mm) would be small because the relatively few clams represented would not be expected to stay within the size range for any length of time.

For further information concerning growth rate in *Rangia* the percent frequency of lines of growth interruption of 40 specimens collected in the north shore on

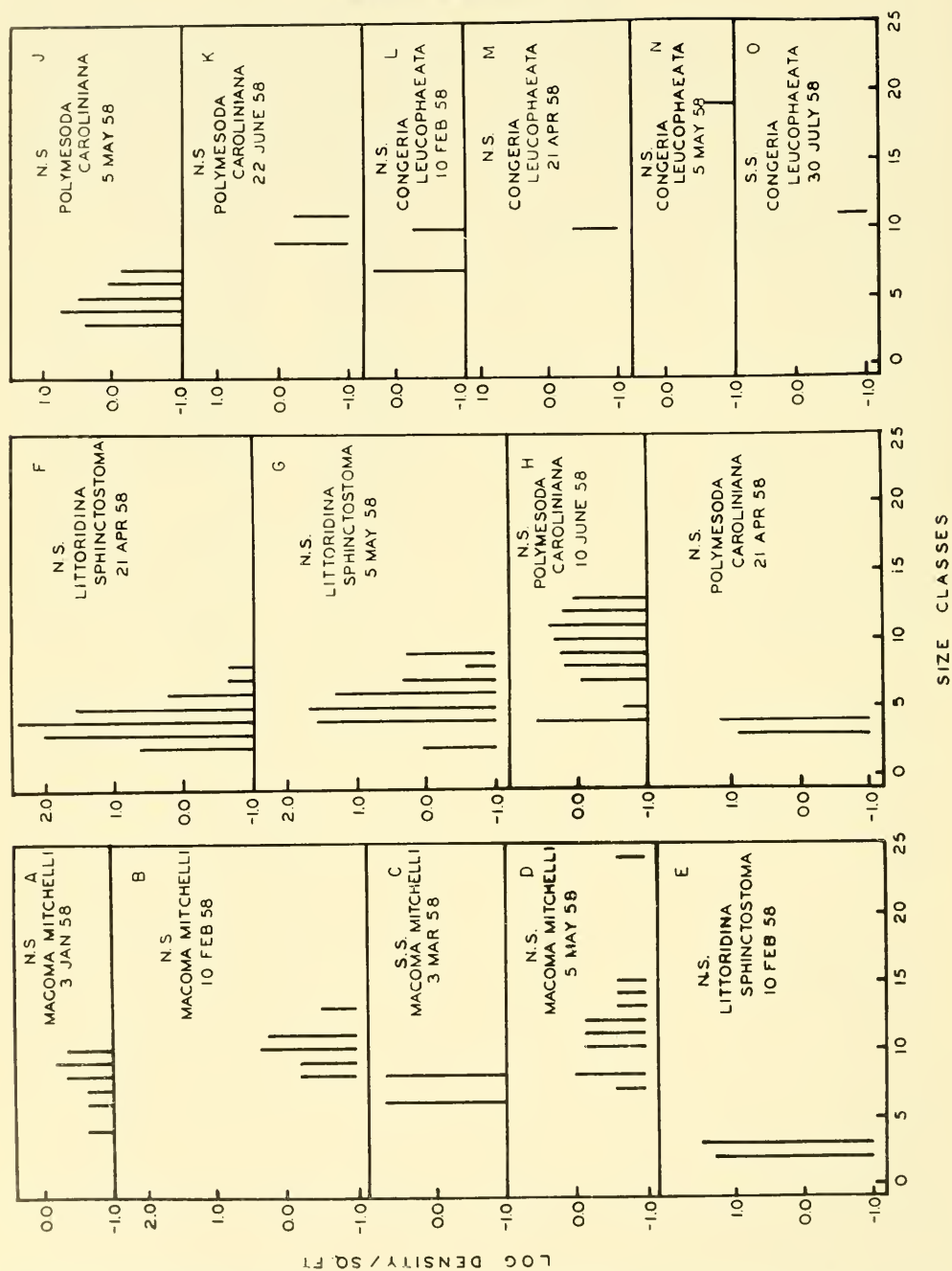
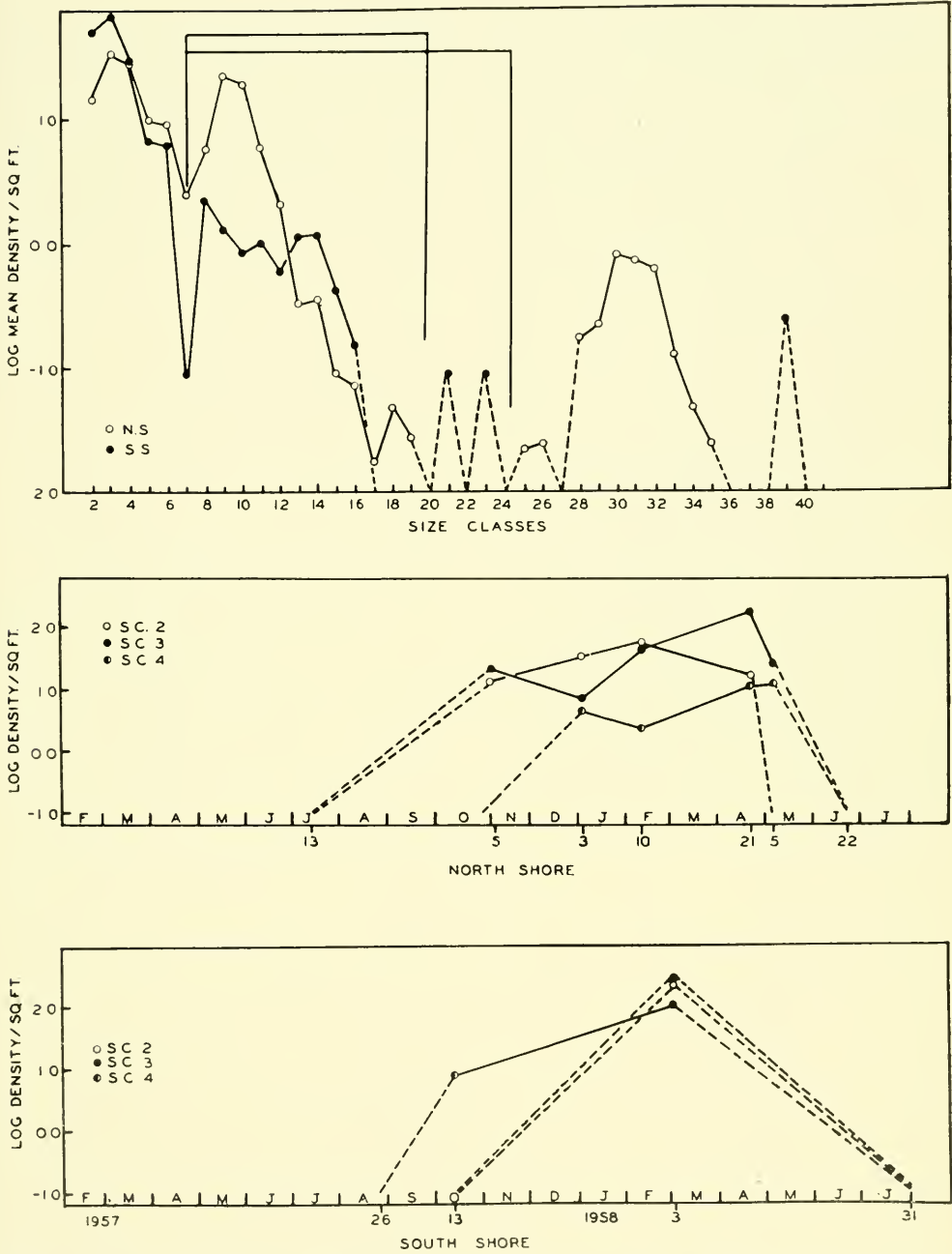


Figure 12. Distributions of population densities of associated mollusks; NS=north shore area, SS=south shore area (see Table 2 for actual sizes).

September 15, 1958 and 60 specimens taken from the south shore area on July 30, 1958 were plotted (figs. 17, 18). The peaks in these distributions were assumed to indicate: (a) the sizes at which shell growth was most

frequently interrupted; and (b) that the space between the peaks generally indicated most frequent size intervals in which growth increment occurred. There were growth interruption lines at nearly all diameters above



Figures 13-15. 13. (Top) Distributions of mean density of size classes; dashed lines indicate size classes having densities estimated to be no greater than the antilog of -2.0 (0.1/sq. ft.), NS=north shore area, SS=south shore area; right angle lines delimit size classes involved in testing the density estimates of juveniles (see text). 14. (Middle) Seasonal distributions of density of the three smallest size classes of the north shore area; dashed lines indicate dates for which densities were estimated to be no greater than the antilog of -1.0 (0.1/sq. ft.), SC=size class (see Table 2 for actual sizes). 15. (Bottom) Seasonal distributions of density of the three smallest size classes of the south shore area (symbols as in fig. 14).

7 mm. Mid-winter interruptions due to cold temperatures seem to be responsible for the majority of the modal peaks although spring and fall interruptions caused by stormy periods may have been recorded (*cf.*, Coe, 1947). In the north shore specimens (fig. 17) the first major peak occurred at 15 mm (size class 21) and probably indicates the end of the first year's growth, as indicated by the rate of shift in modes of Figure 11 and the modal positions in Figure 16. The second major peak occurs at 20 mm (size class 23) but is flanked on either side by smaller peaks at 17 mm and 22 mm. This second major peak probably indicates the average increment at the end of the second year's growth. The flanking minor peaks may indicate the end of the second year depending upon whether the interruptions occurred in the fall or the spring stormy periods. (The flanking peaks may also depend upon whether the individual had arisen from spawn in fall or spring). A period of interruption in the fall would be followed by an immediate delay, if not interruption, by winter cold temperature, producing a lesser increment by the end of the second year. On the other hand, since these individuals were of different sizes and had experienced different seasons, a relatively mild fall and winter but with severe conditions in the

spring could produce an interruption to be followed shortly by warm temperatures and increase in available food resulting in a greater increment than 20 mm for the same period of time. To what extent the timing of these interruptions affects the total increment in yearling juveniles is impossible to determine from these data. However, the higher growth rate of yearlings makes reasonable an expectation of an increment of 15 mm for their first year. The peaks beyond 23 mm (size class 25) appear more regularly spaced but cannot be relied upon to indicate age of the animal at the time of their formation because of preceding variable growth and variously prolonged interruptions. The same difficulty is met in plotting the frequencies of actual lengths for older year classes; a greater spread of sizes is sometimes shown with overlapping of classes and complete obscuring of the modes (Haskin, 1954: 300). Additional factors affecting growth rate of pelecypods is the energy required by the gametogenic cycle, extent of spawning and resorption of unspawned gametes, and timing of the cycle in the individual (*cf.*, Orton, 1928: 365; Coe and Turner, 1938: 99; Coe, 1947: 13).

The distribution of frequencies for clams from the south shore area (fig. 18) similarly indicates the age of the smaller clams. A greater annual increment is indicated for these clams at least during their first two years and possibly for the third. The first major peak is at 20 mm (size class 23) indicating the end of the first year's growth. The peak is flanked on the left by a smaller peak at 16 mm which may also indicate the end of the first year's growth or the end of the growing season for some individuals. Absence of the 16 mm peak in association with the presumed first year peak of the north shore shells may be due directly to the difference in growth rate, regardless of what the causes are. The obtuse peak centering on 29 mm (size class 28) seems to indicate the average increment by the end of the second year. Like the distribution for the north shore this second major peak is flanked on either side by minor peaks which probably have the same possible causes as those for the north shore. The separation of the second major peaks of both distributions from the third major peaks, by dips representing much lower frequencies than for adjacent sizes, must indicate that a high proportion

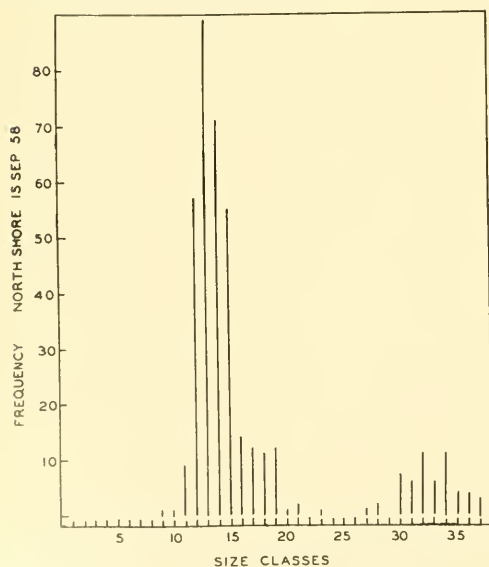


Figure 16. Size distribution of 314 individuals collected on September 15, 1958 in the north shore area (see Table 2 for actual sizes).

of the clams was undergoing rapid continuous growth during the time they were in the respective size intervals. On the average the clams could be in their third summer of growth when these frequencies are low.

The inferred average annual increment for the first three years for the clams from the two areas is as follows:

Year	North Shore	South Shore
1st	15 mm	20 mm
2nd	5 mm	9 mm
3rd	4 mm	5 mm

Accordingly the growth rate in terms of increment in shell length for *Rangia* from the south shore area is initially much greater than for individuals from the north shore but by the end of the third year the rates become nearly equal. The difference in average length for the two areas by the end of the presumed third year is thus 10 mm.

The 90th percentile of the north shore distribution (fig. 9) indicates that 90 percent of the adult population in that area is below 43.0 mm (size class 35) while that of the south shore distribution indicates that 90 percent is below 50.00 mm (size class 38). The difference in these two percentile sizes is 7.0 mm. The shapes of the distribution curves above the 90th percentile are similar and may indicate that growth rate and survival are similar for adults in the two areas only for the upper 10 percent in size. The ages of these clams would be of interest, but data are lacking. The deflection in the distribution of the north shore length weight relationship (fig. 10), in progress when the 90th percentile in size (size class 35) has been attained, is also interesting but not explainable on the basis of present evidence.

The second mode (fig. 13) for the south shore clams, including the mean density estimates for size classes 7-24 (1.62 - 21.75 mm), is considerably in advance of the second mode for the north shore clams, including size classes 7-20 (1.62 - 14.25 mm) supporting the indications of the growth interruption frequencies. (Growth rate is indicated to be greater for south shore clams during the first year at least.) The density estimates for south shore clams in size classes 21 and 23 probably involve clams of about the same age as those in size classes 17-19 of the north shore. The densities of size classes 8-24 inclusive represent clams col-

lected, for the most part, in spring and summer while the densities of size classes 2-7 inclusive are represented in the collections of winter and spring. Comparatively low densities for size class 7 appearing for both areas are probably artificial, owing to change in size class interval. High densities of size class 7 occur in January, April, and May (fig. 11 a, g, j, k) possibly marking intervals between spawning periods.

The similarity in shape of the distributions of Figure 9 to the distributions of mean densities for size classes 7-24 in Figure 13 is notable and probably means that a differential growth rate exists between the clams of the two areas, regardless of age of the juveniles and bulk of the adult population, *i.e.*, below the 90th percentile of a size frequency distribution.

The estimated density for the north shore adult clams (above size class 24) was 2.88 per square foot while that for the south shore was 0.25 per square foot. Since the distribution of adult *Rangia* in either of the two areas is not believed to be either random or uniform but is clumped in varying degrees, particularly in the south shore area, the difference cannot be tested satisfactorily by statistical analyses without further extensive and careful sampling. The distribution of juveniles in the two areas may be more uniform but occasionally single samples from a collection yielded extremely high or low density estimates. The highest density estimates of juveniles in size classes two and three, for example, came from one sample of the collection of March 3, 1958 from the south shore area. This caused the means of these two classes to be about four times higher for this collection than for the same two classes of any other collection. The bottom material brought up in the sample contained a high proportion of black organic material, rare for the south shore area. This suggests that the pelagic larvae tend to select a bottom high in organic matter for settling and supports the contention of Thorson (1946: 464, 465) that pelagic larvae exercise some selection of substrate for settling rather than simply drifting by chance to any type of bottom. The overall mean density for juveniles (size classes 2-24 inclusive) in the north shore area was 167.95 per square foot and for the south shore, 175.42. The difference is not significant when the data are tested by Student's *t*-test ($p > .50$). The

mean densities for size classes 2-7 inclusive were 17.00 per square foot for the north shore and 27.72 for the south shore ($p>.40$). For size classes 8-16 inclusive (delimited by right-angle lines in fig. 13) mean densities were 6.45 for the north shore and 0.99 for the south shore area ($p<.10$). If the difference between the density estimates of the adults in the two areas is tested it may be regarded as conclusive ($p<.02$). Although the results of testing data of this kind may be misleading, there is a tendency for the observed increasing differences between the two areas (fig. 13) to become significant with increasing size from class 2 to adult sizes of class 25 and above. The density data, as such, support the empirical differences found in the qualitative sampling of the adults and suggest that the settling of newly metamorphosed juveniles is no different in one area from the other but that mortality is greater, or survival less, in the south shore area during growth to reproductive size.

If the animals represented by the mean density estimate of size classes 25 and 26 (0.047) for the north shore (fig. 13) were added to the adult (reproducing) population near the end of their third year, as indicated by the data concerning growth rate, then hypothetically about 1.62 percent can be estimated as the mean yearly addition to the north shore adult population, and if the population tends to be stable the same figure could represent yearly mortality. If the frequencies representing size classes 27 and 28 (fig. 16) represent new additions to the adult population following a summer of apparently favorable growth conditions they represent 5.45 percent of the total. That the adult population is stable from year to year is unlikely and whether 1957 and 1958 were representative years for *Rangia* in Lake Pontchartrain, in so far as unknown environmental conditions are concerned, is not known.

The proportions (in different collections) of probably new recruits to the adult population sampled in 1960 and 1961 are listed in the last column of Table 6 and indicate an average yearly recruitment of about 11 percent.

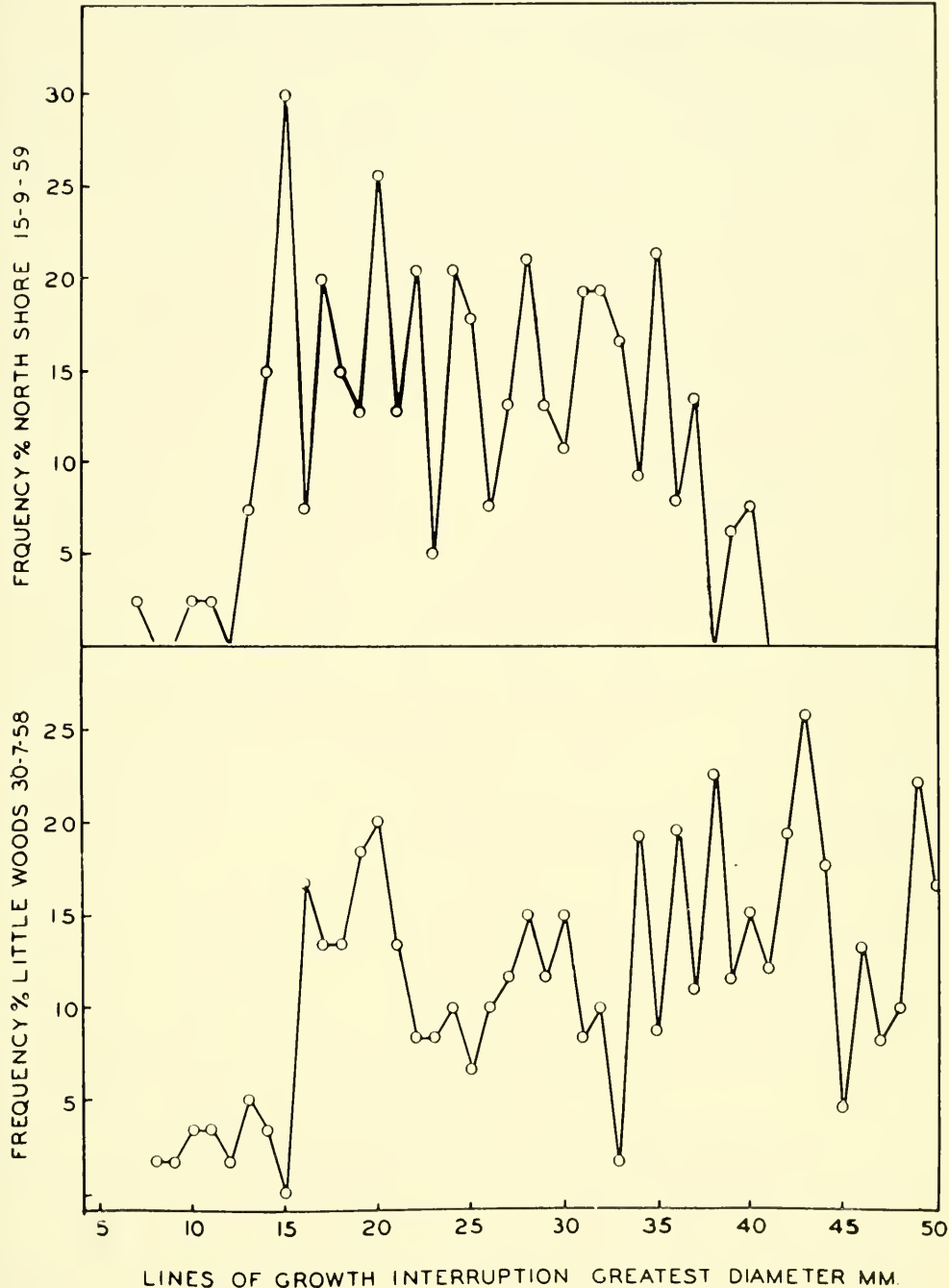
The seasonal mean lengths, as computed from the density data, of adults (above 23.75 mm) from the north shore area and juveniles from both areas are plotted in Figure 19. A discrepancy occurs between the

mean length (38.5 mm) of the north shore adults as computed for the specimens from the qualitative samples (fig. 9), collected chiefly for gonadal analysis, and the mean length as computed from the quantitative samples (34.9 mm) in Figure 19. This is probably attributable partly to bias in the earlier qualitative samples in which some smaller specimens were ignored to insure the inclusion of potentially sexually mature individuals in the gonadal inspections. Also the qualitative samples were consistently collected from north shore locations 1 and 7 (fig. 1) which may not have been representative for size in the general north shore area. Another possibility is that the quantitative dredging may have failed to yield a representative sample of larger specimens because of clumping in distribution over the bottom.

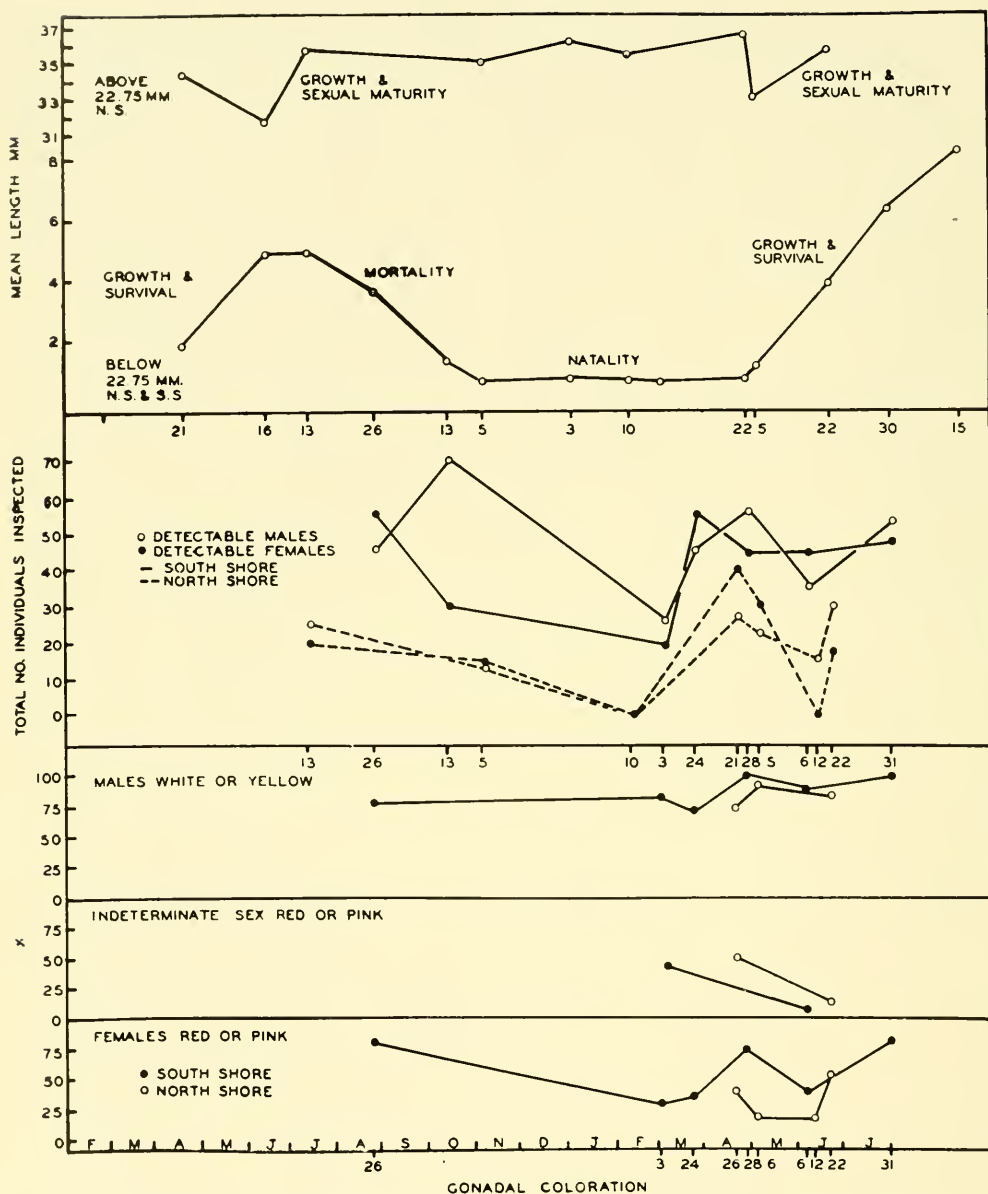
Mean length of the adults (fig. 19) fluctuates sharply above and below the overall mean during the late spring and early summer of both 1957 and 1958. The mean lengths of individuals in qualitative samples having relatively large numbers of specimens seem to show the same thing for both the north shore and the south shore:

North Shore		
Mean = 38.5 mm		
Date	Mean	Sample Size
Nov. 5, 1957	38.57 mm	39
Feb. 10, 1958	37.92	48
April 21, 1958	37.54	227
May 5, 1958	38.91	159
June 12, 1958	41.97	90
South Shore		
Mean = 42.4 mm		
Aug. 26, 1957	44.13 mm	58
March 3, 1958	44.68	60
March 24, 1958	41.44	52
April 28, 1958	41.82	111
June 6, 1958	44.77	82

If the seasonal differences for both areas are significant they are indicative of a slightly higher mortality rate for the larger adults (above the mean) coinciding with the end of the spawning season, a higher growth rate for adults of all sizes, particularly for those below the mean, and the addition of younger members to the adult population coinciding with high temperature and more available food during summer. If the fluctuations in mean length occur annually,



Figures 17-18. 17. (Top) Frequency of lines of growth interruption in 40 specimens from the north shore area. 18. (Bottom) Frequency of lines of growth interruption in 60 specimens from the south shore area.



Figures 19-21. 19. (Top) Distributions of seasonal mean length of north shore adults and of combined north and south shore juveniles; NS=north shore area, SS=south shore area. 20. (Middle) Seasonal distributions of determinable sexes in the study areas; detectable=determinable. 21. (Bottom) Seasonal distributions of gonadal coloration according to sex; indeterminate=non-determinable.

possibly they may have been greater for the interval between the springs of 1957 and 1958 than for previous years particularly in view of the trend toward higher amounts of available food indicated by the data concerning pigment and organic matter (figs. 7, 8).

Mean length of juveniles of both areas (fig. 19) was greater in the summer of 1958 than in the summer of 1957. (The curve is an expression of survival or mortality as well as of growth.) By far the greater part of the annual increment in shell length of the

adults appears to occur within a period of about two months.

A similar rapid growth rate was found for the Pismo clam, *Tivela stultorum*, in June (Coe, 1947: 10-15) along the California shores near La Jolla in marked individuals planted several months previously. As much as 4 mm was recorded for some clams within a month. The average was 2.6 mm for June, but less than 1.0 mm per month during the winter. The author did not state the size limits of individuals in which these rates occurred. The Pismo clam has a second period of increased growth rate beginning in September near the end of its spawning period which lasts about three months. (The temperature range of the habitat was only about 8° C). This clam is about 42 mm in length at the end of its second year and may reach lengths of about 70 mm during its life-time. In *Mercenaria* Pratt and Campbell (1956) found that more than half the year's growth occurred before mid July.

H. Predators

No observations were made that provided a basis for either a qualitative or quantitative account of predators. However, the appearance of considerable amounts of freshly broken adult and juvenile shells with periostracum intact indicated heavy predation by either fishes or crabs or both.

Suttkus *et al.* (1953-54) reported "clams" among the stomach contents of 14 species (representing eight families) of "the 74 different fish forms" found in Lake Pontchartrain. Five of these species were of the Family Sciaenidae and one of these, the Atlantic croaker *Micropogon undulatus*, was one of the three most numerous species found in either trawl or seine catches during the period reported. The authors also reported "clams" among the stomach contents of the blue crab *Callinectes sapidus*, commonly found throughout the period, and among the stomach contents of the white shrimp *Penaus setiferus* found abundantly in July through November of 1953. Gunter and Shell (1958) reported catfish (*Ictalurus furcatus*) living on *Rangia* and the attached *Conger*.

I. Associated Mollusks

Other mollusks in the two areas were the pelecypods *Polymesoda caroliniana* Bosc, *Macoma mitchelli* Dall, *Conger* *leucophaeata* Conrad, and one small gastropod *Littori-*

dina (*Texadina*) *sphinctostoma* Abbott and Ladd. The shells, but no living representatives of the two other species, *Brachidontes recurvus* Rafinesque and *Tagelus plebius* Solander, occasionally were found in both areas and more frequently in the south shore area. The latter two species may have become established temporarily in the lake during preceding years when salinity in the lake was higher or they may have been carried in by fishes that could have passed them through the digestive tract whole. Shells of these species were sent to The Academy of Natural Sciences of Philadelphia where they were identified by Dr. R. Tucker Abbott.

Polymesoda, comparable in size to *Rangia*, was found in relatively small numbers in both areas, and was seemingly more abundant in the north shore area but the largest specimens were found in the south shore area. The differences in shell erosion were comparable to those of *Rangia*, being more extensive in north shore specimens. The other associated species also seemed to be more abundant in the north shore area, although this is based on empirical observations since counts of these species were not made for every collection. The density distributions of size classes (fig. 12) indicate that the peak in the spawning activity of these mollusks may occur simultaneously with that of *Rangia* or at least that their spawning periods are overlapped by the most intense part of the breeding cycle of *Rangia*. Growth rate of north shore mollusks as indicated by shifts to the right of modal peaks seems to be constant regardless of species and size if only individuals under about 9 mm (size class 15) are considered. Maximum size of presumed adults of *Macoma mitchelli* was about 22 mm, and 3 mm for the gastropod *Littoridina*, when measured from the tip of the spire to the base of the aperture.

V. REPRODUCTION

A. Gonadal Analysis

Sex ratio and the gametogenic cycle.—The gonad in *Rangia* is similar to that of other pelecypods, not a discrete organ, but a mass of specialized tissue within the mantle enveloping the ramified digestive gland and loops of the intestine. The gonad develops seasonally to greater proportions, swelling the mantle tissues, and effecting more firmness and opacity just before presumed spawn-

ing periods. At this time recognizable gametes have suddenly become differentiated and the sex of the individuals can be distinguished.

The percent of individuals in which the sex was determinable or non-determinable for each qualitative collection is represented in Table 3 for each study area. The percent of the total individuals of a collection that were male or female is plotted in Figure 20 for each study area. The difference between 50 percent and the percent of one sex or the other of the total number in which sex was determinable was tested either by a simple test of proportions, when the sample number was above 30, or otherwise by application of the binomial distribution, for each collection. The probabilities ranged between 0.18 and 0.85 for all collections except that of June 12, 1958 from the north shore area in which no determinable males were found (p , approximately 0.03). No indications of hermaphroditism or juvenile sexual phases such as those known in *Mercenaria mercenaria* and *Crassostrea virginica* were found (*cf.*, Coe, 1943: 161).

In other pelecypods whose seasonal gonadal changes have been studied (Loosanoff, 1937; Coe and Turner, 1938; Coe, 1947; Tranter, 1958a, 1958b) the rate of which gametogenesis proceeds is variable depending upon environmental conditions and may not be the same in all individuals of a population. In general, spawning is followed by

a gonadal recovery phase in which non-spawned residual gametes are resorbed by autolytic processes and phagocytosis. Mitosis and gametogenic proliferation follow this into the next spawning period. These periods or phases may or may not be clear cut. In *Mya arenaria* (Coe and Turner, 1938: 99) continued intermittent spawning may occur after the first spawning of the season early in June. In *Mercenaria mercenaria* (Loosanoff, 1937: 408-409) at least a few ripe appearing ova and mature spermatozoa can be found at all seasons of the year except for a brief post-spawning period when no mature spermatozoa are likely to be found.

According to Tranter (1958b: 150-152) no distinction can be made between the developing and the declining phases nor can the degree of development or regression be estimated except by microscopic examination of stained gonad sections, at least for *Pinctada albina*. In the latter species the gonad may develop more than once in the same season with overlapping of breeding cycles; spawning frequently may be incomplete in both sexes and there are occasional instances of non-spawning in which cases the entire gametic production is resorbed. Spawning usually continues for 3-4 months and recovery for 2-3 months, but it is not unusual for gametogenesis to continue after the first spawning of the season nor for the resorption of gonad material to commence before spawning is complete.

TABLE 3.
Proportions of sexes and gonadal parasitism.
(ND, non-determinable sex; NS, north shore area; SS, south shore area.)

Date and Location	Females %	% ND	% Males	No. of Specimens	Size Range mm	% Infested by Trematodes	Sizes of Individuals Infested with Trematodes (in mm)
7/13/57 NS	25	55	20	40	24-50	0	
11/ 5/57 NS	13	72	15	39	27-44	5.13	40, 41
2/10/58 NS	0	100	0	49	32-46	6.12	33, 38, 41
4/21/58 NS	27	33	40	67	31-48	6.00	36, 39, 41, 42
5/ 5/58 NS	22	48	30	50	27-48	4.00	12, 47
6/12/58 NS	15	85	0	40	33-51	1.76	38, 45
6/22/58 NS	20	54	17	48	28-41	4.00	39, 40
NS Average	18.7	63.9	17.4	total=333			Mean size infected—40.13 Total inspected for Trematodes—337 % infected—4.45
8/26/57 SS	45	0	55	58	34-56	1.72	52
10/13/57 SS	70	0	30	23	33-47	0	
3/ 3/58 SS	26	55	19	58	36-55	3.45	15, 53
3/24/58 SS	15	0	55	51	27-58	0	
4/28/58 SS	56	0	44	52	27-56	0	
6/ 6/58 SS	35	21	44	81	27-56	3.57	49, 50, 51
7/31/58 SS	53	0	47	40	34-48	2.50	47
SS Average	47.1	10.9	42	total=363			Mean size infected—49.57 Total inspected for Trematodes—366 % infected—1.91

The gametogenic cycle in *Rangia* may be little different from that of other pelecypods except in the timing of spawning and recovery. The percentage distributions of determinable sexes for the study areas appear almost identical in timing but consistently different in proportions of individuals whose sex is determinable (fig. 20). The proportion of determinable sexes evidently depends upon extent of spawning. The mean percent of individuals of non-determinable sex (Table 3) for the north shore collections was considerably greater than for the south shore collections (p, infinitesimal). The highest percentages of individuals of non-determinable sex in the collections from both areas (or lowest percentages of determinable sex, fig. 20), occurred within at least a month of each other. The gonads of clams collected on February 10, 1958 from the north shore area and those collected on March 3, 1958 from the south shore area were firmer, more well filled, and milkier in appearance than those seen in any of the other collections. The condition can undoubtedly be regarded as one of prespawning development and imminent ripeness. Apparently this phase was preceded by a long recovery phase with some individuals spawning later than others in the fall in view of the large numbers of juveniles represented in the January and February quantitative collections. Artificial fertilization of eggs taken from females collected October 13, 1957 was relatively successful, but difficult with eggs from females of the November 5 collection. Development of fertilized eggs from females collected 24 March and 6 and 12 of June, 1958 appeared normal. The collections of April and May, 1958 showed high proportions of individuals with ripe gametes; also, the corresponding quantitative bottom samples had high proportions of small juveniles. Low percentages of clams with recognizable gametes were evident again in the early June collection but collections later in June and July indicated a rapid increase in gametic production.

That the first maturation of gametes in the spring occurs only after water temperatures begin to rise (figs. 2, 3) is probably significant and indicates that the effect of temperature upon the gametogenic cycle is as important for *Rangia* as for other pelecypods in which temperature has been experi-

mentally raised in laboratory situations to induce spawning (Loosanoff, 1954).

The data suggest that *Rangia* has two incompletely definitive spawning periods per year with post-spawning recovery phases indicated by low percentages of individuals with recognizably mature gametes. A spring spawning period of about three months duration (March, April, May) and a more prolonged but less intense spawning beginning in late summer and lasting at least into November is indicated. Many individuals during the latter period may be undergoing recovery at a more rapid rate than others and some may be spawning more intensely than others. The post-spawning recovery phase apparently occurring in mid-summer is more rapid or intense than that occurring in fall and mid-winter.

In general there was a distinct difference in the gross appearance of the gonadal tissues of the north shore and south shore clams. The north shore specimens were nearly always flaccid and pale in coloration while those of the south shore were generally firm, opaque, and of definite color. This difference in appearance and the differences in percentages of clams of determinable sex probably indicate that spawning is more complete in the north shore clams.

Gonadal coloration.—Distinctive gonadal coloration is found generally throughout the pelecypods (Coe, 1943: 156; Ricci, 1957: 13; Tranter, 1958a: 136) and depends directly upon the sexual type of the mature gametes, the mass of mature ova being more richly colored than the gonad with mature spermatozoa which is opaque and white, or cream, or some other light shade. The color is seen through the transparent epithelium of the mantle. Even in truly hermaphroditic species such as *Pecten irridians* (Coe, 1943: 156) the male part of the gonad is distinct in color from the part producing ova.

Data concerning the intensity of coloration of gonadal tissues of *Rangia* were recorded for most of the collections at the time of inspection determining sexuality. The percentages of individuals of each sex and of indeterminable sex fitting four categories of color ranging from white to red are represented in Table 4 and their seasonal distributions of color intensity are plotted in Figure 21. Generally, few males were found that could be classified as red, but either white or red females were not uncommon.

TABLE 4.
Gonadal coloration in proportions of the population.
(NS, north shore area; SS, south shore area; R, red; P, pink; Y, yellow or cream; W, white; ND, non-determinable as to sex.)

Date and Location	Females						Non-determinable						Males						No. Animals Inspected		
	R %	P %	Y %	W %	R %	P %	Y %	W %	R %	P %	Y %	W %	R %	P %	Y %	W %	female	male	total		
21 April 58	X	0	40	20	40	6	44	17	33	0	27	21	52	0	29	15	9	22	15	62	
5 May 58	X	9	73	9	14	0	0	14	86	7	0	53	40	0	46	11	0	31	0	48	
12 June 58	X	0	17	50	33	9	0	12	86	0	0	—	—	0	6	—	—	0	0	40	
22 June 58	X	13	40	40	7	0	13	48	39	0	16	42	42	0	23	15	23	50	12	50	
NS Average	5.5	26.5	45.8	22.3	1.5	14.3	22.8	61.5	2.3	14.3	38.7	44.7	0	2.3	14	14	0	23	12	300	
26 Aug. 57	X	36	0	21	—	—	—	—	—	0	23	12	65	0	17	14	0	0	17	31	
3 Mar. 58	X	0	29	0	71	13	30	0	57	0	17	0	83	0	23	14	0	23	12	49	
24 Mar. 58	X	0	35	35	30	—	—	—	—	0	29	0	46	0	25	23	0	0	28	51	
28 April 58	X	45	25	17	10	—	—	—	—	0	0	52	48	0	32	23	0	0	33	52	
6 June 58	X	11	28	29	32	6	0	19	75	3	8	0	33	3	16	29	0	16	36	80	
31 July 58	X	27	55	0	18	—	—	—	—	0	0	6	94	0	0	12	0	0	18	40	
SS Average	21.0	35.2	13.5	30.3	9.5	15.0	9.5	66.0	0.5	12.8	25.2	61.5	0	0.5	12.8	25.2	61.5	0	0	303	

Those of indeterminable sex were more often white or translucent.

The following statements are based on tests of proportions concerning the observed differences (Table 4) in gonadal coloration of clams of the two study areas: (a) the proportion of south shore females that were red or pink was higher than the proportion of north shore females that were red or pink ($p=0.019$); (b) the proportion of south shore males that were white or yellow was not significantly different from the proportion of north shore males that were white or yellow ($p=0.28$); (c) the proportion of individuals of indeterminable sex from the north shore did not differ significantly (at the five percent level) from the proportion from the south shore in intensity of red coloration ($p=0.11$).

The data in Figure 21, when compared to Figure 20, show that the intensity of coloration for each sex is greatest at times of greatest gonadal development, and that periods of least distinctive coloration for the sexes coincide with periods when sex is least distinct, (i.e., presumed post-spawning recovery or prespawning phases). The individuals of indeterminable sex had least coloration at the end of the first, and apparently more intense, spawning period of the season.

The gonadal coloration of clams from the south shore was at all times more intense than in clams from the north shore (fig. 21) and supports the data of Figure 20 in indicating a more extensive release of mature gametes (spawning) among the north shore clams. Presumably the current load of unspawned gametes of the south shore clams is resorbed and proliferation recurs before spawning in the spring.

Gonadal parasitism.—Occasionally individuals were found whose gonads were spotted with distinct orange coloration. The gonadal fluid of these clams contained larvae of trematodes (cercariae, and often sporocysts). Only rarely did such clams have mature gametes. Specimens of the trematode larvae preserved in formalin were sent for identification to Dr. Franklin Sogandares (then, of the Florida State Board of Conservation). They appear to be fellodistomatids, but the adult form is not known and no positive identification could be made without further investigation involving possible secondary hosts. The suggestion was made that

pinfishes (*Lagodon rhomboides*) might harbor the adults.

In Table 3 the sizes of parasitized individuals found in both study areas are given together with the extent of parasitism in terms of percent infected in the respective areas. The mean size of those infected appears to be greater than the mean size for the population in the areas concerned. This may mean that the infected clams have had better chances of becoming parasitized because of greater age as indicated by the size, or that they are larger because parasitic castration has allowed them to put more energy into shell growth in lieu of the energy required for gametogenesis as in the gastropod *Peringia ulvae* (Rothschild, 1935). The difference in extent of parasitism between the two areas is conclusive ($p = 0.05$).

B. Early Embryonic Development

The eggs of *Rangia cuneata* are about 69 μ in diameter. Immature ova, often seen in gonadal fluid samples are likely to have rather long attachment stems such as those described by Tranter (1958b) for *Pinctada albina*, and do not develop normally, even if penetrated by spermatozoa, when artificial fertilization is attempted. But, a female may contain both mature and immature ova so that some of the eggs may develop normally.

Eggs from females collected in October, March, and June were artificially fertilized and development was observed to a veliger stage from eggs of all three collections. Following is a developmental sequence with descriptions based on the observations of several larvae, hatched from eggs at temperatures between 73 and 80° F:

Hours after fertilization

Description

- | | |
|-------|---|
| 0.00 | Egg or zygote, 69 μ |
| 8.50 | First appearance of spheroidal ciliated blastula and movement (rotating or rolling along bottom). |
| 26.25 | First appearance of pelagic trochophore (acorn-shaped with long stiff flagellum protruding from obtuse end, surrounded by ring of cilia at base, no other cilia present). |
| 34.25 | First appearance of veliger, 93 μ (flattened, with thin growth of shell, ciliated velum well developed, flagellum retained, apparent early differentiation of gut; swimming rapid). |

C. Larvae

The most abundant animal organisms found in the plankton collections were copepods and the nauplius and cypris stages of higher crustaceans. Molluscan larvae in the collections were either absent or non-recognizable. What may or may not have been molluscan larvae appeared only in the January collections. Since all of the collections were taken from near the surface most molluscan larvae present may have been excluded from the collections. According to Thorson (1946: 462) "indications are that newly hatched larvae will either rise to the surface after hatching or react indifferently to light" and old larvae are likely to stay near the bottom and many are photonegative.

Had more extensive collections of plankton been made, the larvae of *Rangia* would likely have appeared but their identification by the investigator may not have been reliable. Pelecypod larvae of identical age and species are known to vary greatly in size and shape with some individuals being more than twice the size of others. Published photographs and descriptions of the larvae of some species do not agree with observations of the larvae grown in the laboratory under controlled but apparently healthy conditions (*cf.*, Loosanoff, 1954: 609, 621).

The sizes of pelecypod larvae are apparently highly variable. Descriptions by Thorson (1946: 287) includes a range of 245 to 400 μ for the veliger of one species and comparable variability for other species. Sizes above 500 μ seem to represent the beginning stages, at least, of post-larval life. Loosanoff (1954: 621) described sizes from 100 to 236 μ for larvae reared in the laboratory.

Since no shells of juvenile *Rangia* were found that were less than 375 μ this may be the minimum size at which settling occurs, or this size may be slightly larger than minimum size at metamorphosis for this species. Duration of larval life and larval size of *Rangia* is probably dependent, as in other species, on temperature and food. Duration of the larval period of some pelecypods is known to be two to four weeks (Thorson, 1946: 453) or seven to sixteen days under laboratory conditions (Loosanoff, 1954: 621).

The trochophores and veligers developed in the laboratory from *in vitro* fertilized eggs proved to be fragile organisms and difficult

to transfer with a pipette. The larvae frequently broke up into their constituent cells, particularly when released from a small pipette onto a cover slip. Occasionally while their swimming movements in a hanging drop were being observed they became entangled in the surface film near the edge of the drop and disintegrated, the constituent cells subsequently agglomerating without organization. This fragility seemed more common in the trochophores than in the veligers. Because of the short duration of this stage before the shell develops the risk of disintegration may not be great under natural conditions, although attempts at collecting with a plankton net may have been destructive for such small ($90\ \mu$) veligers. Time spent in the pelagic stage will have to be established by further investigation.

However, speculation to the effect that a pelagic existence for *Rangia* is of short duration seems reasonable in view of what is known of the life history, habitat, and physiology of other members of the Phylum. Of the five classes of mollusks only the two largest (in number of species) have representatives in freshwater. Adaptation to freshwater by the gastropods has apparently come about by evolution through at least two different routes, one involving primary adaptation to the terrestrial habitat with pulmonary specializations and secondary adaptation to freshwater, the other route undoubtedly by way of brackish-water and these are few in comparison to the great numbers of marine and pulmonate species. To the writer's knowledge no freshwater gastropod has a pelagic developmental stage. The advantages during development of a nidamental enclosure or ovoviviparity, common to the fresh-water gastropods and to shallow water coastal marine forms such as *Buccinum*, *Urosalpinx*, *Lacuna* (cf., Abbott, 1954: 225, 212, 131; Lankester, 1906: 139), *Littorina* (cf., Lankester, 1906: 139; Abbot, 1954: 133), and *Acteonia* (*Cenio* of Lankester, 1906: 139; Thiele, 1931: 416), apparently have outweighed any potential for adaptation to freshwater by pelagic larvae. The pelecypods have relatively few families represented in freshwater and their adaptation may have depended greatly, if not entirely, upon a modified sequence of development such as that characteristic of the Unionidae, incubation in the parental gills, formation of the glochidium and parasitism

upon fishes. The latter modification has been held responsible for their extensive world-wide dispersion within the freshwater habitat (Thiele, 1935: 1149). Incubation in the Sphaeriidae until the young are well developed also may represent fortuitous circumvention of exposing the early developmental stages to the medium of freshwater. Pelecypods inhabiting shallow-water coastal areas, subject to vicissitudes in salinity, commonly have what may be regarded as adaptive modifications benefiting survival of the young. The latter include: nidamentous forms such as *Nucula delphinodonta* and *Milneria kelseyi* (cf., Abbott, 1954: 42, 380); incubatory genera such as *Gemma*, *Parasterte*, *Transennella* (cf., Abbott, 1954: 42, 412-19); species with testaceous larvae characteristic of some of the Nuculidae (cf., Lankester, 1906: 248-249; Abbott, 1954: 334-335); and, the incubatory oysters of the genus *Ostrea* (cf., Abbott, 1954: 373-374). Pelecypods inhabiting low salinity brackish waters, without obvious modification of the early developmental stages, seem rare and with little or nothing known of the duration of their pelagic stages nor size attained before settling (or, e.g., affixation as in the case of the Dreissenidae). The problem of buoyancy would seem to be particularly cogent for molluscan larvae in a medium so much less dense than that of a strictly marine environment, and the problem becomes greater with increasing size. One solution might be a shortening of the pelagic stage and an early metamorphosis (perhaps accompanied by adaptive decreased density of the body and cell fluids, i.e. osmotic adjustment, of developmental stages and adults). Maintaining a pelagic existence in low salinity waters is also made more difficult by shell growth resulting in increased relative density of the organism.

The lack of observed sizes of *Rangia* between 93 and $375\ \mu$ either as pelagic larvae or metamorphosed juveniles calls for a tentative explanation to the effect either that the young, if pelagic during this size, are confined to the bottom (and were missed in the plankton samples, all taken from near the surface), or that they were destroyed or rendered unrecognizable in taking and preserving the plankton samples. On the other hand, smaller sizes (than $375\ \mu$) of juvenile shells of *Rangia* may have been present on the bottom at times of collection and

could have been missed in the counting due to breaking up or chemical disintegration during storage of the bottom samples, due to their extreme fragility.

VI. INCLUSION OF AN UNDESCRIBED SPECIES OF RANGIA (RANGIANELLA)
In July, 1960 the existence of a small undescribed species of *Rangia* (*Rangianella*) occurring in Lake Pontchartrain was made

TABLE 5.
Qualitative collections of clams within size range limits of Rangianella sp.

Collection Dates	<i>Rangianella</i> sp. in Proportion to Total Number of Small Clams Collected			
	Range (4-12 mm)		Range (4-10 mm)	
	Number	Percent	Number	Percent
16 July 1960	567	4.2	557	4.3
21 Oct. 1960	121	19.8	65	37.0
24 Jan. 1961	56	8.9	43	11.6
4 April 1961	58	6.9	26	7.7

known to this writer by the late Mr. Percy Viosca Jr. of the Louisiana Wild Life and Fisheries Commission and Dr. J. P. E. Morrison of the U. S. National Museum. The maximum size of this species was said to be 10 mm. The inclusion of this small species as juveniles of *R. cuneata* in the 1957-58 collections by the present unsuspecting investigator seems certain. An adequate estimate of the error involved in estimates of population density of juveniles of *R. cuneata* 10 mm and under cannot be made because complete quantitative collections were not kept beyond 1959.

Additional collections were made in 1960 and 1961, however, in an attempt to clarify the relation between the densities of the two species. What the relation was in 1957 and 1958 can only be inferred with reservation from these later findings.

The morphological differences between equal sized individuals of the two species are distinct. The *Rangianella* have the sub-generic distinction of short non-serrated lateral hinge teeth; the pallial sinus is shallow, wide and only slightly evident. Externally they are more triangular in outline, narrower in transverse diameter; the beaks are lower, less divergent and projecting and more likely to be eroded than in the juveniles of *R. cuneata* of corresponding size (from correspondence between Morrison and the editor of T.S.Z., August, 1960).

Qualitative and quantitative collections made in 1960 and 1961 are represented in

Tables 5-8 and Figure 22. The qualitative collections were made at north shore station Number 1 (fig. 1). Because the meshes of the dredge retained clams 4 mm and over the critical size range in comparing proportions of the two species would be 4-10 mm. In some collections a few specimens of *Rangianella* were as large as 12 mm. As Dr. Morrison has stated the maximum size to be 10 mm, and this seems to be generally true, comparison was made on the basis of two size ranges (4-10 mm and 4-12 mm).

Data showing the proportion of small clams recognizable as *Rangianella* are presented in Table 5. More than half the July collection of 1960 was sent to Dr. Morrison for identification of the *Rangianella*. Three and six tenths percent of the small clams 10 mm and under were identified as *Rangianella*. *Rangianella* in the remainder of the collection (as well as the *Rangianella* in the later collections) were identified by me. In the entire July collection 4.3 percent of the clams 4-10 mm in length were *Rangianella* (Table 5). The distributions of sizes are shown diagrammatically for both species in Figure 22. The proportion of *Rangianella* was at its highest in the October collection while the following January and April collections showed a progressive decline in the proportion. This decline was accompanied by an increase in maximum size of *Rangianella*: 7 mm in July, 8 mm in October, 11 mm in January, and 12 mm in April (fig. 22).

Examination of gonadal fluid from specimens of *Rangianella* revealed mature eggs and spermatozoa in individuals as small as 4.75 mm, hence individuals of this size and larger can be considered potentially sexually mature. Only five specimens of the July collection were examined; each contained mature gametes. Specimens from the other collections were examined; the results are presented in Table 8 in comparison with findings from gonadal fluid examinations of *Rangia cuneata* collected on the same dates. Mature eggs of *Rangianella* were 30 μ in diameter (cf., 69 μ for *Rangia cuneata*). In the October and January collections proportionally more *Rangianella* were found with recognizable gametes than *R. cuneata*. In the April collection, however, no significant difference was indicated. This infers that spawning by *Rangianella* may extend later

into the fall and winter than that of *R. cuneata*.

Apparently this small species of *Rangianella* is short lived; some may live as long as one year perhaps, with few adults and a greater number of juveniles surviving the winter to initiate repopulation of the habitat each spring. Mortality due to predation and physical hazards seem to be especially heavy in the fall. Early sexual maturity conveys the impression that with rapid growth in the spring reproductive age may be attained easily within a few weeks after the initial spawning of the season when temperature is rising. By the end of the summer or in mid-autumn several generations may be added to the population, thus explaining the great contrast in the July and October proportions of *Rangianella* to *Rangia cuneata*. The production of several generations rapidly in one year may be one reason why this small clam, having a ratio of egg size

to parental biomass many times greater than that of *R. cuneata*, can compete with the latter species which has an advantage in obviously producing greater numbers of young per female early in the spring and summer.

The collections made in 1960 and 1961 indicate that the greatest error caused by inclusion of *Rangianella* in the 1957-58 collections was an over-estimation of juveniles (under about 10 mm, size class 15) in the later summer and fall collections. The two quantitative collections (Table 7, fig. 22) were intended to provide additional information, concerning relative density of the two species, in comparison with the qualitative collections and particularly to provide specimens smaller than 4 mm (because these were not taken by the qualitative dredge). The October quantitative collection was based on eight hauls of the small Ekman dredge "randomly" taken in the north shore

TABLE 6.
Qualitative collections of clams within size range limits of *Rangia cuneata*.

Collection Dates	<i>Rangianella</i> sp. and Juveniles of <i>R. cuneata</i> combined (4-24 mm)	Juveniles of <i>R. cuneata</i> (4-24 mm)		Adults of <i>R. cuneata</i> —24 mm	Adults of <i>R. cuneata</i> (25-30 mm incl.)	
		Number	Percent of Total		Number	Percent of Total Adults
16 July 60	575	551	95.8	—	—	—
21 Oct. 60	137	113	82.5	51	3	5.9
24 Jan. 61	92	87	94.6	86	12	14.0
4 April 61	158	154	97.5	84	2	2.4

TABLE 7.
Quantitative estimates of population density (North Shore area, 1960-61).

Collection Dates	Density/sq. ft. 4-24 mm <i>Rangianella</i> sp. and Juveniles of <i>Rangia cuneata</i>	4-24 mm Juveniles of <i>Rangia cuneata</i> Density/sq. ft.	—24 mm Adults of <i>Rangia cuneata</i> Density/sq. ft.
21 Oct. 60	165,500	96,500 (58.3%)	.500
24 Jan. 61	7,637	7,637	1,455

TABLE 8.
Results of gonadal inspection of clams collected in 1960 and 1961.

Collection Dates	Species	Number Examined	Females	Males	Sex Undeterminable	Number Parasitized
16 July 60	<i>Rangia cuneata</i>	0	—	—	—	—
	<i>Rangianella</i> sp.	5	1	4	0	0
21 Oct. 60	<i>Rangia cuneata</i>	33	19 (57.6%)	5 (15.1%)	9 (27.2%)	3 (9.1%)
	<i>Rangianella</i> sp.	23	10 (43.5%)	11 (47.8%)	2 (8.7%)	0
24 Jan. 61	<i>Rangia cuneata</i>	32	0	0	32	1 (3.1%)
	<i>Rangianella</i> sp.	5	1	2	2	0
4 April 61	<i>Rangia cuneata</i>	30	2	5	23	0
	<i>Rangianella</i> sp.	1	0	1	3	0

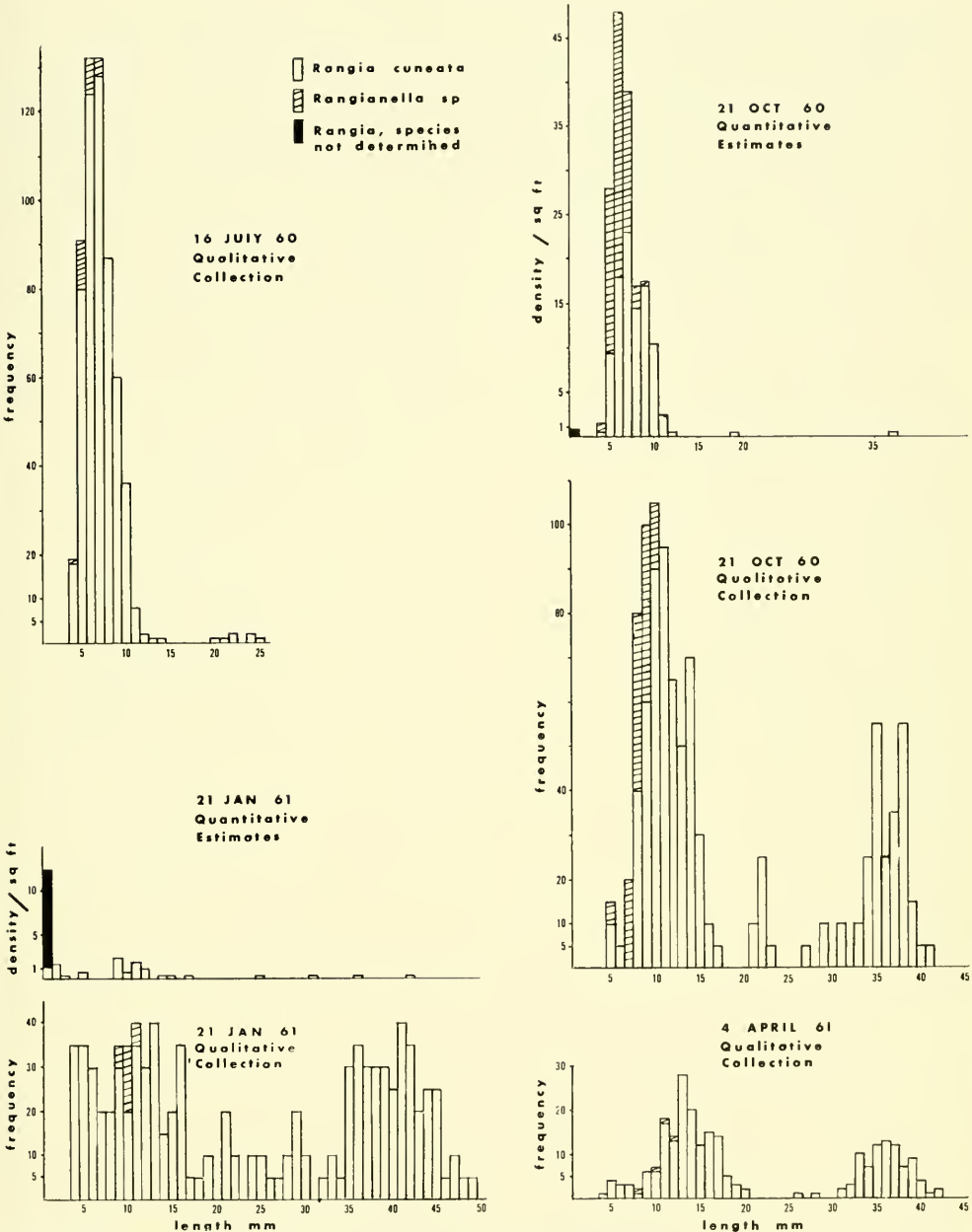


Figure 22. Proportional relations of *Rangia* and *Rangiaella* in collections from the north shore area.

area among the several collecting stations. The January collection was based on twelve hauls in the same area. Small specimens of *Rangia* were found in both the October and the January quantitative collections but *Rangianella* smaller than 2 mm were not dis-

tinguishable with any certainty from *Rangia cuneata* among these small clams. In January quantitative collections all specimens except those under 2 mm were identified as *R. cuneata* and in the qualitative collection taken in January no specimens of *Rangia*-

nella were found that were less than 9 mm. The large numbers of juveniles less than 2 mm in length may have included *Rangia-nella* and *Rangia cuneata* as well.

Agreement between the qualitative collections (Table 6) and the quantitative collections (Table 7) of the two species is not exact as would be expected because of both paucity of quantitative samples and the effect of clumping. However, the essential reduction in *Rangianella* is clear in both sets of data.

VII. DISCUSSION

The data present the impression that Lake Pontchartrain is highly productive as indicated by criteria such as the littoral qualities, shallow water and long shore line (when marshland extensions are included), and high concentration of total phosphorus, variable electrolytes, relatively high amounts of organic matter (both in suspension and in bottom deposits), and the presence of large aquatic plants. However, physical factors such as temperature changes, high winds that disturb bottom deposits and increase turbidity thereby interfering with light and consequently phytoplankton growth, connection with waters of contrasting salinity and tidal fluctuation, periodic influxes of fresh water, and dark coloration of the latter, probably tend to reduce biological productivity.

The immoderate nature of these contrasting conditions can only prohibit the establishment of many species and allow a few to dominate. A direct relation between size and salinity of the water has been found for many species of fish and invertebrates (Gunter, 1950: 48-50) in Gulf coastal regions and the significance of this has been considered to be better adaptation to fresh water or low salinity on the part of younger members of species the adults of which are recognized as marine forms. That possibilities of high potential food supply for growth and development, relative to that of the marine environment (and aside from protection afforded from marine predators and parasites) aid in such an adaptation appear not to have been investigated extensively by anyone. Strictly brackish water species of invertebrates in the Louisiana marshlands are apparently few (Gunter and Shell, 1958: 14, 19, 20) but there seems to be little doubt that *Rangia cuneata* could be assigned to any other categorical rank based on salinity, since

it is not found in freshwater nor commonly in seawater.

The paucity of other molluscan species in the areas studied and the small adult sizes of those present seems to indicate that *Rangia* has few competitors as a filter feeder and does not suffer greatly from intraspecific competition when the tendency for clumping is taken into account.

The utilization of a wide variety of organic matter by pelecypods has been deduced by authors (e.g., Coe, 1947) on the basis of discoveries of weak cellulases in the crystalline style as well as amylase and glycogenase. Experiments with filtered phagocyte-free stomach juice of *Tridacna* and *Pinctada* supposedly have proved the presence of free proteolytic and lipolytic enzymes as well as those acting on carbohydrates (Mansour, 1946: 482). Yonge (1946: 729), however, maintained that lamellibranchs are specialized herbivores and stated that the proteolytic and lipolytic enzymes were probably from ruptured phagocytes and that there is no cytological or histochemical evidence for extracellular enzymes of this nature in lamellibranchs. Whatever the case may be, the variety of organic matter in Lake Pontchartrain seems to offer abundant possibilities of food for *Rangia cuneata*.

Pelecypod larvae reared by Loosanoff (1954: 614-615) and his associates could be classified into two general types based on food requirements. The oyster larvae, both Atlantic and Pacific species, apparently were able to utilize only a few species of marine bacteria, while clam and mussel larvae thrived on almost any organism small enough to be ingested. *Rangia* seems to belong to the latter group unless dependency for food upon some particular organisms in its environment can be demonstrated.

The problems of population sampling in ecological investigations are still to be solved, according to Odum (1953: 156-157), before dependable estimates of density can be obtained. One suggestion made by Odum was the selection of as homogeneous an area as possible for sampling and caution was advised concerning the possibility that the organisms to be sampled could be responding to local factors unknown to the investigator. The writer's estimates of 1.62 or 5.45 percent adult *Rangia* added to the population each year, on the basis of certain size class densities observed, appear small assuming a

theoretically stable population. If 5 percent of the adult population was added annually, 20 years of general stability would be required for one year class to enter and leave the population. Marked specimens of different sizes allowed to remain in the habitat and recovered after one or two years are needed to establish the growth rate of certain sizes of adults and to better infer the life span of *Rangia*. Assuming that the population fluctuates yearly and in some years greater numbers are added or lost or die would seem logical considering environmental differences from one year to another. Extreme fluctuation in bottom populations from one year to another seems to be associated with possession of a pelagic larvae (cf., Moore, 1958: 317). Maintenance of the breeding population undoubtedly depends upon a combination of many factors including number spawned and settled in any one year which in turn depends upon food and temperature, accidental death due to unfavorable physical environment, and predation of both adults and juveniles which probably varies from one year to another. An average life span of eight years, for example, does not preclude the possibility that some adults may live much longer and, in view of the possible large numbers spawned, a large area reasonably could be repopulated in a relatively short time even if the major part of the breeding population were suddenly eliminated.

In this investigation of *Rangia* local factors were expected to influence population density. Since several were possibly involved in the differences found between the two study areas the consideration of some of these factors separately is reasonable.

Among the environmental conditions measured, temperature, although important in a general way to the species, or as a primary factor in controlling both maturation of gametes and spawning, cannot be held responsible for the difference found in *Rangia cuneata* of the two areas. Temperature was not greatly different in the two areas. This is not surprising considering the shallow depth, wind action and response of water temperature to that of the air in both areas.

Salinity was slightly different in the two areas and because of proximity to fresh-water inlets the north shore area may, at times, be greatly different in regard to this

factor. If salinity were a factor responsible for the differences (in sizes of adults, shell thickness, population density of adults, incidence of unreleased mature gametes, and extent of parasitism) in *R. cuneata* of the two areas, a gradient extending away from the mouth of Bayou Bonfouca involving some of these characteristics (e.g., size of adults) would be expected. The only such gradient indicated by the collections was that of increasing population density toward the mouth of the bayou (where decaying vegetation in the bottom deposits was noticeably plentiful). Specimens taken from near the mouth of Bayou Bonfouca, where salinity was most likely to have been lowest and more variable in the north shore area, were not noticeably different in size or incidence of unreleased gametes from specimens taken two miles further west where there were no major inlets. The extent of any differences seen in *Rangia cuneata* of the north shore area, as compared to south shore specimens, that may be attributable to salinity differences is not readily apparent.

Since animals generally obtain phosphorus secondarily from plants, the population density and/or growth of *Rangia* would necessarily first be limited by lack of living or dead plant matter. Since all total phosphorus values were high, this element cannot be considered limiting either to plants or *Rangia* in the lake. According to Hutchinson (1948: 232) rooted aquatic plants are capable of taking up phosphorus from the water and storing this element until released by decomposition after the plant dies; also bottom sediments release part of their phosphorus content back into the water. In view of the great extent of marshland whose waters are directly connected with Lake Pontchartrain, its sediments of high organic content and its "freedom of expanse" (Steinmayer, 1939) the high total phosphorus values might be explained by regarding the entire lake and its adjacent marshland as a storage area for this element, with possible additions from some inorganic sources by erosion and leaching.

On the basis of the differences in phytoplankton pigment concentration there may be reason to suspect that phytoplankton could be more abundant in the north shore area, particularly if species are involved that may be better adapted to fresh-water. More food might explain greater population den-

sity but does not reasonably account for smaller size and the differences in the gonadal condition. On the other hand, the differences in pigment values were not great and may not have been conclusively different. Wind action may effect considerably homogeneity in plankton concentration in the east end of the lake, except perhaps at certain times of the year, or depending upon differences in seasons from one year to another.

The remaining major accountable factor to be considered is organic matter, both in solution and in the bottom deposits. Wind action may be expected to keep the lake water fairly homogeneous part of the time during the year so that organic matter in solution might generally be little different in concentration from one area to the other. However, a considerable difference appeared in the estimates for the two areas in the spring and early summer of 1958. On the basis of empirical observations organic matter in the bottom deposits is unquestionably greater in the north shore area. Steinmayer (1939: 17-19), in describing the sediments from Lake Pontchartrain, stated "In general, high organic content is associated with low texture, and conversely low organic content implies high coarse grain content. . . . The size of the sediment varies from coarse to fine out from the shore in some places and at other places varies in the other direction. A section normal to Little Woods is an example of the former, and a section normal to Bayou Lacombe is an example of the latter." According to this author organic material is chiefly of plant origin and varies in average percentage from 0.528 in bottom sediments classified as "sands" to 6.72 in bottom classified as "clays".

In recent years a few authors have studied a direct correlation between organic matter in bottom deposits and population density of pelecypods of several species. The correlation has apparently been noticed by several investigators through the years but the explanations were that pelecypod larvae settled in regions of high organic matter or mud bottom because those areas were in locations where reductions in current velocity left deposits of silt and mud (organic matter) as well as the settling spat (*cf.* Pratt, 1953: 66-67; Moore, 1958: 317).

Newcombe and Kessler (1936), in a study of growth indices of *Mya arenaria*, compared plots of shell weight on shell

length and dry body weight on shell length in specimens from the Bay of Fundy, the Gulf of Maine, the Gulf of St. Lawrence and Chesapeake Bay. The ratios of shell weight per shell length were higher for clams from the Bay of Fundy and the Gulf of Maine (a twofold difference in the larger specimens from the Bay of Fundy). Both areas were similar in salinity and in having a high "mud" content although they differed in temperature. The Gulf of St. Lawrence and Chesapeake Bay were characterized predominantly by "sand" bottom but salinity was considerably lower in Chesapeake Bay. The ratios of shell length to shell weight were nearly identical for the latter two areas. The bottom deposits of these two areas were described as differing from those of the Bay of Fundy "in that the soil is not nearly as compact." Apparently the differences in salinity had no effect on the ratio of shell length to shell weight. Salinity in the Gulf of St. Lawrence was said to be comparable to that in the Bay of Fundy. The ratio values of dry body weight on shell length were determined for clams from the Bay of Fundy and Chesapeake Bay only. The values of this ratio were considerably lower for clams from the Bay of Fundy.

The study of Newcombe and Kessler suggests that mud or organic content in bottom deposits may have been partly responsible for greater shell weight per unit length and lesser percentage dry body weight (perhaps involving the gonadal condition) although the authors emphasized the correlation of shell weight with temperature, an inverse relation resulting. An opposite trend was found in the case of body weights.

Swan (1952: 530-531) reported a difference in shell weight for comparable lengths in populations of *Mya arenaria* living only a few miles apart. The longer but relatively lighter shells were from clams grown in a bottom type varying from slightly muddy sand to sand and fine gravel mixture. The heavier shorter shells were from clams living in a compact mud-gravel-mixture. In experimentally planted clams in sand and a combination of mud-gravel side by side, the clams grown in sand averaged roughly twice the gain in length of those in the mud-gravel mixture and had shells of appreciably lighter weight and of proportionally smaller width and thickness.

Pratt (1953) studied abundance and

growth of *Mercenaria mercenaria* and *Callocardia morhuana* in relation to bottom sediments. He found that population density was negatively correlated with the particle size of the major bottom constituent; greatest average concentration was in predominantly muddy grounds, less in sandy bottoms and least in rocky areas. *Mercenaria* was most abundant in predominantly fine sediments, but in such sediments the abundance was generally a function of the coarseness of the minor constituents. Both species occurred in greater average numbers in predominantly muddy bottoms than in sandy or rocky areas, and where sand was the major constituent the presence of mud favored both species. In experimental plantings of *Mercenaria* in contiguous frames, one with sand and the other with soil of high organic content, the specimens in sand grew 24 percent faster than those in mud. The difference was "highly significant" and "no observations were made which might have explained the difference in growth". Pratt reasoned that the difference in growth rate must have arisen directly or indirectly from benthonic factors and suggested that a mud bottom, rich in decomposing organic matter might reduce the oxygen content of the water much more than does the sand.

Pratt and Campbell (1956) studied the growth rate of *Mercenaria mercenaria* in Narragansett Bay over a five year period by using retrievable boxes placed on the bottom and containing natural sediments and individually identifiable animals. Growth rates in different parts of the bay showed variations up to nearly three-fold in any given year and were consistently slower in sediments with higher silt-clay content although growth rates were not strictly proportional to this or any other observed property of the sediment. The authors stated that growth was not appreciably influenced by existing differences in the speed of current, dissolved oxygen, or salinity of the bottom water. In discussing the relationship between slower growth rate and mud or silt-clay bottom the authors included the possibility that fine sediments may cause interruptions in feeding and additional expenditure of energy occasioned by the necessity for frequent clearing of the animal's filtering apparatus, also the possibility that mud may produce harmful or inhibitory substances. Experiments by these authors, unfortunately

interrupted before completion, involving the pH of mud and sand bottom deposits in aquaria showed a minutely higher value for mud than for sand.

Growth rate of *Mya arenaria* on sandy bottom was over four times greater than in clams less than one-half mile away on silted bottom (Spear and Glude, 1957).

High densities of juvenile clams in the Chesapeake Bay area reported by Manning and Pfitzenmeyer (1958) were associated with bottom deposits of mud over clay.

Bader (1954) studied organic matter of bottom deposits in relation to the distribution and population density of 16 species of pelecypods in the Gulf of Maine. There appeared to be an overall potential toward an increase in pelecypod density as the median diameter of sedimentary particles decreased and approached a range of 0.15 to 0.05 mm, beyond this toward the extremely fine sizes there was a sharp drop in the densities. Salinity in the area varied only 0.2 ‰ and temperature only 4° F so there was no relation apparent between the two factors and the pelecypod populations. In consideration of the abrupt decline in population density with decrease in particle size beyond a certain point an investigation was made concerning the state of decomposition of the organic matter. This was done by subjecting samples to chemical analysis and comparing the proportion of lignin which is highly refractory to the non-refractory portion by the coefficient or ratio, L/R_n (L = lignin, R_n = total non-refractory or readily decomposable organic matter) which was taken to indicate a stage of decomposition of the organic matter in the bottom deposits. As the numerical value of the ratio increased an increase in the degree of decomposition was indicated. The plotted relationship of the decomposition coefficient of organic matter in the sediment to pelecypod density showed that the population density was lowered sharply when the coefficient exceeded 1.0. The pelecypod density increased initially with increase in organic content of the sediment, but beyond 3 percent organic content "the products of decomposition and/or decline in available oxygen became limiting variables". No pelecypods were found at 4.5 percent organic content. Bader discussed the possibility that microbiological decomposition of organic matter in sediments can produce aldehydes, hydrogen sul-

phide, methane, and many other toxic products and that degree of decomposition is correlated with abundance of bacteria which can cause serious drain in available oxygen supply.

Moore (1958: 95-99) discussed possibilities of specific reactions to particular organic compounds in seawater. Collier, *et. al.* (1953) showed a correlation between the activity of oysters and the abundance of an unidentified carbohydrate in the water. Clam beds (*Mercenaria mercenaria*) which have declined in value through failure of spat to settle may be recolonized when soil is spread over the bottom surface or even if the surface is ploughed (Moore, 1958: 309).

According to Loosanoff (1954) clam larvae may be specialized as to food type according to their age and size, smaller specimens requiring smaller food organisms such as bacteria and other small types of nanoplankton. If larger amounts of bacteria are commonly associated with bottom sediments high in organic content this may be an explanation, in part at least, for greater abundance and possibly survival of older juveniles in this type of bottom, if older juveniles (one year of age) also may be somewhat specialized. This could partly account for the apparent greater survival of young *Rangia* in the north shore area, or lack of survival in the south shore area. On the other hand comparatively high density of tiny juveniles in the south shore area may not be a regular occurrence but occasionally may follow temporary high organic content on the surface of the sand in that area.

Publications concerning comparisons of gonadal conditions of clams from bottom types differing in organic content are unknown to this writer. Since the gametogenic cycle appears to be a dominating physiological response to environmental conditions, it could be as profoundly affected by such conditions as shell growth and population density. At least this appears to be a possibility in *Rangia*. Larger size in *Rangia* grown on more sandy bottom such as that of the south shore area may result from more energy being available for growth since the gametes apparently are not spawned out completely but are resorbed. This does not appear to be the case for *Rangia* of all ages, however, because growth rate is already considerably greater in the south shore clams in the first and second year sizes before

gonadal development is complete. Whether or not the differences in length/weight relationship hold for young clams of the two areas before reaching sexual maturity would be interesting to know. The differences both in growth rate and gonadal condition appear to be separate direct results of the environment. That the difference in shell weight in comparable sizes is more closely related to growth rate differences seems logical if shell thickness is affected at the expense of shell area. If this is true an explanation is necessary to account for the greater relative weight and smaller size of the north shore shells. Since the pelecypod shell is decalcified or eroded on its inner surfaces when the animal is exposed to increases in CO_2 (Dugal and Irving, 1937), greater shell thickness or weight may be the result of physiological compensation as a protective reaction to carbonic acid or any other acid present. A low pH value might well be suspected for the highly organic subsurface bottom deposits of the north shore area, particularly in view of the greater umbonal erosion of the shells in that area. A smaller size and greater shell thickness might have two advantages in such an environment: less surface area exposed and greater reserve of calcium carbonate per size for buffering.

That the gonadal condition of north shore *Rangia* generally appears to be more "spawned out" than that of the south shore clams may indicate that the full extent of gonadal development comparable to the latter is never or rarely attained. This difference may also mean that spawning continues for equally long periods in both areas but the "spawned out" condition is seen more often in the north shore clams, because these animals might have had fewer gametes to shed and recovery may take longer. The latter view of the differences in gonadal condition allows the possibility that gonadal fullness or ripeness may be positively correlated with growth rate and negatively correlated with shell weight, or at least that the differences in shell weight and gonadal condition are caused by the same factor or factors. On the other hand, possibly more extensive spawning may be caused simply by greater chemical stimulation due to the greater density of clams in the north shore area since the spawning of one individual is known to initiate spawning in others in many pelecypods (Loosanoff, 1954). Cer-

tainly the concentration of the substance eliciting spawning would be greater in the north shore area if population density there is as much greater as the quantitative bottom samples indicate.

The bearing that this question, of causal factors in differential spawning in pelecypods, may have upon the commercial problem of "watery" oysters produced each summer in Gulf coastal waters may be important in indicating need for greater attention to control of bottom conditions (e.g., selection of bottom for "seeding", or for seasonal exploitation). This is of particular interest if high growth rate and incomplete spawning in oysters are ecologically linked and determined largely by bottom type. Retention of gametes seems certain to make for better quality in the oyster as a commercial product, while high growth rate has obvious economic advantages.

Evidence presented by investigators (e.g., Orton, 1928; Coe, 1947) supporting the conclusion that growth rate of adults (sexually mature individuals) is modified by the gametogenic cycle seems sufficient to warrant the possibility that the growth rate of the north shore adult *Rangia*, presumably at the height of sexual maturity, is greatly curtailed by increased gametogenic activity and spawning over and above that from the south shore clams. The shape of the curve of size distribution from the north shore clams leads one to suspect that the majority nearly cease growing at a certain size since a greater percentage of the entire population of adults represented falls within a narrow range of size limits about the mean. The comparative gonadal condition can only support the assumption that greater spawning activity slows the growth rate of these clams. The relatively few individuals achieving larger sizes in the area may be less active in spawning and have higher growth rates. The small modal peak on the left in the distribution of south shore sizes (fig. 9) may indicate something of the same phenomena in the south shore clams shortly after achieving sexual maturity, namely slowed growth rate affected by slightly greater spawning activity which does not continue, as indicated by the plateau to the right in the distribution curve. That the shape of the size distribution curves of the larger sizes (larger 10 percent of the adult population) in both areas is similar and that

the length/weight ratio is similar for this portion of the population may indicate that a differential reaction to the respective environments is non-functional after a certain age has been reached. This would affect the north shore clams more than the south shore clams because the former hypothetically would have been restrained from expressing full growth rate potential. The size or age at which this differential reaction ceases to function is represented in the length weight distributions where the differences in the ratio values become non-significant with increasing size. The irregularity in the north shore distribution clearly indicates a greater comparative increase in rate of linear increment, "overshoot" or possibly over-compensation and recovery with further increase in size or age.

That the larger north shore clams were grown in sandy places in that area, and were large because of this, is improbable since no clams were found in that area equaling the largest sizes of the south shore area. The possibility that smaller size of the north shore *Rangia* is due exclusively to crowding seems untenable because, on an empirical basis, adults of maximal size (for the north shore area) were more commonly found where population density was highest in that area; i.e., there were no indications that within the general area a negative correlation existed between maximal size and population density. However, an investigation producing conclusive results concerning this question is certainly in order.

Local environmental conditions other than salinity or temperature are known to affect the growth rate, size, and shape of non-burrowing pelecypods such as *Mytilus* (Lubinsky, 1958) and *Crassostrea* (Butler, 1954). The effects of mud on oysters are fairly well known but are generally believed to result from the direct inhibitory effects of particles in suspension and crowding in such environments. The extent of the differences, seen in pelecypods living on muddy bottoms, directly referable to chemical and physical phenomena would be difficult to separate from other influential factors abounding in these habitats, e.g., inter- and intra-specific competition, predation, and parasitism. The significantly higher percentage of *Rangia* infected with trematodes in the north shore area and the empirically observed greater densities of other mollusks

and annelids and the probability of high density of unobserved microorganisms in this area as well as the possibility of great fluctuation in the physical environment suggest a gradation in an estuarine ecotone as described by Odum (1953: 283).

VIII. SUMMARY AND CONCLUSIONS

Between February 10, 1957 and July 30, 1958 the habitat of *Rangia cuneata* in Lake Pontchartrain varied in temperature between 47 and 90° F. Monthly mean lake temperatures varied between 48.2 and 85.1 in close conformity with monthly mean air temperatures which varied between 48.1 and 84.2° F.

Salinity varied between 0.5 ‰ and 5.7 ‰ during the period but is known to vary between 1.5 and 9.78 ‰ within a year. Salinity is influenced chiefly by run-off into the lake and tide level and partly by wind direction and velocity.

Total phosphorus values representing the two study areas ranged between 0.0035 and 0.0113 µg at/ml, a range considerably higher than that for seawater generally, and indicative of potentially high productivity. Phosphorus cannot be considered a limiting element in the environment. Total phosphorus varied directly with salinity during the period.

Phytoplankton pigment values were highly variable; highest values occurred in the early summer of 1958.

Estimates of oxidizable organic matter in solution were higher in the early summers of both 1957 and 1958, with the highest estimates representing the north shore area in the early summer of 1958. All values were generally higher than average values recorded for certain other coastal waters.

With the exception of organic matter in solution the physical and biological environmental factors that were quantitatively measured or estimated did not differ greatly between the two study areas. With reference to the north shore area the greatest differences in the two environments were: (1) empirically determined higher organic content of the bottom deposits; (2) greater general variability in (a) salinity, (b) organic matter in solution, and possibly (c) phytoplankton concentration.

The north shore area has a greater population density of adult (sexually mature) *Rangia* than the south shore area. The adults of the north shore area are smaller

and less variable in length than those of the south shore area. A majority (90 percent) of the smaller of the north shore adults have heavier shells than adults of comparable size in the south shore area. The shells of the north shore clams are generally darker in color and more extensively eroded than those of the south shore area.

Sex is more frequently distinguishable and the gonad firmer in the south shore clams; also coloration of the gonadal tissues is more distinctive in the south shore clams. Sex was least distinguishable in the clams of both areas in early March and in June coinciding with times of least gonadal color distinction. Gonadal parasitism is more extensive in clams of the north shore.

The growth rate of *Rangia* of all sizes is highest in early summer. Growth rate of all sizes, except approximately the larger 10 percent of adults in each area, is consistently higher in the south shore area.

Evidence was presented suggesting that the observed differences in *Rangia cuneata* of the two areas investigated were attributable chiefly to differences in organic content of bottom deposits and organic matter in solution.

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ABSTRACT

Rangia cuneata, a pelecypod mollusk commonly inhabiting brackish water coastal areas of the northern Gulf of Mexico, is known from Neocene fossiliferous deposits of the Mississippi embayment and is abundantly represented into the Recent epoch. References to

this species in the literature are generally limited to mention in faunistic and geological surveys and species checklists. An investigation was made to determine pertinent physical and biological factors in the habitat of *R. cuneata* concerning population density, sizes of individuals, and the reproductive cycle. Two areas, approximately ten miles apart in Lake Pontchartrain, Louisiana were selected for the investigation carried out from February, 1957 to September, 1958. Temperature, salinity, total phosphorus, phytoplankton pigment concentration, and oxidizable organic matter in solution were measured and/or estimated. Population densities by size classes of adult clams and juveniles greater than 0.375 mm in length were estimated for the two areas from quantitative bottom samples collected throughout the period. Non-quantitative samples of adults were collected routinely for gonadal analysis to elucidate the reproductive cycle and estimate the extent of gonadal parasitism. Growth rates of clams under three years of age were estimated from analyses of the quantitative bottom samples and lines of growth interruption in the shells of adults.

Water temperature varied between 47° and 90° F. Salinity ranged between 0.5 and 5.77 o/oo. Total phosphorus ranged between 0.0035 and 0.0113 μg at/ml, values considerably higher than average for seawater indicating potentially high productivity.

Total phosphorus varied directly with salinity (lowest in the summer of 1958) during the period. Phytoplankton pigment values were highly variable with the highest values representing the early summer of 1958. Estimates of oxidizable organic matter in solution were higher in the early summers of both 1957 and 1958. The environments of the two study areas differed chiefly in textural type and concentration of organic matter in the bottom deposits, and organic matter in solution.

Greater density (estimated 2.88 per sq. ft.) of adults occurred in the area having higher concentrations of organic matter. Also, in the area having higher organic matter mean size of adults and growth rate of clams under three years of age were less, and shell weights of comparable sizes were greater in the smaller 90 percent of adults (size frequency distribution). Survival of juveniles and spawning by the adults were indicated to be greater in the area of higher concentration of organic material. Sex was more frequently distinguishable and the gonadal tissue firmer and more distinctly colored among clams of the area having a sandy bottom with less organic matter.

Density of juvenile clams was not significantly different in the two areas.

Spawning of *Rangia* may occur at any time but is more extensive in late spring and early summer and least during mid-summer.