CHAPTER V

PLANT AND ANIMAL COMMUNITIES

PHYTOPLANKTON OF THE GULF OF MEXICO

By CHARLES C. DAVIS, *Western Reserve University*

As late as 1944 Dr. B. F. Osorio Tafall, writing concerning the interesting distribution of *Biddulphia sinensis* Greville, found it necessary to speak of "La carenzia absoluta de estudios sistemáticos del plancton en años anteriores en las aguas del Caribe y del Golfo de México . . ." It is true still that little has been done on taxonomic studies of Gulf of Mexico phytoplankters, and even fewer ecological studies have been made.

The earliest published observations on the phytoplankton of the Gulf of Mexico appear to be those of Alexander Agassiz (1888) who mentioned, in very general terms, the occurrence of Coccolithophoridae in the central regions of the Gulf. He mentioned more specifically the occurrence of large chains and patches "of dirty yellow color" of the filamentous blue-green alga he identified as "probably" the same as the *Trichodesmium erythraeum* that is so famous in the Red Sea. Dr. Drouet of the Chicago Natural History Museum has identified the most common filamentous blue-green alga from Florida and Texas marine waters as *Skujaella* [*Trichodesmium*] *thiebauti* (Davis, 1950), and probably this is the species referred to above. Agassiz also referred to the occurrence everywhere, but in small patches only, of a species of *Sargassum*.

From the time of Agassiz' (op. cit.) early superficial report until 1937 there were no detailed reports on Gulf of Mexico phytoplankters other than individual species records such as that of Taylor (1928) who listed the occurrence of *Skujaella* [*Trichodesmium*] *thiebauti* and of two common pelagic species of *Sargassum* (*S. natans* and *S. fluitans*) near or at the Tortugas Laboratory. In addition, there were certain other studies made at the Tortugas Laboratory which, however, appear not to have been reported in detail. Thus, Grave and Burkenroad (1928–29) reported diatoms among those plankters that were abundant or that occurred regularly, while Conger (1925–26, 1926–27, 1927–28, 1928–29, 1937–38, 1938–39) briefly summarized his work on diatoms, some of them planktonic. Conger (1926–27) found that the diatom flora of the Dry Tortugas was strongly local in character and that it had its nearest affinities to the West Indian flora. His (Conger 1937–38) investigations showed that there was little change of quantity or kinds of the planktonic diatoms during his 10-week (summer) stay at the laboratory except that there was "some slight increase" in abundance after a period of heavy wind. He emphasized that the region of the Dry Tortugas is a silica-poor region and that Si is a limiting factor there in diatom production. For comparative purposes he (Conger 1927–28) also studied some samples from Tampa Bay and found the water rich with plankton. He stated that the "richness of this area in diatoms may account for the abundance of marine life there."

Riley (1937, 1938) studied phytoplankton production in Gulf waters, largely through the plant pigment method. In his former report (Riley 1937) he considered the influence of the Mississippi River drainage upon the phytoplankton in the northern portion of the Gulf. A number of stations were established from Galveston to Mobile and south to the thousand-fathom line (fig. 44). Analyses were made of salinity, phosphate, copper, plant pigments, and weight of organic matter. It was found that the water of the Mississippi River itself was very rich in phosphates and that this water spread over the surface of the northern Gulf both to the east and to the west but especially to the east in the direction of Mobile (fig. 45). Plant pigments were highest in the waters richest in phosphates (fig. 46). Samples obtained from completely fresh river water contained higher values for plant pigments than elsewhere, but these values were not especially high for fresh waters. This indicated that the high turbidity of the river water was a deterrent to phytoplankton growth, for nutrient conditions were especially favorable for phytoplankton production. Analyses in the open Gulf showed typically low values.

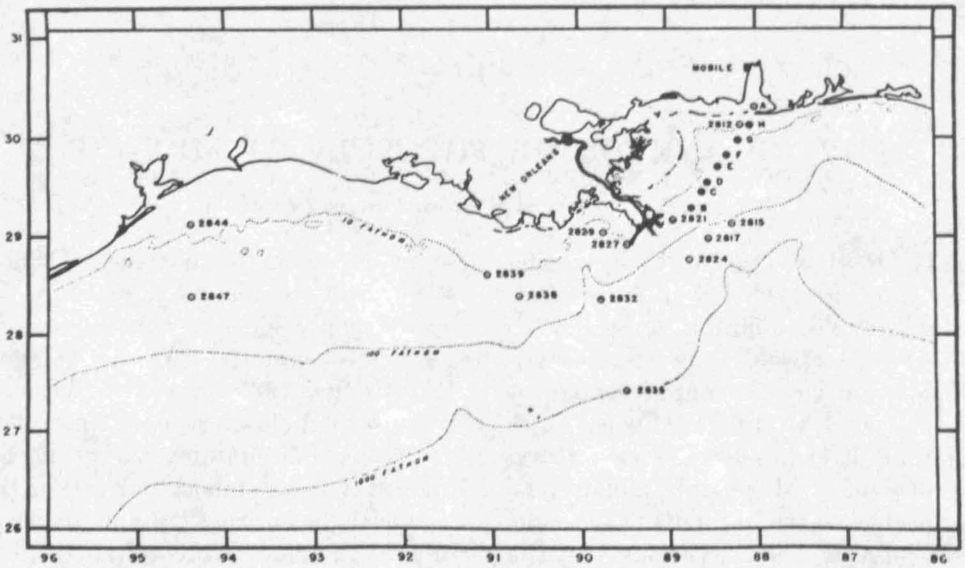

FIGURE 44.—Stations established by Riley (1937) in the northern portion of the Gulf of Mexico.

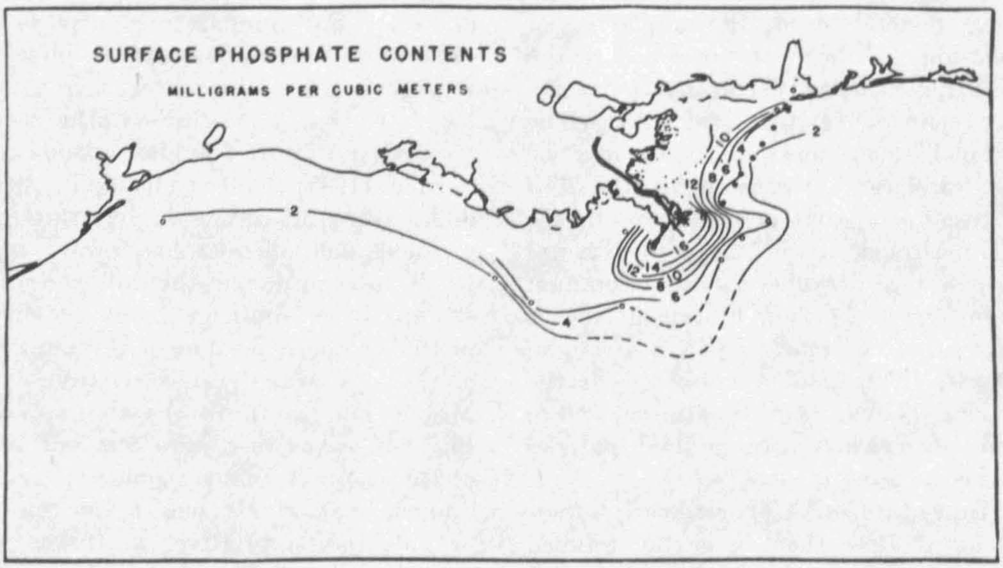

FIGURE 45.—Distribution of phosphates in the waters of the northern portion of the Gulf of Mexico.

The later work by Riley (1938) was done in the Dry Tortugas at the end of the chain of the Florida Keys in the eastern part of the Gulf. Here the water was shallow and with no influence of land drainage of any consequence. Some samples were taken at the edge of the Gulf Stream, but most of them were taken at two regular stations between Loggerhead Key and Garden Key. Plankton samples were obtained by sieving 400 liters of water through a No. 20 silk net, and a second set of samples was obtained by filtering from 3 to 10 liters through a Whatman No. 2 filter paper. Part of each net sample was studied for number of animals present, for plankton weight, and for organic material weight, while the remainder was studied for the quantity of plant pigments. It was found that the plant pigments of the net plankton constituted less than 2 percent of that occurring in the filtered samples. Thus, the mean value for the net plankton was 17 Harvey units per m.^{3}, while the average for the total plankton was 924 Harvey units per m.^{3}, indicating a very high proportion of nannoplankton. The total quantity of plankton

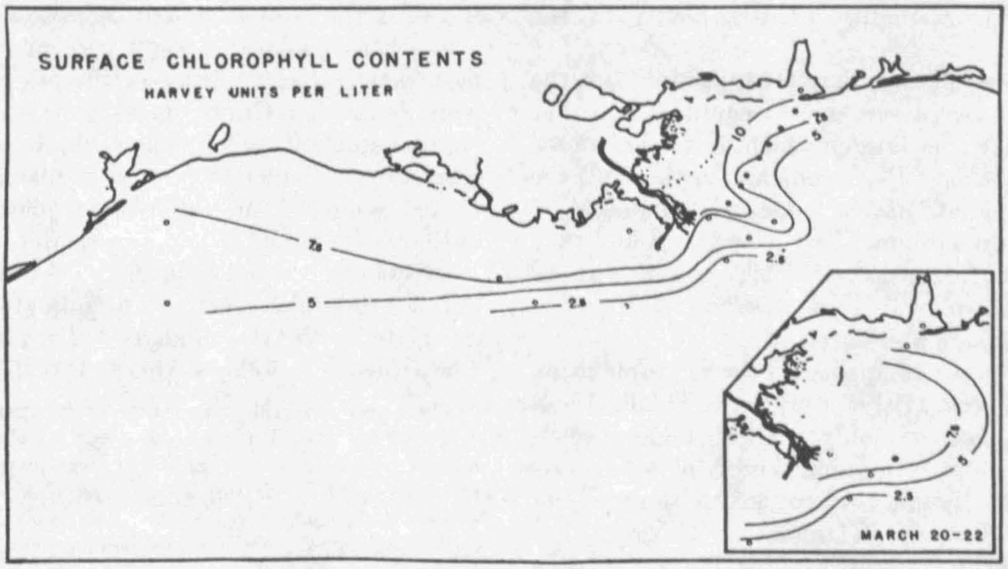

FIGURE 46.—Distribution of plant pigments in the waters of the northern portion of the Gulf of Mexico.

was much less than that to be found in most higher latitudes, the net plankton being approximately 1 percent of the spring bloom conditions in the English Channel. The total chlorophyll at the station that lay closest to Loggerhead Key (it was the less productive of Riley's two main stations) was only about 4 percent of the summer crop determined by the same author in Long Island Sound by similar methods.

Riley (1938) also attempted to study productivity and limiting factors in productivity by means of oxygen determinations in sea water samples that had been confined in white and dark bottles. To some of these, nitrates and phosphates had been added. He found that in the waters of the Tortugas region the nitrates were more important than the phosphates as limiting factors in phytoplankton production.

Parr (1939) made a quantitative study of pelagic species of *Sargassum* in the western North Atlantic, the Caribbean Sea, Cayman Sea, and the Gulf of Mexico. Samples were obtained by dragging a special net at the surface of the water while the *Atlantis* was traveling from station to station on hydrographic cruises. For each sample, the catch was sorted as to species and weighed on board ship. Within the Gulf of Mexico proper, a total of 26 samples was obtained during the spring months (February 16 to April 12) of 1935. To obtain these samples, the net was dragged through the water for 1,230.5 miles. *Sargassum* was not uniformly distributed in the Gulf. The outer portions of the Gulf had a very sparse population of the weed, whereas, the concentration in the inner portion was second only to that of the Sargasso Sea itself. Parr (op. cit.) calculated that within the region of abundance, which he thought to occupy about 90,000 square miles, the crop of *Sargassum* amounted to approximately 1 ton per square mile.

The *Sargassum* crop, at the time of sampling in the Gulf of Mexico, was in very poor physical condition, the plants being small and moribund. The occurrence of the maximum in the inner portion of the Gulf, completely isolated as it was from the primary maximum in the Sargasso Sea by a wide expanse of *Sargassum*-poor water, agrees with the results of hydrographic work published by Parr (1935) and reported on elsewhere in this book, to the effect that there appears to be no great volume of surface water floating from the Gulf of Mexico to Florida Strait during the period of examination. The nearly complete isolation of the Gulf maximum from the maximum of the Sargasso Sea is also emphasized by the fact that the epizoan fauna in the two regions is very different. From his observations, Parr (1939) believes, however, that the Gulf community is not a self-sustaining community in the same way that the Sargasso Sea community is. He based this belief on the comparatively poor quality of the plants in the Gulf.

In his investigation, Parr (1939) found that the taxonomy of *Sargassum* is very confused and that there are many variations which, however, merge into one another. He found that in the Gulf the form he designated as *S. natans* (I) composed 87 percent of the specimens with approximately 6.5 percent each for *S. natans* (VIII) and *S. fluitans* (III). Small quantities of *S. natans* (II) and *S. fluitans* (X) were also observed.

The next paper to appear on the phytoplankton of the Gulf was written by Osorio Tafall (1944) who dealt, however, only with a single species, namely, with the diatom, *Biddulphia sinensis* Greville. He found this species in samples obtained near Tampico, Tamaulipas, Mexico. The species has an interesting distribution in the oceans of the world, but on the Atlantic Coast of the New World it had previously been described only from off the coast of South America. Osorio Tafall discussed the manner in which *B. sinensis* may have reached the waters of the Gulf of Mexico but was unable to come to any definite conclusions because of a lack of previous investigations of the phytoplankton of the Gulf. He thought it might be a relic of a previous flora, or that it might have been carried to the Tampico region from the North Sea on the hulls of boats, or that it might have been carried there by currents from its center of distribution off the east coast of South America. He favored the last-mentioned hypothesis and pointed out that if the hypothesis were correct the species would be widespread along the coasts south of Tampico, a matter easily determined by further investigation.

The disastrous "red tide" of the southwestern coast of Florida in 1946 and 1947 stimulated considerable interest in the phytoplankton of the whole Gulf. It became painfully evident that all investigations of the phytoplankton bloom that was associated with the catastrophe were greatly hampered by the lack of previous knowledge of conditions in the Gulf. Red tide is being discussed elsewhere in the present book (p. 173), and only those aspects that could not be adequately dealt with at that place will be discussed here.

Davis (1948a) mentioned cases in which *Gymnodinium brevis* Davis occurred in the plankton in very large numbers, up to 60 million cells per liter. The same author (1951) pointed out that in two of the samples under discussion this species constituted 99.28 and 98.99 percent of the total organisms present. Most of the other organisms were diatoms. Gunter et al. (1948), in addition to discussing the red tide as such, discussed other associated phenomena in the plankton cycle. Color changes of the water, as deciphered by these authors, are described in the section on the red tide. Gunter et al. (op. cit.) described in some detail other plankters, both animal and plant, associated with these changes. They summarized the sequence as follows (pp. 318–319):

> There was first the appearance of numbers of *Gymnodinium brevis* mixed in with other normal plankton types, mostly diatoms . . . Locally, or over large areas there then appeared a "bloom" of *Gymnodinium*, and in these areas the mortality occurred. This was then followed by the decomposition of many dead organisms, with the consequent release into the water of much nutrient material. Bacteria and/or phytoplankton utilized this nutrient material, and then were themselves utilized, especially by the Copepoda, which consequently increased enormously in the plankton . . . The Copepoda devoured all the suitable diatoms, and left only the species of *Rhizosolenia*, which would be very difficult for the copepods to handle . . .

Davis (1948b) described a plankton tow taken in Long Lake, a brackish-water tributary to Florida Bay. He mentioned naviculoid diatoms and *Ceratium furca* as being present but not abundant, and as being far overshadowed by large numbers of copepods.[1] Davis and Williams (1950) described a more extensive series of samples obtained from 28 lakes, bays, and sounds in the mangrove areas of southern Florida. All samples were obtained from brackish bodies of water including Florida Bay and bodies tributary to Florida Bay or directly tributary to the Gulf of Mexico. They made few identifications of phytoplankters to species. Such forms as *Rhabdonema*, *Skeletonema*, and *Ceratium* were confined to those bodies of water that were most saline, while *Coscinodiscus* was much more abundant in such localities. On the other hand, *Chaetoceros* was not so greatly limited by salt content, though it did not occur in localities with less than 3.06 parts per thousand salinity. They found that desmids were confined to the freshest bay and that green algae and blue-green algae (with the exception of *Skujaella thiebauti*) were found only in those lakes and bays with the lowest salinities. *Gonyaulax*

[1] See article on zooplankton by H. B. Moore, pp. 117–172.

spinifera (?) occurred in vast swarms in many localities on the south coast (parts of Florida Bay and some of its tributaries) and in salinities ranging from 8.60 parts per thousand in Seven Palm Lake to 25.12 parts per thousand in Upper Terrapin Bay.

In addition, Davis (1950) has dealt with phytoplankton and zooplankton from various Florida marine waters. Many of the samples analyzed were taken in the Gulf of Mexico (as far out as 60 miles west of Anclote Light) and its inland tidal waters. A large proportion of the inshore and inland-water plankters was obtained coincident to the study of the red tide, and they were reported in more detail than was possible in Gunter et al. (1948). Davis (op. cit.) stated that: ". . . the plankton appears to be richer on the west coast [than on the east coast of the peninsula], and a number of important species were confined to west coast waters." He listed, among the plants, the following that were confined to the west coast: *Baccilaria* sp., *Cerataulina* sp., *Hemiaulus* sp., *Gymnodinium brevis*, *Striatella* sp., and *Noctiluca scintillans*.

Joseph King (1950) also discussed both phytoplankters and zooplankters collected during 1949 from the west coast of Florida. He established a series of stations extending off shore to the 100-fathom line in the Fort Myers region, and these were visited several times. In addition, samples were obtained one or more times from certain other locations near the coast (fig. 47). He found that the waters in question were poor in plankton. Greatest plankton volumes were obtained at the station established over a 5-fathom depth of water. He observed a sporadic bloom of the blue-green alga, *Trichodesmium* [*Skujaella*] *erythraeum*, which at the height of growth formed yellowish flocculent windrows on the surface. He found diatoms to be numerous, especially in the inshore waters, the most abundant being *Coscinodiscus*, *Skeletonema*, *Navicula*, *Nitzschia*, *Surirella*, *Chaetoceros*, and *Rhizosolenia*. Fresh-water green algae, including desmids, were encountered at two of the stations located in estuaries. Dinoflagellates were abundant in his samples only on three occasions, all of them in inside waters (twice in Sarasota Bay and once in the estuary at Fort Myers). In each of these three cases there was a dense bloom of *Gonyaulax*, forming scattered streaks and patches of a reddish-brown film over the surface of the water. Mullet appeared to be feeding voraciously on this bloom. The species of *Gonyaulax*, or else the conditions in which it was living, may have been very different from those described by Connell and Cross (1950) in Offatts Bayou near Galveston, Texas, for in the latter case the regularly occurring red water of the bloom of *Gonyaulax* was accompanied by fish mortality and foul odors. Gunter (1951), on the other hand, believes that the occurrence of *Gonyaulax* in Offatts Bayou is only incidental to the mortality and that the mortality was directly caused by a seasonal stagnation and putrefaction accompanied by oxygen depletion. This view also had been previously expressed by Gunter (1942).

King (op. cit.) found that in the offshore waters of the open Gulf all forms of phytoplankton were very scarce. Several diatom genera were represented: the most common were *Chaetoceros*, *Rhizosolenia*, and *Thalassiothrix*, but none occurred in any abundance.

From the above it is fairly obvious that the greatest immediate need in the field of phytoplankton research in the Gulf of Mexico is a thoroughgoing quantitative study of the seasonal distribution of the phytoplankton in all portions of the Gulf. True as this statement is for the net plankton, it is far more true for the nannoplankton which has hardly been considered at all except to a limited extent in the studies of *Gymnodinium brevis* and the red tide (Davis 1948a, 1951; King 1949).

Also needed are (1) further production studies such as those attempted on a small scale by Riley (1938), (2) detailed studies of the phytoplankton-zooplankton interrelationships in the Gulf, a field practically untouched by previous investigators, (3) studies of the nutrient needs of the more abundant individual species, and (4) studies of the utilization of the Gulf phytoplankton by benthic and nektonic animals.

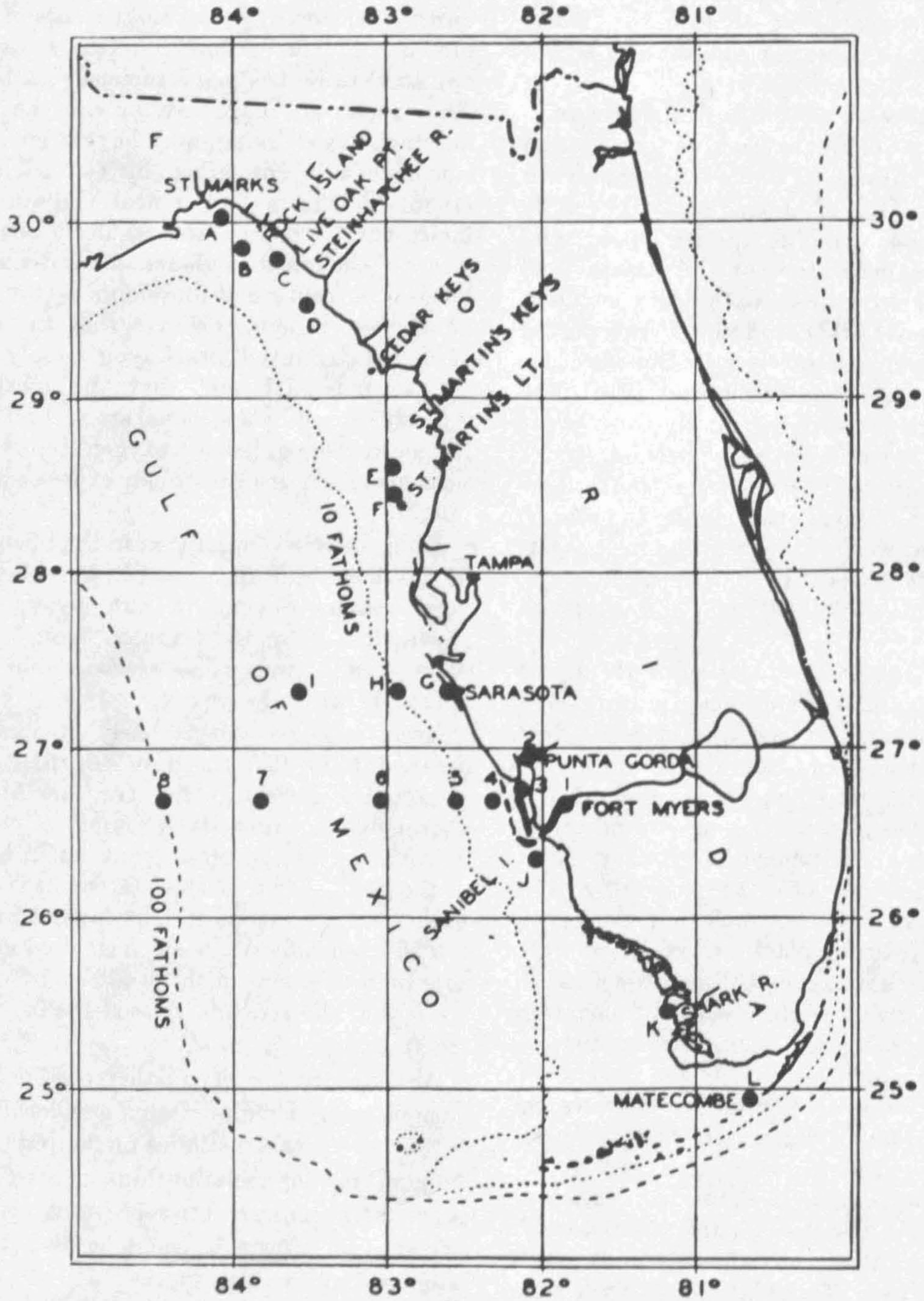

FIGURE 47.—Stations established by Joseph King in Florida west coast waters.

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THE ZOOPLANKTON OF THE GULF OF MEXICO

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No major expeditions have collected zooplankton from the Gulf area. Most of the collections which have been made were from coastal waters, and none of these have been completely described. Some of the collections are still being worked on, while others could no doubt be available for study if required. No complete reference collection of the various species appears to exist.

Those published accounts of the zooplankton which have been traced are listed below. In view of their scattered nature and the fact that brief reference to material from the area may occur in papers on other areas, the list is almost certainly incomplete. A list of known collections and what could be ascertained on their present status is also included.

Burkenroad (1932) reports on nine species of euthecosomatous and one of gymnosomatous pteropods from Louisiana. Davis (1948) lists three species, one of them new, of copepods from a brackish habitat and mentions unidentified ctenophores. In another paper (1950) he gives a full account of 35 open water and 10 inshore hauls from the area. None of the hauls were from deep water. This paper also contains a survey of his own data and references to related work.

King (1950) describes the samples taken over a 10-month period in the St. Marks-Fort Myers region. Except for some copepods, few specific identifications are given.[2]

Osorio Tafall (1942) reviews previous work on Mexican rotifers and gives a detailed study of certain genera including fresh water, brackish, and marine species.

Riley's (1937) work is mainly concerned with phytoplankton–nutrient salt relations but is important in indicating an area of high standing crop off the mouth of the Mississippi. The productivity of the waters emerging from the Gulf of Mexico into the Florida current is discussed in his paper on the plankton of the Tortugas region (Riley 1938).

An ecological survey of the waters adjacent to Miami (Smith et al., 1950), although not within the area, deals with the water of primarily Gulf origin and is therefore relevant for Gulf of Mexico studies.

MATERIAL

Various plankton collections made in the Gulf of Mexico are now located in the following institutions:

Scripps Institution of Oceanography.—F. B. Phleger is working on Foraminifera from 27 series of tow-nettings taken from the surface to 2,000 meters. He states that the remainder of the material has been passed on to Yale University.

Texas Christian University.—W. G. Hewatt has a considerable amount of material which is still being worked on. In 1944–46 frequent samples were taken from Barataria Bay, Louisiana; in 1947 samples were taken from an extended area of Louisiana embayments; in 1948 samples were taken from the east side of the Mississippi Delta, Mobile Bay, and Pensacola Bay.

Texas Game and Fish Commission.—J. L. Baughman has a collection of samples from the Rockport neighborhood.

Fish and Wildlife Service, United States Department of the Interior.—P. A. Butler has a series of weekly samples for a period of about 18 months taken in Santa Rosa Sound. These are partially worked up.

United States National Museum.—Has a partly identified collection of medusae from the Gulf made by M. D. Burkenroad.

Institute of Marine Science.—Has a collection of Gulf copepods which are being worked on. To date, 11 species have been identified.

Zoological Museum of Copenhagen.—P. Heegard of the Zoological Museum of Copenhagen made collections of larval penaeid shrimp from the Gulf.

[1] Contribution No. 102 from the Marine Laboratory, University of Miami.
[2] See article on Copepoda by W. L. Schmitt, pp. 439–442.

Marine Laboratory, University of Miami.—H. B. Moore has a named collection of oceanic copepods, chaetognathes, siphonophores, and tunicates from the Florida current and Sargasso Sea. This collection is being extended to cover other groups and should prove useful in identification of Gulf material.

It is apparent from the paucity of material presented in this section that we know next to nothing of the zooplankton of the Gulf of Mexico. The importance of improving our knowledge is obvious. To mention only a few reasons: plankton forms the major fraction of the food of many fishes; it contributes largely to the food of bottom-living organisms; it contributes to bottom sediments; it can provide a valuable indicator of water movements; it may be used as an indicator of good fishing areas; and it is sometimes the cause of catastrophic mortality in fishes.

Probably the first essential step in any plankton investigation of the area must be the identification of the species present. Here a little is known from inshore waters and almost nothing from deep water. Next, or in parallel with this, a survey is needed to show the geographic distribution and relative abundance of the various species throughout the area. While the more common species call for particular study here, some of the rarer ones may prove particularly suitable for use as "indicator species." From there on, different types of investigations will call for more detailed studies of different aspects of the plankton. Fishery investigations will be concerned with the distribution and life histories of fishes and economically important invertebrates whose larvae are planktonic at some stage. It will also be concerned with the ecology of those species, probably copepods in particular, which are important as fish food. It will be concerned in the water movements in the area and so of indicator species useful in tracing these movements. Finally, it will be concerned in the details of the productivity of the various areas insofar as these bear on fish production. To the hydrographer, also, this latter aspect is of importance. To the geologist concerned with the formation of sediments the shelled forms, such as Foraminifera and pteropods and all aspects of their ecology, are of classic importance, but all organisms which contribute to the sediments are significant, and those which contribute organic matter may be of particular importance to the petroleum geologist.

It is, in fact, clear that almost all aspects of investigation of the waters of the Gulf will be directly or indirectly concerned with plankton. There are, at present, few investigators working on plankton problems of the area. More are needed, and the available supply is so small that they will probably have to be specially trained. It is to be hoped that adequately supported projects may be forthcoming to carry on at least some of the lines of work which have been suggested.

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RED TIDE

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The nature of phytoplankton blooms, i. e., the extensive production of microscopic aquatic flora in localized areas, is today, as in the past, an unsolved problem facing the biologist, oceanographer, and limnologist. Many scientific reports attribute the wholesale death of fishes and other marine organisms to these phenomena. Since the water which is affected is discolored, resulting in an amber or red color, the popular terminology has provided names for an outburst of this sort ranging from "yellow water," "rotten water," and "red plague," to the term now in common use, the "red tide."

Outbreaks of discolored water are common throughout the oceans of the world. These may or may not be associated with fish mortalities. A comprehensive record of fish mortalities due to poisoning of water by dinoflagellates and other phytoplankton is given by Bröngersma–Sanders (1948).

The Gulf of Mexico has probably been the scene of fish mortalities throughout its geological history (Bröngersma–Sanders, 1948). Written records, however, date back only to 1844. Recorded fish mortalities took place in the Gulf of Mexico in the years 1844, 1854, 1878, 1880, 1882, 1883, 1908, 1916, and 1946. In some places, such as Offatts Bayou in Galveston Bay, there is an annual recurring mortality (Connell and Cross, 1950).

The events associated with the 1844 and 1854 incidents are briefly recorded by Ingersoll (1882) in the Proceedings of the U. S. National Museum. The 1878 outburst was located near Cedar Keys and particularly off the Anclotes. Vast quantities of dead sponges were found, and the profitable sponging grounds in that area were badly depleted. In 1880 an area extending from the southern shore of Tampa Bay, from Egmont Key at its mouth, southward to Shark River and Whitewater Bay, was the scene of mass fish mortalities. Hordes of fishes and other aquatic animals were found dead and dying. Fatal patches were also found southward through Bahia Honda passage, beyond Key West, and in some places as far as the Tortugas.

Another account of "poisoned water" in the Gulf (Anonymous, 1883) cited an area off Indian Pass, approximately 1 mile long, between Clearwater and Egmont Light. The streak of "poisoned water" was covered with all varieties of dead fish. The total of individual fish deaths was not estimated.

Similar mortalities broke out in this area in 1883, 1908, and 1916. The 1916 instance was particularly severe and lasted from October 3 until the end of November of that year. Representatives of all fishes local to the area between Boca Grande and Marco were killed, although few other aquatic animals were affected. Taylor (1917) found no extraordinary numbers of dinoflagellates but observed that "the evidences contrary to such an explanation [were] not altogether convincing." His late arrival on the scene of the then current red tide may have accounted for the absence of the organisms.

In most cases, nauseating odors and the tendency for sneezing and respiratory distress were present. Discolored water was reported in all but a few accounts of mortality. It is quite plausible that the noxiousness, and particularly the discoloration of the water, was due to heavy concentrations of toxigenic phytoplanktonic organisms in practically all the cited cases.

Most of our information regarding recent outbreaks of red tide in the Gulf of Mexico stems from investigations made by several independent workers and organizations during the red tide of 1946–1947. (Gunter, 1947; Gunter et al., 1948; Davis, 1948; Ketchum and Keen, 1948; King, 1950; Smith, 1949; Woodcock, 1948.) An excellent review is offered by Galtsoff (1948, 1949).

Between November 1946 and August 1947 approximately half a million fish were annihilated. The Florida west coast fishery industry suffered

[1] Contribution No. 104 from the Marine Laboratory, University of Miami.

heavily from this loss. The area affected by this red tide extended from Sarasota southward to the Dry Tortugas. This was approximately 150 miles long and encompassed an area of several thousand square miles.

Davis (1948) identified the causative agent of the noxious water and the consequent fish deaths as *Gymnodinium brevis*, a new species of dinoflagellate. In some places the concentration of the organism was nearly 15 million cells per liter. Also, a definite sequence of discoloration took place. The initial discolored water was an "opaque" green as distinguished from the normal clear green. Following this came a yellowish green and later a greenish yellow. The water next took on a bright saffron yellow and became viscid and oily to the touch. This yellow water was associated with dying fish and was apparently caused by *G. brevis*; this organism contained individually several yellow-green chloroplasts. Other organisms were dominant at the same time and will be given consideration later. After the yellow water stage the water turned brown slowly and then "red." The "red" was actually an opaque, dull, dark amber with a greenish yellow cast. At the end of the cycle the water reverted to an opaque green and finally to its normal appearance.

Red water similar to that which appeared at the end of the discoloration cycle is believed to be caused by purple sulfur bacteria (Hayes and Austin, 1950). ZoBell (1946, p. 165) states, "Extensive populations of purple sulfur bacteria . . . growing associated with decomposing plankton including algae, jellyfish, etc., imparted a distinctly red coloration to the sea. . . . It is significant that the hydrographic conditions in 'Bloody seas' are generally precisely those which would promote the growth of purple sulfur bacteria; namely, the presence of an abundance of decomposing plankton material which provides for H_2S production and reduced oxygen tension." In the red water stage in the Gulf few *Gymnodinium* were found, since most had previously perished. Animal plankton was found to dominate at that time but did not cause the red water (Gunter et al., 1948).

The poison produced by huge numbers of *G. brevis* is a powerful toxic agent to fish. This was proved experimentally in the laboratory by placing live and healthy fishes into Florida Bay water containing dense masses of *Gymnodinium*; similar fishes were placed into a control tank containing Biscayne Bay water. Both tanks were aerated strongly by means of electric pumps. All the fishes in the test tank died, while those in the control were unaffected (Gunter et al., 1948).

Pharmacological studies have been made of a dinoflagellate-produced poison which infected shellfish off the coast of California (Sommer et al., 1948; Riegel et al., 1949), but as yet its exact chemical structure has not been described.

Connell and Cross (1950) state that a species of the dinoflagellate *Gonyaulax* produces a lethal anaerobic condition in Offatts Bayou (Galveston Bay) by its own high biochemical oxygen demand. This condition was suggested as the cause of the fish deaths that took place therein. In the red tide observations of 1946–1947 the oxygen content in the affected waters, as a rule, was normal.

It is evident that one or several genera of dinoflagellates are the causative agents of death-producing blooms of phytoplankton. These organisms, studied by both botanists and zoologists, exhibit a wide range of morphological and physiological differentiation. Thus, any satisfactory explanation of the red tide must take into account their diverse physiological characteristics.

The conditions necessary for the growth of phytoplankton and for its maintenance include proper temperature, salinity, dissolved oxygen, illumination, hydrogen-ion concentration, the presence of mineral nutrient salts, and possibly of organic substances as well as other less known factors. In the ocean, under normal conditions, the quantity of nutrient salts, particularly the phosphate-phosphorus content, is believed to be the factor limiting the growth of phytoplankton, although the role of organic nutrients cannot be dismissed as unimportant.

The areas in which the outbreaks of red tide occur in the Gulf of Mexico are those where normally a low plankton content is coupled with a low phosphorus content (Smith 1949). In the red tide waters of 1946–47, Ketchum and Keen (1948) discovered that waters containing a dense *G. brevis* population have 2½ to 10 times the maximum total phosphorus concentration, both organic and inorganic, to be found normally in the Gulf (table 1). Dissolved oxygen, salinity, and other conditions deviated little from the average for the areas involved.

TABLE 1.—*Phosphate-phosphorus determinations (Smith 1949)*

Location	Date	μ gram-atoms/L
North side of Big Bird Key, Terra Ceia Bay, R. H. Williams.	June 3, 1946	4.80
Middle of Terra Ceia Bay, R. H. Williams	do	3.60
East side of Green Key, Hillsborough, R. H. Williams.	June 4, 1946	12.00
One mile west of Green Key, Hillsborough Bay, R. H. Williams.	do	8.40
Neighborhood of Sarasota, B. H. Ketchum	July 1947	4.5 to 7 4

The source of this increased phosphorus is the main problem faced by the red tide scientist. Smith (1949), Ketchum and Keen (1948) suspect that the presence of this element can be explained by a simple process of accumulation. If the initial absorption of phosphorus by *G. brevis* takes place over an entire water column (approximately 10 meters in depth), it is possible for the organism to concentrate this element by migrating to, and aggregating at, the surface. Unfortunately, chemical analyses of the water at different depths were not made, hence, no direct evidence is available to test this hypothesis. It appears that even with the removal of all the phosphorus from the water column, the phosphorus content was excessive. George L. Clarke of Harvard (personal communication) theorizes that vertical migration linked with a subsequent horizontal concentration due to convergences of water masses may be the complete solution.

Coincident with the large amount of total phosphorus the total nitrogen in red tide waters bears consideration. Sverdrup et al. (1942), indicate that the ratio of nitrogen to phosphorus in phytoplankton is about 15 atoms to 1. Although no analysis for this element was made, its presence or absence has a bearing on the problem. In order to provide for the large quantity of nitrogen that ordinarily accompanies the metabolic absorption of phosphorus, it is possible that red tide organisms might be able to utilize atmospheric nitrogen as some of the blue-green algae are capable of doing. On the other hand, if this is not so, the organism must be able to survive and develop under far lower nitrogen concentrations than ever before were recorded.

King (1950), while attempting to produce red tide in the laboratory, states that *Gymnodinium simplex*, a dinoflagellate closely related to *G. brevis*, was able to utilize dissolved organic nitrogenous matter. Though the concept of organic utilization by obligate phototrophs is not a new one to the field of protozoology (Lwoff 1947), it does suggest that in red tide dissolved organic material could be a source of nitrogen.

The concentration of nutrients may have been the result of the lateral or vertical migration of some organism or organisms other than *Gymnodinium*. Coincident blooming of other phytoplankton was pointed out by Gunter et al. (1948). These were primarily naviculoids and other diatoms. Utilization of phosphorus accumulated this way and later released could account for the bloom of the death-causing *Gymnodinium*.

The theory of accumulation as it stands does not explain the fact that swarming occurs at infrequent intervals as much as 30 years apart, nor does it explain any possible causative mechanism.

The upwelling of nutrient–rich water has been proposed but is not known to occur normally in the Gulf of Mexico. For red tide in other areas of the world, such as along the coast of Peru, this is an adequate explanation. However, the phosphorus present in the Gulf as reported by Ketchum and Keen was far in excess of that found normally in deep water. Nor are the deeper water layers of the Gulf rich enough in nutrient content to provide the amount found.

The presence of nutrient salts in bottom sediments is a likely source of nitrate and phosphate concentrations. Recently, Robert H. Stewart, a government geologist, in 1950 discovered phosphate deposits covering a 25-mile area off Tampa, Florida. Unfortunately, he has not supplied the authors with any further information. The coincidence of these deposits with the area in which red tide outbreaks have occurred suggests that this may be a partial explanation of phosphorus availability.

The problem presented is to account for periodic releases of nutrient salts from these bottom deposits. Possible explanations include shifts due to cataclysmic upsets in the ocean bottom or simple mechanical shifting of bottom muds due to strong bottom currents. These, of course, are still speculative.

River drainage as a source of mineral deposits in the Gulf has been suggested (Smith 1949). Since Florida is a major source of rock phosphates, this possible origin cannot be discarded. The remoteness of places like Key West and Cape

Sable from river drainage areas where rich phosphate deposits are known to exist renders this explanation doubtful. Ocean drifts seem to be northward in the region involved, though information on shore circulation and surface wind drifts is lacking.

The problem of the red tide as presented leaves a great deal of room for scientific investigation. The physiology, metabolism, and tactic responses of *Gymnodinium brevis* must be understood, and the source and mode of distribution of increased nutrients determined before it is possible to suggest a solution or remedy.

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SKETCH OF THE CHARACTER OF THE MARINE ALGAL VEGETATION OF THE SHORES OF THE GULF OF MEXICO

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GENERAL NATURE OF THE FLORA

The warm tropical current from Central America sweeps between Cuba and Yucatán to find its way into the Atlantic between Florida and Cuba or to swing into the Gulf of Mexico. With this as a striking feature of the environment, it is natural to expect, and to find confirmed in fact, that the marine algal flora is altogether tropical in character. Countercurrents alongshore do not carry northern plants southward. Where species known in the north are found here, they are ubiquitous types which range widely into the American tropics. Though much of the coast with which we are concerned is above the Tropic of Cancer—indeed all of the United States coast—where the land climate is no more than subtropical, this does not alter the character of the marine vegetation. The tropical currents from the southeast determine what species can migrate here, and the limited physical variety of much of the shore determines what species establish themselves. One may justly contrast the conditions at the Bermudas which, though in a much more northern latitude, are affected by the northward effluent stream through the Straits of Florida and have a highly varied shoreline and a similar, though much richer and more diverse, tropical marine vegetation.

Within our range one may generalize by saying that the most varied algal flora exists on the eastern shores, the Florida Keys certainly, and probably Cuba and Yucatán, and that as one progresses toward the north the flora becomes simpler and less spectacular. This is due, in part, to the physical nature of the shore, in part to the somewhat lower water temperatures and lower concentration of nutrient materials, and in part, at least locally, to the dilution of the sea water by the great rivers which empty into the Gulf in this sector.

MARINE BOTANICAL STUDIES OF THE GULF OF MEXICO

Studies of the algae of the shores of the Gulf have been so very few that, alone, they would hardly serve as a useful base of reference for the beginner. Nevertheless, they are adequate to show the main peculiarities of the flora, and by supplementing these lists with the more comprehensive literature of the West Indian islands one may approach the identification of Gulf algae with confidence.

Bounding our area on the east lies the Florida Peninsula and its appendage of keys. The eastern coast of this and the keys have been given quite a little attention. The first significant list of the algae of Florida is that of Bailey (1848) which was amplified and made much more useful a few years later by the illustrated volumes of Harvey (1852–58) and the more complete list of Farlow (1875). The bulk of the information to which this development was due came from the collection of Mrs. F. A. Curtiss (A. H. Curtiss, 1899) and Mrs. G. A. Hall who collected extensively and sent valuable series of plants to Harvey, Farlow, Collins, and experts abroad. Murray (1888–89), in bringing together all the lists of West Indian algae, included many references to those of Florida, and Collins et al., in their exsiccata (1895–1919) and his account of American Chlorophyceae (1909–18), greatly enhanced our knowledge of Florida algae.

However, it is obvious that these collections and records were of east-coast observations; though they include Key West, they give us practically no knowledge of the flora of the Gulf side of the peninsula. The writer (1928) was able from his study of the algae of the Dry Tortugas to greatly amplify the records from the Florida Keys in an area as much related to the Gulf as to the Straits of Florida, but only in a later (1936) paper did he specifically treat of a few west Florida records. Nielsen and Madsen (1949a, b) and Madsen and Nielsen (1950) have recently extended considerably the records of northwest Florida species.

Westward to Texas the coastal flora is essentially unknown. There are no lists of importance and only occasional mention of algae in botanical works (Cox 1901, Taylor 1936). The Texas coast, fortunately, has received a little attention. A long-neglected set of specimens collected by A. C. V. Schott in 1853–65 came to the attention of the writer. It fell to him to publish on them (1941b), as he had previously studied recent collections by E. U. Clover, E. L. Cheatum, B. Smith, and C. T. Reed (Taylor 1941a).

Mexico entered the algal records early, with the Yucatán collection of Liebmann (Agardh 1847); numerous other specimens were in the Schott collection when it came to the attention of the writer (1941b); and he has studied Yucatán material collected by W. C. Steere (Taylor 1935). Other than in these three papers the algae of the Gulf coast of Mexico are unreported.

Finally, our information regarding the Cuban algal flora is slight. More than a century ago Ramon de la Sagra (Montagne 1842) listed 52 species, which was very creditable for the time. Farlow (1871), reporting on the collections of Wright, and Castellanos (1945) have dealt with the flora in general terms, while Howe (1918), writing on specimens of the *Tomas Barrera* Expedition, the writer (1941b), on the collections of Schott, and Sanchez Alfonso (1930) with material from the Havana area, have added numerous others. Curiously, the three detailed lists all deal with the flora of the Gulf sector of the coast.

Respecting work in progress from which future publications may result, it is known that collections have been made in Texas toward an amplification of the known flora of that State. We badly need information on the Mexican sector eastward, Dr. Francis Drouet and Dr. E. Y. Dawson have both collected substantially on the shores of the Gulf, and the latter from Cuba as well, and this material should add much to the exactitude of our knowledge. The Louisiana-northwest-Florida sector, while probably producing only a limited and specialized flora, still needs study. Extension of the Nielsen-Madsen reports would help with respect to northwest Florida. The richer west coast of peninsular Florida (like the northern east coast) needs active field work. Cuba is almost completely unknown and will prove rich in variety, though probably few novelties are to be expected. The writer has in manuscript an account of tropical flora, Gulf and Caribbean, for which many illustrations have been drawn, but early completion of this is not expected because of the hope of filling obvious gaps in our knowledge of the botany of the area. In short, the Gulf coast is the least known, as to marine plants, of the mainland coasts of Mexico and the United States.

COLLATERAL WORKS OF REFERENCE FOR THE GULF ALGAL FLORA

Recognizing the absence of any contemporary text to which we can turn for direct information on Gulf algae, we must consider the floras of neighboring areas that are most reliable and helpful in analyzing the flora of the Gulf itself. It is possible to set up a small working reference shelf, provided the books can be obtained. Therein lies the chief difficulty. Most of them are out of print and seldom appear in the catalogs of secondhand dealers.

One must distinguish between primary sources of the descriptions and figures of marine algae which have been found in the Gulf area and such floristic works as may be useful for the identification of specimens in general collections. For the former, we must refer to such works as those of J. G. Agardh (1872–90, 1892–99), of Harvey (1852–58), and the scattered notes of Howe (1905–09). Monographic works dealing with tropical genera will, in many cases, be needed, as those of Barton (1901) on *Halimeda* and the Gepps (1911) on other Codiaceae in the *Siboga* reports, and of A. Weber-van Bosse (1898) on *Caulerpa* from Buitenzorg. For early illustrations, not only these but the famous and regrettably rare *Tabulae Phycologicae* of Kützing (1845–71) will frequently be consulted. For the second purpose, we turn to local floras.

The most complete West Indian reference work is that of Børgesen (1913–20) on the former Danish West Indies. Its critical notes and numerous illustrations are very valuable, but keys and formal descriptions are not provided. Howe's algal flora of the Bahamas (1920) gives keys to some difficult genera, but generally not species descriptions or illustrations. Collins and Hervey (1917), in their Algae of Bermuda give, in addition, critical notes and much useful information on algal habitats, and Collins (1909–18) treats the Chlorophyceae adequately, with keys and brief descriptions. Hoyt (1920), writing of the Beaufort, N. C., algae, deals with some species also found in the Gulf and gives keys, descriptions, and illustrations. The present writer published, in

1928, an account of the algae of Florida, now urgently in need of revision but giving keys, descriptions, and many illustrations. Some of the needed changes were incorporated in his notes on Caribbean Marine Algae . . . (1942), where keys and additional illustrations are given. For Myxophyceae, Tilden's volume (1910) is still the only general American source, but this will need to be supplemented and corrected by that of Geitler (1932) and the current publications of Drouet. Outside of these few works, the investigator must rely on the great *Sylloge Algarum* of De Toni (1889–1924) and on a few score of brief papers scattered through botanical journals.

The chief reference collections containing algae of the species found in the Gulf are easily designated. Most generally available are those distributed in Collins, Holden, and Setchell's Phycotheca Boreali-Americana (1895–1919), of which numerous sets are held in institutions about the country, but in the use of these exsiccatae the usual attention must be given to corrections in nomenclature and identification. Many Florida algae appear in this series. The main Curtiss collection is in the U. S. National Herbarium. Because of his early dominance of phycological studies in America, Farlow accumulated valuable early reference materials at Harvard University. Howe did far more field work himself and acquired Collins' personal herbarium for the New York Botanical Garden so that the Gulf collections there are the most extensive in the country. The writer in his personal collections and the herbarium of the University of Michigan has a most valuable resource. While no other collections in this country contain many specimens from this area, one may list the very important herbaria at the University of California and the Chicago Natural History Museum, both of which have useful auxiliary collections.

CHIEF TYPES OF ALGAL VEGETATION

Since for great stretches of the Gulf coast no lists have been published, it is impossible to tabulate known floras. By describing here the more striking floristic elements of a few selected types of locality, it is hoped that future students may, through these characterizations, be guided in what to expect under similar conditions.

SHIFTING SANDY BEACHES AND ESTUARINE MUD FLATS

The great extent of the Gulf coast line which consists of unconsolidated sand and mud militates against the production of a complicated flora. Where every wave turns over the sand or stirs up a cloud of mud, algae do not colonize. Few microscopic forms are able to live mixed with the unstable sediments; few large species long survive adrift above them, and these accidental elements constitute no real flora. Such a region, regardless of the chemical nature of the sediments, is consistently an algal desert. The great areas of recently transported silt in estuarine regions and deltas are equally barren.

STABLE SAND AND MUD; POOLS, SMALL LAGOONS, AND COVES

When such sediments become stabilized, a different situation is presented. If the tidal rise and fall is considerable, broad zones of beach which were immersed at high water of spring tides are exposed at times of neap tide and such zones may show an algal flora. If they receive enough moisture from salt-marsh pools by percolation, or from rain or by other means, they may support a considerable and recognizable vegetation of such Myxophyceae as *Lyngbya aestuarii* and *Microcoleus chthonoplastes*, or on the surface mats of *Rhizoclonium riparium*. Such a vegetation may even be able to survive a little gentle wave action undisturbed. Where silt transported by stream movement in flood is left stable by recession, it, likewise, may develop similar colonies in brackish estuaries.

When waves throw up barrier beaches of calcareous sand and coral rubble, pools, or lagoons are cut off in which surf action is absent and tidal action greatly reduced or eliminated. Rains serve to dilute the water, especially at the surface. On sunny days, the temperature rises greatly. Under such circumstances, few algae except Myxophyceae can survive, but at times these form a heavy sludge over the bottom, where *Chroococcus turgidus*, *Gomphosphaeria aponina*, Oscillatorias, and Lyngbyas dominate. If there is a direct communication with the sea and some circulation, if the area is relatively large, and especially if there is a moderate depth of 3 to 12

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dm. of water at low tide, then colonization by marine vascular plants, such as *Ruppia maritima* L., *Halodule wrightii* Asch., or perhaps *Zannichellia palustris* L., may occur, and the flora resembles that of the next section. With or without this colonization, the growing conditions are so greatly improved that many larger algae grow in abundance. The Myxophyceae form larger masses of such coarser species as *L. majuscula*, and on the vascular plants occur epiphytic growths of other species, Myxophycean, diatomaceous, or of larger types, inconspicuous in form and color but very general.

PROTECTED COVES AND POOLS WITH A MARINE CHANNEL

The numerous deeper pools near the edges of salt marshes partake of the character of these ponds barricaded from the sea, though they may show a distinctive growth of algae including *Bostrychia rivularis*. Others receive too much fresh water to have a well-developed marine flora, while on the contrary yet others are more like protected coves.

The floras of these smaller coves vary greatly one from another, but no one in itself shows much range. One will have the bottom studded with *Penicillus capitatus* (fig. 48–d), another will be dominated by *Thalassia testudinum* K. & S., or *Halodule*, bearing epiphytes, another by *Amphiroa fragilissima*, by *Spyridia filamentosa*, or by *Gracilaria confervoides* (fig. 50–e). This last is sometimes exceedingly abundant and is harvested commercially for its gel content. It is about the only economically important alga recognized in the area. Others have advantageous features of their own, however, and await the discovery of harvestable quantities.

PROTECTED BAYS AND LAGOONS

The transition from these small coves to large ones, to protected bays and lagoons, is easy and is accompanied by an increase in the variety of the marine flora. In shallow water the same species are found and many others in addition. Characteristic is the excellence of vegetative development of all the plants whenever there is a good circulation of sea water. On the other hand, even if the lagoon is large, a muddy bottom and a reduced communication with the sea generally will be reflected in a poor flora of Myxophyceae and a few Chlorophyceae. Under good conditions, *Sargassum* is tall and freely branched, *Ectocarpus* and *Padina vickersiae* flourish, as do *Acetabularia crenulata* (fig. 48–a), *Batophora oerstedi*, *Cymopolia barbata*, *Codium decorticatum*, *Udotea flabellum* (fig. 49–e), and many other Codiaceae and Caulerpas, especially *C. racemosa* (fig. 49–c) and *C. sertularioides*, which form magnificent colonies. A great many of the species common on the more open rocky coasts and reefs may appear here, more luxuriant and loosely branched than elsewhere. The list is too long to give here, but it points sharply to a greater variety in the Florida Keys sector and a poorer one on the northern shores of the Gulf.

The larger area of these bodies of water involves the occurrence of natural or artificial rock or concrete walls, jetties, piers, or other solid structures which afford a new type of habitat, and here an intertidal zoned band will often be recognized in which *Enteromorpha*, *Caloglossa*, *Catenella*, and especially *Bostrychia tenella* will generally be conspicuous features.

MANGROVE THICKETS

These lagoons, inlets, and coastal islands may, in some localities, especially in southern Florida, be bordered or even nearly filled by mangroves, primarily *Rhizophora mangle*, with *Avicennia nitida* higher along the shore. The prop roots of *Rhizophora* and the pneumatophores of *Avicennia* offer excellent support for algae, and a strongly developed belt of *Bostrychia tenella*, or even more conspicuously *B. montagnei* (fig. 50–c) may encircle each root, with *Polysiphonia macrocarpa* a little lower down, while on emerging ground which receives a little sunlight between the mangroves there may be a green mat of *Vaucheria* or a mossy growth of brighter *Cladophoropsis membranacea*. Around the border of such a thicket where light is ample, a few species of other larger algae may grow luxuriantly attached to the submerged parts of the roots, as *Padina vickersiae*, but the flora of mangrove thickets is not marked by great variety.

TIDAL STREAMS

Tidal streams commonly discharge through these protected coves and thickets. Their flora is largely determined by the light received and the admixture of fresh water. Near the mouth, marine Myxophyceae, *Vaucheria*, *Enteromorpha*,

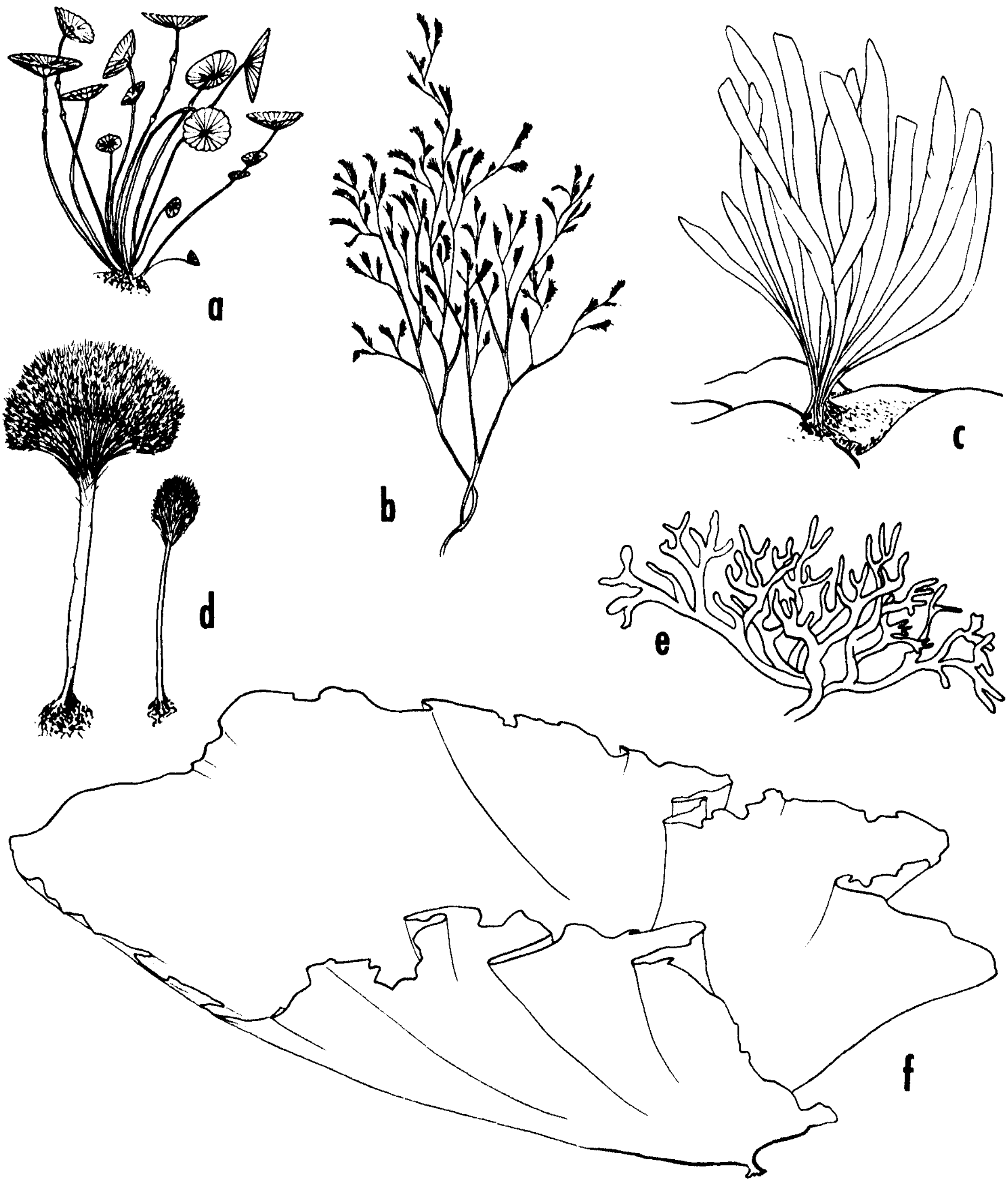

FIGURE 48.—*a*, *Acetabularia crenulata*, several plants, × 0.4; *b*, *Cladophora fascicularis*, a small portion of a branch, × 0.8; *c*, *Enteromorpha flexuosa*, several plants, × 0.7; *d*, *Penicillus capitatus*, a young and a mature plant, × 0.4; *e*, *Codium dichotomum*, a small portion of a clump, × 0.2; *f*, *Ulva lactuca* var. *rigida*, a single plant, × 0.4. Drawings by C. V. Cangemi.

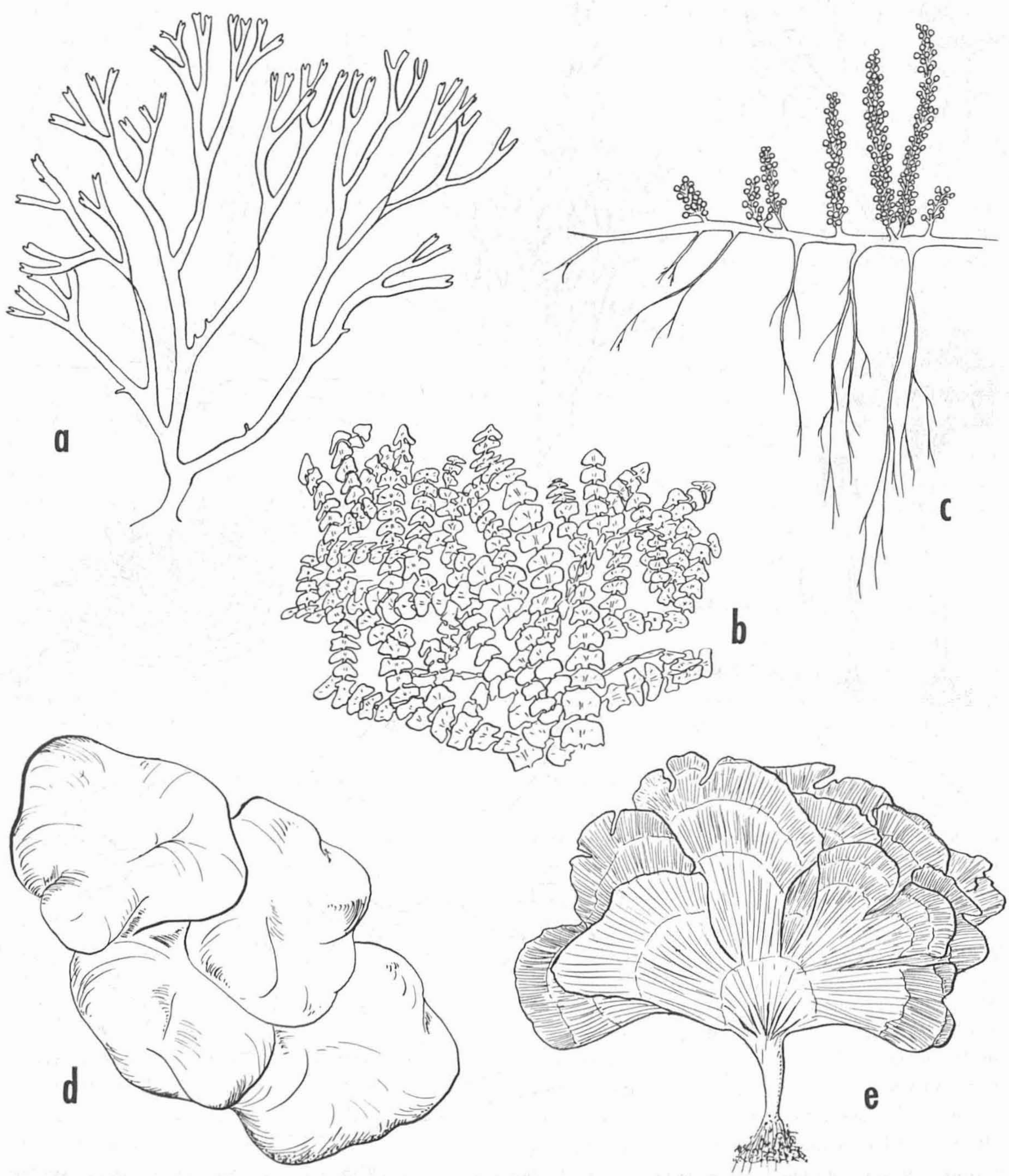

FIGURE 49.—*a*, *Dictyota cervicornis*, a small portion of a plant, × 0.7; *b*, *Halimeda opuntia*, a small portion of a clump, × 0.4; *c*, *Caulerpa racemosa*, portion of a stolon with erect green branches, × 1.3; *d*, *Colpomenia sinuosa*, a single plant, × 0.4; *e*, *Udotea flabellum*, a single plant, × 0.7. Drawings by C. V. Cangemi.

Caloglossa, and *Bostrychia* will generally be important, while much farther up, fresh-water genera including, particularly, the peculiar *Compsopogon*, will dominate. It is notable, however, how far upstream the adaptable genera mentioned may, in the absence of pollution, be found.

SANDY SHALLOWS AND "REEFS" OF SHELL AND CORAL RUBBLE

Shallow water among the keys combines the advantages of shelter from storms with ample water circulation, sunshine, and freedom from fresh water and mud. Sometimes similar sandy flats extend out far from the shore but are less protected toward the sea than those among the keys. Often the white coral sand is directly exposed and is only partly covered by the vegetation which is chiefly limited by the number of suitable objects on which algae may attach. Over the soft sand bottom the marine vascular plants may form vast "sea grass" meadows with *Halodule wrightii*, *Cymodocea manatorum* Asch. (manatee grass), and especially *Thalassia testudinum* (turtle grass) in shallow water, and with *Halophila baillonis* Asch., at a depth of several meters, generally 5 or more, exceeded by *H. engelmanni* Asch., which may go as deep as 75 meters, probably much more. While little grows on the *Halophila*, there may be a great variety of epiphytes on the *Thalassia* and other shoal-water types. Most ubiquitous of these are the thin encrusting species of *Fosliella*. Also common are species of *Spyridia*, *Hypnea*, small Laurencias and Chondrias, slippery brown *Aegira* and *Ectocarpus*, and many others. Nowhere is one feature of the subtropical and tropical marine flora, the extreme etiolation of the Rhodophyceae, more evident than on these sandy shoals. The Chlorophyceae are just as green here as elsewhere, the Phaeophyceae as brown, but the Rhodophyceae do not have much need for and so do not develop their phycoerythrin pigment, and their small proportion of green chlorophyll is not conspicuous, so their aspect is light and dull purplish to straw-colored.

Apart from epiphytes, many other algae grow in these "grass" beds. Mats of *Amphiroa fragilissima* are common as are scattered plants of *Penicillus capitatus*, *P. pyriformis* and *P. dumetosus*, *Avrainvillea nigricans*, *Udotea flabellum*, *Halimeda tridens*, and *H. monile*. Others, like the Caulerpas, rather tend to replace the "grass" beds as they have similar spreading rhizomes. While *C. sertularioides* and *C. cupressoides* may be commonest, other species also occur, such as *C. paspaloides* and particularly *C. prolifera*.

In more open water where "grass" beds are lacking, great beds of *Halimeda opuntia* (fig. 49–b) occur, a plant of different habit from its congeners, and, if large shells and coral fragments abound, many species typical of coralline reefs also find footing, particularly *Laurencia obtusa* (fig. 50–b), *Padina sanctae-crucis*, *Dictyota divaricata*, *Caulerpa racemosa*, *Batophora oerstedi*, and *Acetabularia crenulata*. The presence of a slight ridge or "reef" of shell fragments may, for instance, determine the presence of a striking local colony of *Acetabularia* or of its relative, *Neomeris annulata*.

ROCKY SHORES AND INSHORE REEFS

The area under consideration is exceptionally poor in tracts of rocky shoreline. The only portion of shoreline with such a substratum of whose algae we have any detailed account is that of south Florida, particularly the Florida Keys, where a certain amount of calcareous rock may lie at the waters' edge, and where old coral formations in shallow water afford even better attachments for algae. Equally promising stretches of shoreline occur in Cuba and Mexico, but of their productivity we have no detailed account. Marine algae do not flourish in tracts preempted by vigorous, actively growing corals and gorgonians. It is on these older reefs, on submerged structures built of stone, and in lesser degree on concrete, wood, and iron structures, that the vegetation gives us our chief view of algae suited to these stable anchorages. Through much of Florida and all the north and northwestern sectors only these artificial structures support what in a completely natural state would only occur as lithophilic colonies, and being relatively recent, small, and scattered, the variety of plants they support is far less than one would expect on the rocky shores of West Indian islands.

In dealing with so great a coastline, much quite unknown as to vegetation, and considering all seasons of the year, it is impossible to be specific as to algal communities, though some suggestions can be made. If circumstances permit, the upper zone of algal growth will be one of marine Myxophyceae in a black or olive crust, with below it very usually a clear zone of *Bostrychia tenella* or

FIGURE 50.—*a*, *Sargassum natans*, a small portion of a plant, × 0.4; *b*, *Laurencia obtusa*, a small portion of a plant, × 1.0; *c*, *Bostrychia montagnei*, a small portion of a plant, × 1.0; *d*, *Digenia simplex*, a portion of a large plant, × 0.8; *e*, *Gracilaria confervoides*, a small portion of a plant, × 0.7. Drawings by C. V. Cangemi.

B. binderi, more or less intermixed with *Enteromorpha* (fig. 48–c) and *Rhizoclonium*. Green turfs of *Cladophoropsis membranacea* and darker ones of *Cladophora fuliginosa* may be close by, with mats of *Wurdemannia miniata* and closer-attached *Gelidium pusillum*, but *Catenella* and *Caloglossa* are less important than in localities discussed earlier. Seasonal growths of *Colpomenia sinuosa* (fig. 49–d), *Hydroclathrus clathratus* and perhaps *Codium intertextum* are to be expected near the low-tide line, with *Laurencia papillosa* and *Sphacelaria*, stunted *Sargassum*, *Amphiroa*, and *Centroceras*.

At levels primarily submerged or laid bare only by the backwash of the waves, we have a richer and sometimes spectacular vegetation. Near the surface a new group of Chlorophyceae appear: *Caulerpa racemosa* and *C. verticillata*, *C. sertularioides*, *C. cupressoides*, *Dictyosphaeria cavernosa*, and *Dasycladus vermicularis* on the rock faces, *Anadyomene stellata* and *Valonia macrophysa* more in crevices or other protected spots. We also have such Phaeophyceae as *Ectocarpus duchassaignianus*, *Pocockiella variegata*, and Dictyotas. Somewhat deeper, we may have the brilliant peacock colors of great masses of *Zonaria zonalis*, and at this level, abundant Padinas, Sargassums, *Cladophora fascicularis* (fig. 48–b), and more Dictyotas, among which *D. cervicornis* (fig. 49–a), may be the most common, but *D. ciliolata* and *D. dentata* will reach the greatest size and are often irridescent. Here, also, come a few species of conspicuous Rhodophyceae, Galaxauras, and Liagoras, with lower down *Heterosiphonia wurdemanni*, *Centroceras*, and *Spyridia* in masses, and some showy Halymenias. The number of other kinds at this and nearby levels makes continued detailed listing unprofitable.

PELAGIC SEAWEEDS

The fact that the term "gulfweed" for our drifting algae has arisen at all is suggestive of the conspicuousness of these plants in our area. Although the term has long been known, one has come to think of these plants more in relation to an ill-defined "Sargasso-Sea" in the North Atlantic. However, while the abundance of the "weed" in the Sargasso Sea is perhaps greater than in the Gulf of Mexico, the amount is nevertheless considerable in the northwestern parts even if less conspicuous in the literature. The best general account of the distribution and ecology of the gulfweeds is that of Parr (1939), and it particularly deals with *Sargassum* as found in the Gulf. The taxonomic segregation of the Gulf and the Caribbean benthonic and pelagic species is far less difficult than that of the Pacific species but still is exceedingly confusing to an inexperienced student of them. The books mentioned for the general flora will clear up most points; the summaries of information regarding the species of the world in DeToni (1895) and Grunow (1915–16) will be necessary to the advanced student.

First of all, it is to be recognized that the benthonic sargassums are particularly suited to transport by currents once they come adrift, and any such species may travel among the driftweeds for a long distance from their origin. Thus, *Sargassum hystrix* v. *buxifolium* has been collected on the coast of Nantucket among gulfweeds as a very exceptional occurrence (1938, for example). However, the new growth on these plants is not so altered from the parts developed during the attached growth period as to resemble the pelagic species. Of these, there are two: The classic *Sargassum natans* (L.) J. Meyen (fig. 50–a) and *S. fluitans* Børg., each somewhat variable. However, the former has much narrower leaves with more terete teeth than the latter, and the vesicles are characteristically long-apiculate. While the leaves of *S. natans* never have cryptostomata, rudiments of them may occasionally be seen in the latter species. Neither has been convincingly reported in fruit, contrary to the common state of mature benthonic plants. Parr (1939) reports that significant amounts of drifting gulfweed are not found south of a line extending from approximately the latitude of 16°–17° near the Lesser Antilles to 14° near the Central American coast. We may accept it that there is very rapid growth and fragmentation of the floating plants north of this line, and there is no evidence that the pelagic flora needs to be initiated by a constantly replenished nucleus of benthonic origin. Both species of gulfweed, passing out through the Straits of Florida, continue in excellent health into the drift area called the "Sargasso Sea" and multiply vegetatively there. The wind and the water currents also bring the sargassums into the Gulf of Mexico. While there seems to be some growth of the plants within the Gulf, especially during the summer, it is clear that it is not very considerable, and the flora comes to consist of more than 90 percent *S. natans* which gradually passes into an unhealthy state, particularly in the latter part of the year and in the more northwesterly area.

LOCAL FEATURES OF THE GULF COAST MARINE ALGAL FLORA [1]

Since the algal vegetation of most of the shoreline of the Gulf of Mexico has not been studied, a review of what has been done is in order and an application of the information derived from this to the rest of the coast. Such an analysis will show what work needs to be done and what areas may be expected to yield the greatest rewards.

The Florida Keys, as far as we yet know, support much the richest algal flora in our area. About 400 species of marine algae are known from the State, and most of them have been found among the Keys. The fact that intensive study has been limited to the Dry Tortugas was a matter of chance; probably the other more exposed Keys are equally rich. Fortunately, a very helpful study of the littoral ecology of these islands has recently been presented by the Stephensons (1950) which relates the plant and animal components. The presence of offshore corals, in itself, is of no present advantage because algae do not grow to any extent on living corals, but the older portions of reefs, dead masses of coral rock and debris form an excellent foundation for algal colonies. Many spectacular ones appear: great beds of *Halimeda opuntia* and Caulerpas in shallow water, of living brown and white *Padina* fans, golden clumps of Dictyotas and iridescent *Zonaria zonalis* a little deeper. In the next lower depths and in shaded areas, a great variety of "red" algae appear. Beach rock outcrops, the foundation and moat of Fort Jefferson, wide stretches of soft muddy sand, ridges of shell and small coral fragments, all have special advantages and are favored by particular species, as discussed elsewhere. The proximity of the Gulf Stream to the east gives good circulation of the water, and at times an abundance of the species of pelagic sargassums is evident.

When one crosses Florida Bay to Cape Sable one leaves behind the area of most favorable growth conditions, and the floras around the Gulf are thenceforth restricted ones. The west coast of Florida, without the advantage of a strong offshore current and considerably encroached upon by the red mangrove, *Rhizophora mangle*, offers a less favorable habitat which continues unimproved for many miles to the north since only at isolated spots such as Cape Sable, Pavilion Key, and Marco are large sandy beaches reported and no extensive suitable rocky shore. In the Florida Bay area Davis (1940) reports turtle grass with *Acetabularia*, *Caulerpa*, and *Gracilaria* growing among the pioneer *Rhizophora* colonies. The mangrove roots may well support the typical *Bostrychia* vegetation, some suitable mud-favoring species like *Penicillus* may occur in the shallow open areas, but the vegetation is not likely to be a rich or varied one for neither these inshore features nor the sand of the offshore islands favor any variety of algae. The Ten Thousand Islands area is especially characterized by the great development of red mangroves over much shell and marl beneath with beaches showing on the largest islands (Davis 1940). A collection made at Naples shows a poor flora of *Enteromorpha*, *Ectocarpus*, *Spyridia*, and the like. The configuration outside Fort Myers and Punta Gorda promises better conditions, but we have no reports, and the amount of fresh water discharged may restrict the flora. The Tampa Bay area is certainly different, for rock outcrops, as on Hillsboro Bay, locally offer a good substratum for algal growth. Limited though the collections we have seen have been, they certainly indicate that there is a good, though not very complex, shallow-water flora of well-developed specimens. However, a good deal of the shoreline is sandy or of shell reefs, with considerable mangrove thickets, and proceeding northward we again come upon an inhospitable, swampy coast. From Cedar Key, we have received collections indicating a rather limited flora but by no means an extremely reduced one including several typical tropical genera like *Codium*, *Caulerpa*, *Padina*, *Laurencia*,

[1] Owing to lack of personal familiarity with most of the Gulf coastline and the fact that published marine botanical studies are generally lacking or poorly documented, the writer has appealed for help and information to several persons, many of whom are not botanists, but each is well informed regarding some part of the coast. Among these may be mentioned with especial gratitude: Professor Clair A. Brown, University of Louisiana, Baton Rouge, Dr. P. A. Butler, Fish and Wildlife Service, Pensacola, Fla., Professor John H. Davis, University of Florida, Gainesville, Dr. Francis Drouet, Chicago Natural History Museum, for the northern shores of the Gulf, Dr. Joel W. Hedgpeth, University of Texas Marine Station, Port Aransas, Roy N. Jervis, University of Michigan, for the Cuban coast, Director of the Herbarium, Hno. León, Colegio de la Salle, Habana, Cuba, Professor W. Armstrong Price, Agricultural and Mechanical College of Texas, College Station, Dr. Paul Weaver, Houston, Texas, for the Mexican coast, and Professor R. H. Williams, University of Miami, Coral Gables, Fla.

and *Digenia*, with genera which, like *Hypnea* and *Gracilaria*, are suited to and widespread in warm, quiet water. On a nearby rocky causeway appear *Ectocarpus*, *Caloglossa*, and other Rhodophyceae and marine Myxophyceae, but apparently Dasycladaceae are already few and do not go much farther.

From this point the red mangrove ceases to play a significant part in the shore vegetation, and the black or *Avicennia* mangrove which is present but not exclusive to the South takes over and continues, somewhat reduced in stature, around the coast. The pneumatophores of *Avicennia*, like the prop-roots of *Rhizophora*, can support a *Bostrychia-Caloglossa-Catenella* algal association but arise from the tidally immersed mud for only a few inches and do not extend out into water of more than a very slight depth. While the flora here includes an abundance of *Gracilaria* and other mud-favoring, widespread types, there are still many characteristically tropical species.

North and west of Cedar Keys the algal flora changes much for the worse owing to the unfavorable factors suggested earlier. Although *Batophora* has been reported from Adams Beach and *Acetabularia* from near Panama City, the family Dasycladaceae is now unimportant. The last records of Caulerpas and Codiaceae are from about Apalachee Bay. Unfortunately, the data for Phaeophyceae and Rhodophyceae are not so sharp, for the more distinctive, less cosmopolitan types disappear early as we go up the coast. The remaining flora of *Gracilaria* and *Hypnea* in protected bays, of *Bostrychia* and its associates on the mangrove roots, with Ulva (fig. 48–f), Enteromorpha (fig. 48–c), and Myxophyceae, dominates the vegetation throughout the northern arc, so far as it is known. As studies progress with the establishment of marine laboratories, doubtless numerous other species will be recorded, and more exact details will become available, but the general pattern probably will not change, i. e., nowhere will a diversified flora of conspicuous species appear. Near Carrabelle there is some *Thalassia*, and some associated small forms like *Fosliella* may be expected. Near and a little west of Pensacola considerable growths of attached *Sargassum* are reported. However, this district represents the outpost of numerous things, for on causeway rocks east of here *Bryothamnion*, *Laurencia*, and other tropical Rhodophyceae appear. This is our last reported outpost of *Catenella* of the mangrove association. Still, the most characteristic red algal flora is that of the bays and swamp mangroves associated with Ulvaceae and blue-green algae.

Alabama's short coastline is phycologically little known. There seems to be some growth of *Polysiphonia* where it can become attached. *Sargassum*, apparently the pelagic gulfweed, is washed ashore in the Mobile area. More conspicuous on docks, walls, and such constructions are growths of *Enteromorpha*, *Rhizoclonium*, and blue-green algae, but there is very little natural opportunity for coarser algae, and these forms adapted to mud are the most widespread.

Mississippi is in the same unreported condition. There is much shoal water off shore. The coast is guarded by a line of sandy islands, and itself is of sand and mud with some swamp areas approaching the shoreline to the west. The flora reported is limited to observations about Biloxi, Ocean Springs, and Bay St. Louis. The flora is much the same as in Alabama and restricted by the same factors except that we have no reports of *Sargassum*, though doubtless gales can throw gulfweed ashore upon the outer islands.

In fact, the general limitation of the algal vegetation of the north and northwest sector has now been completed. The prevalence of muddy shores will explain the dominance of a flora composed of *Rhizoclonium*, *Vaucheria*, and numerous Myxophyceae. For a long distance to the west this is seldom relieved by sandy beaches. Occasional accumulations of shells permit the appearance of *Enteromorpha* and *Ulva* which can also grow on exposed roots and tree balks projecting from the mud. The exposed black mangrove roots permit the *Bostrychia-Caloglossa* vegetation to appear, often with elements from the last-named mud and shell flora. All these also appear on wharves and stone jetties but with almost none of the larger types added that flourish in like situations to the east.

Louisiana has a highly dissected coastline with swampy land almost everywhere descending to the sea. Off the coast between the Sabine and Atchafalaya Rivers just inside the 183-meter line, Trask, Phleger, and Stetson (1947) report flat-topped hills which rise to within 18 meters of the surface, and which in 18 to 36 meters of water support a dominating flora of *Lithothamnion* balls associated locally with corals, a very remarkable flora to be discovered in this area. Offshore on the east the sandy Chandeleur Islands with shell ridges shield a shallow, sandy sound. Even marshy islands like Isle au Pitre to the northeast of the delta may be margined by beaches of shells. In the outer delta region at Grand Isle and near the western side of the State south of Lake Calcasieu we again have a sandy shore. Unstable sand subject to wave action is not favorable to growth of algae, and only the more sheltered muddy shores can maintain the flora outlined in the paragraph above. A particular feature of the tidal marsh streams emptying into the northern part of the Gulf may be introduced here. These are reported to support a flora similar to the above near the sea but with the very curious *Compsopogon* in fresher water. There is no reported work dealing with Louisiana marine algae, but considerable collections from the north Gulf coast are now being studied and will add to the details of this account. In salt marshes and tidal lakes on the Calcasieu River the usual limited flora prevails. Weeks Bay and the Canal are similarly but sparsely populated. Lake Pontchartrain on its southeast side is again similar but with more evidence of *Cladophora*, *Ectocarpus*, *Polysiphonia*, and *Bostrychia* where these are favored by rocks and wharf piles. On the north shore and at the east end, only *Rhizoclonium* and blue-green algae appear. The tidal marshes at the south delta extension of Chenier Caminada and Grand Isle show the usual flora including *Compsopogon*; on the outer beaches much *Sargassum* is washed ashore by storms. In the bay to the west the same flora occurs again, but by virtue of pilings and other firm attachments we have there the *Bostrychia* flora. In general, because the shores of most of the state are marshy, the opportunities for algal colonization are restricted.

A great change appears as one crosses the State line into Texas. Only a very short coastal section below Port Arthur is marshy; thenceforth sandy shores face the sea nearly everywhere. Immensely long and narrow peninsulas and islands line the coast with relatively shallow bays behind them. These unstable, sandy, outer shores discourage algae effectively, but in the bays behind and on the rocks of the jetties and other harbor structures a much enhanced (though still not a rich) flora appears, of 60 or more macroscopic species. The neighborhood of Galveston and Texas City yield few of these: *Ulva lactuca* (fig. 48–f), *Gelidium crinale* var. *platycladum*, *Agardhiella tenera*, and *Gracilaria confervoides* (fig. 50–e) slightly enrich the sparseness of the continued Louisiana type of marsh flora, and of these only the *Gelidium* really is additional to the Gulf north shore flora and only in its variety among the four seems at all tropical.

The next group of reported stations centers about Matagorda Bay and its offshoots; Schott, nearly a century ago (Taylor 1941a, 1941b), found it a profitable collecting ground. Here the flora again includes *Centroceras*, *Digenia simplex* (fig. 50–d), and less distinctive tropical additions. However, the flora between Copano Bay and Corpus Christi Bay is much richer. *Ulva fasciata*, *Cladophora fascicularis* (fig. 48–b), *Acetabularia* (fig. 48–a), *Batophora*, *Padina*, *Corallina cubensis*, *Ceramium subtile*, and Laurencias greatly accentuate the tropical character of the flora despite limited suitable substrata. It is not solely this feature which restricts the flora, of course, for the sandy to muddy inner bays might be suitable for Caulerpaceae and Codiaceae, not yet reported from the State, were it not for unrecognized limiting factors. Where muddy, the great shallows behind Padre Island may show an enormous development of an almost leathery blue-green algal flora. On the outer islands *Sargassum* is washed ashore in conspicuous amounts. This is partly, but not solely, of the pelagic species, for *S. filipendula* and *S. pteropleuron* are also reported. Otherwise, nothing distinguishes the flora hence to the Mexican boundary.

The marine flora of the east coast of Mexico is far less known than that of the west coast and both shores much less than the land flora of the central parts of the country. For the east coast this is not hard to understand. South from the Rio Grande extend sandy barrier islands which promise little of botanical interest. With the approach to the shore of hills containing calcareous rock the lime content of the sands increases progressively to Tampico. A little to the north at Punta Jerez limestone rocks outcrop in about 18 meters of water and corals occur, so algae may be expected. The calcareous content of the sands, in general, decreases again south of Tampico, but limestone is expected at Lobos Island and other reefs south of Cape Rojo. Lava materials rather replace other elements near Punta Delgada, but as one approaches Veracruz sandy beaches appear, with numerous rocky shoals and reefs where Heilprin (1890) long ago confirmed the presence of actively growing corals and coral reefs (as at Gallega and Anegada de Adentro Reefs), as well as serpulid reefs (Punta Gorda and in part Hornos Reef), the presence of both of which suggests good conditions for algal growth. This had long before been recognized by Liebmann who collected here, from among whose algae Agardh (1847) described five striking species as new. Farther to the east at about longitude 95° W., lava flows account for a rocky coast with cliffs, but the sandy beaches begin again at Punta San Juan and extend until, at the Rio Tonala, mangroves take over and dominate the swampy, rather muddy coast to the Laguna de Terminos, a large body of water with several streams emptying into it and two major passes communicating with the sea. This should support an appropriate algal flora. Hence out the west coast of Yucatán, the presence of underlying limestone rock and the absence of streams substitute an irregular coast with much calcareous sand and mud derived from this rock. It is, curiously, from this unpropitious area that we get most of our few records of Mexican east coast marine algae. Several specimens were collected by Steere in 1932 at Progreso and reported by the writer (1935) together with odd specimens from other sources, especially some collected by A. C. V. Schott who visited Progreso, Sisal, and Celestum in 1865 and made very important collections, indicating that there was here a substantial vegetation characteristic of the Caribbean flora and of a rocky shore. Liebmann (Agardh 1847) had obtained a new *Sargassum* from the Campeche reefs only a little earlier. The Schott algal collections, of some 40 species, in general remained unknown until the present writer reported on them (1941b). Shoal water extends far off shore all along the north and west of the peninsula, and 45 miles off Celestum and Sisal in about 32 meters of water *Sargassum* is sufficiently abundant to appear on the naval charts as a distinctive feature occurring on a coral bottom.

Of Cuban algae, we know even less than we do about those of Mexico. Most of the island has never been surveyed for these plants. Small collections have been made from the Guantanamo area but not reported upon. Fortunately, three considerable lists (Montagne 1842, Howe 1918, Sanchez Alfonso 1930) do apply to the Gulf coast from Habana eastward to Cabo San Antonio. While doubtless only a portion of the flora is represented, it is clear that we have a typical Caribbean tropical assortment in accord with the varied coastline. For example, Mariel, west of Habana, shows a rocky limestone coastline beyond which sandy beaches alternate with rocky shores along the coast. Serpentine rocks are reported to reach the shore in some places. In many areas broad stretches of shallow water extend far out from the shore, and in such shallows near Habana *Thalassia* grows over the sandy bottom, doubtless with its attendant algae, and doubtless occurring also elsewhere along the northwest coast. Many parts of the shore are marked on charts as being mangrove-bordered, so the algae commonly associated with *Rhizophora* are to be expected. The western peninsula of Guanahacabibes is generally low on the north shore and mangrove fringed. A few miles off much of the northwest coast lie the Colorado Reefs, commonly at a depth of 2 to 5 meters, which presumably bear the rich tropical reef flora. Of the shores which face the Gulf of Mexico, Cuba has in its relatively small extent the most promising coast line and should rival Florida in the richness of its algal flora when fully explored.

CITED LITERATURE OF GULF OF MEXICO MARINE ALGAE AND BIBLIOGRAPHY OF PRINCIPAL WORKS ON COMPARABLE WEST INDIAN MARINE ALGAE

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FLOWERING PLANTS OF THE WATERS AND SHORES OF THE GULF OF MEXICO

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The maritime flowering plants of the Gulf of Mexico, because of their dependence on light to carry on photosynthesis and on the substrate to furnish a place of attachment for their roots or underground stems, are confined to shores and shallow coastal waters. No flowering plant has been reported from Gulf waters at depths greater than 100 meters. Taylor (1928) reports that *Halophila engelmannii* Aschers., a sea-grass, was dredged in the transparent waters of the Dry Tortugas area from measured depths up to 73.2 meters and one estimated depth of 91 meters. Thus only the margins of the Gulf of Mexico are of concern to one interested in vascular plants.

Knowledge of the flora and vegetation of the Gulf perimeter is mostly inadequate. Only in very limited areas such as the Florida Keys is information about the plant life extensive. Data on the Gulf maritime flora must be sought in many publications treating limited land areas fringing the Gulf. The appended bibliography attempts to bring together the more important and recent of these references.

Floristic works of the greatest usefulness in the Gulf region because of their wide scope and relatively recent publication are: Small's Flora of the Southeastern United States, 1913, and Manual of the Southeastern Flora, 1933, Leon and Alain's Flora de Cuba, 1947–51, and Standley's Trees and Shrubs of Mexico, 1920–26, and Flora of Yucatán, 1930. Pertaining to smaller areas but often containing much valuable information on the distribution of maritime plants are: Small's Flora of the Florida Keys, 1913, Mohr's Plant Life of Alabama, 1901, Lowe's Plants of Mississippi, 1921, Lloyd and Tracy's The Insular Flora of Mississippi and Louisiana, 1901, and Cory and Parks' Catalogue of the Flora of the State of Texas, 1938. Floristic and ecological treatments of still more limited areas are referred to under the several plant communities.

The marine and strand flowering plants of the Gulf are best considered in the natural groupings in which they usually grow. There are four such major plant communities: submarine meadow, mangrove swamp, salt marsh, and sand-strand vegetation.

SUBMARINE MEADOW

Least collected and studied of all the Gulf plants are the marine spermatophytes or sea-grasses. These aquatic flowering plants, members of the Hydrocharitaceae and Zannichelliaceae rather than true grasses, have received some attention in the waters around the Dry Tortugas. Bowman (1916, 1918) and Taylor (1925, 1928) have contributed original observations on the ecology and morphology of species in that area. For other parts of the Gulf information about them is scanty (Howe 1918; Davis 1940; Hotchkiss 1940; Stephenson and Stephenson 1950). Several authors (Ascherson 1906; Ostenfeld 1914, 1926–27; Setchell 1920, 1934a) have discussed their world distribution, and Balfour (1878), Rydberg (1909), and Bowman (1916) have contributed papers on their morphology. The most thorough taxonomic treatments of the marine spermatophytes are included in Ascherson and Graebner's (1907) monograph of the Potamogetonaceae in Das Pflanzenreich and Ascherson and Gürke's (1889) study of the Hydrocharitaceae in Die Naturalichen Pflanzenfamilien. Descriptions and keys for the identification of Gulf species are available in Small (1933) and Muenscher (1944).

More species of marine flowering plants are found in the Gulf of Mexico and Caribbean Sea than anywhere else in the Western Hemisphere. In the waters around the Florida Keys grow five species belonging to two families: *Diplanthera wrightii* (Aschers.) Aschers. and *Syringodium filiforme* Kutz., manatee-grass, of the Zosteraceae, *Thalassia testudinum* König, turtlegrass, *Halophila baillonis* Aschers. and *H. engelmannii* Aschers. of the Hydrocharitaceae. *Halophila aschersonii* Ostenf., as well as the above, is found in the Caribbean and is reported as far south as Recife, Brazil. The widespread *Ruppia maritima* L., widgeongrass of the Potamogetinaceae and *Zannichellia palustris* L., horned-pondweed of the Zanichelliaceae, though usually not marine, are found in brackish waters along the Gulf coasts.

Only two other genera of marine flowering plants are reported from the New World. *Zostera marina* L., eelgrass of the Zosteraceae is found in shallow, quiet waters of the Pacific and Atlantic coasts of North America, reaching as far south along the latter as North Carolina. Other species of this genus have been collected on the coasts of Chili and Uruguay (Setchell, 1934b, 1935). *Phyllospadix scouleri* Hook. and *P. torreyi* Wats., also of the Zosteraceae, grow along the Pacific coast near low-tide mark where they are exposed to strong wave action.

The Gulf and Caribbean sea-grasses are limited in habitat largely to soft marl, mud, or sand in warm, clear, shallow marine water. *Thalassia, Diplanthera,* and *Syringodium* form extensive submarine meadows or beds in shallow water of bays and lagoons, seldom being exposed except at the lowest tides. These plants extend also into deeper water, having been dredged in the Dry Tortugas area to 11 meters (Taylor 1928). Generally, the species of *Halophila* thrive on calcareous bottoms in much deeper water. *H. baillonis* has been dredged from 5.5 to 29.3 meters but more commonly in 14 to 18 meters and *H. engelmannii* in still deeper water, 4.6 to 73.2 meters and one estimated depth of 91 meters (Taylor 1928). *H. aschersonii* was dredged with *H. baillonis* along the south shore of Puerto Rico from a depth of 18 meters (Howe 1915). These marine plants are usually associated in southern Florida waters with such marine algae as *Acetabulum, Caulerpa, Gracilaria, Halimeda, Hypnea, Penicillus, Polysiphonia, Sargassum,* and *Udotea*. *Thalassia* especially furnishes a good habitat for such algal epiphytes as *Melobesia farinosa* Lamouroux. *Ruppia* is often abundant in shallow water of enclosed bays, tidal estuaries, or other areas where the water is less saline.

The distribution of sea-grasses in the Gulf is poorly known. All five Gulf species grow along the northwestern coast of Cuba and around the Florida Keys. All of these but *H. baillonis* have been collected in the Tampa Bay region by the writer and on the northern Gulf coast of Florida by others. *Thalassia, Diplanthera,* and *Halophila engelmanii* are present in the coastal waters of southern Texas. Several of the species must occur along the Mexican coast. The apparent rarity of marine spermatophytes except *Ruppia* on the northern Gulf coast between Bay County, Florida, and Aransas County, Texas, may be significant. Perhaps the silt and fresh water dumped into the Gulf by the Mississippi and other large rivers are involved.

Outside the Gulf and Caribbean, *Diplanthera* has been collected on the coast of North Carolina and *Diplanthera, Thalassia, Syringodium,* and *H. baillonis* on Bermuda shores. Two species, *Thalassia testudinum* and *Diplanthera wrightii* have been collected on both the Caribbean and Pacific coasts of the Isthmus of Panama, possibly indicating a former water connection across the isthmus. Close relatives of species in each of the four Gulf genera are found in the Indo-Pacific region. In all, approximately 40 species of sea grasses are known, and the largest concentrations of these occur in tropical waters of the Indian Ocean, western Pacific Ocean, and the Red Sea.

MANGROVE SWAMP

Most conspicuous of the plant communities of the Gulf coast is mangrove swamp. There is much literature about this swamp-forest or swamp-thicket that is so characteristic of tropical coasts around the world. Davis (1940) has made a thorough study of mangroves in Florida with emphasis on their ecology and geologic role. Their importance as land-builders in Florida has been emphasized, perhaps overemphasized, by several writers (Curtiss 1888; Sargent 1893; Pollard 1902; Phillips 1903; Vaughan 1910; Harshberger 1914; Simpson 1920). The embryology of *Rhizophora mangle* L. has been studied by Cook (1907), the physiology by Bowman (1917), and the dispersal and establishment by Egler (1948). Dispersal of *Rhizophora* and other mangroves has been considered in some detail by Crossland (1903), Guppy (1906, 1917), Ridley (1930), and other biologists. In addition to some of the above papers good accounts of mangrove swamp on Gulf coasts have been written by Harper (1927) and Davis (1942, 1943). Publications describing mangrove swamp in other regions are listed in the bibliography for Jamaica (Steers et al. 1940), the Virgin Islands (Børgesen 1909; Raunkiaer 1934), Micronesia (Fosberg 1947), Indo-Malaya (Schimper 1891), and for the tropics in general (Schimper and Faber 1935) and (Warming 1909).

The three widely distributed mangroves of Gulf shores are *Rhizophora mangl^* L., the red mangrove, *Avicennia nitida* Jacq., the black or honey mangrove, and *Laguncularia racemosa* (L.) Gaertn. f., the white mangrove. These species grow mixed together or in distinct zones. All are noteworthy for their ability to withstand varying concentrations of salt in the sea water and soil solution in which their roots are buried. They are apparently facultative halophytes, for seedlings of each have been grown in fresh soil and water for at least 6 years (Davis 1943). *Rhizophora* may be readily identified by its peculiar system of branching prop-roots extending downward like stilts from the trunks and lower branches and by the less common flexible air roots dropping from the upper branches. It produces seeds which germinate while attached to the tree to form club-shaped hypocotyls commonly 30 centimeters long. These hang by the two cotyledons from the ovate fruit until they plummet into the water or mud below the tree. *Avicennia* produces an abundance of odd, pencil-like pneumatophores rising through the mud from the shallow horizontal roots. The flowers produce abundant nectar that is manufactured by bees into excellent honey. The fruit is ellipsoid, flattish, and 3 to 5 centimeters long. *Laguncularia* produces fewer and smaller pneumatophores than *Avicennia*. It may be recognized by its fleshy, elliptical leaves and small, ribbed fruit.

In addition to the three mangroves several plants are characteristic of mangrove swamps. A relative of *Laguncularia, Conocarpus erecta* L., called the buttonwood or button mangrove because of its small, button-like or alder-like clusters of flowers and fruit, grows inland from the other mangroves on harder ground that is usually not flooded by normal tides. Its trunks are loose-barked, twisted, and frequently prostrate. It is a common plant also in dune hammocks. Two vine-like shrubs of the Leguminosae, *Caesalpinia crista* L., nicker-bean, and *Dalbergia ecastophyllum* L., coin-vine, often sprawl over the mangrove thickets on their landward margin. Both species are more shrub-like when growing on the dunes. Another vine, of the grape family, *Cissus incisa* (Nutt.) Desmoul., marine-ivy, climbs through the crowns of the mangroves and sends down to the ground long, cord-like aerial roots. *Batis maritima* L., saltwort, a succulent-leaved, spreading or prostrate shrub, is frequently the only species accompanying the mangroves on wet mud. On sandy or marly shores other succulent halophytes, such as *Salicornia virginica* L., glasswort, *Sesuvium portulacastrum* L., sea-purslane, and *Suaeda linearis* (Ell.) Moq., sea-blite, and several grasses may cover the ground on the inner margin of the mangrove thickets.

On drier ground landward from the mangrove thickets several shrubs and herbs associated with *Conocarpus* form an open thicket transitional to shore hammock or pineland. Some of the plants of this transitional zone, flooded by salt water only during spring and storm tides, are *Borrichia frutescens* (L.) DC., sea-oxeye, *Lycium carolinianum* Walt., Christmasberry, *Bumelia celastrina* HBK., saffron-plum, *Coccoloba uvifera* (L.) Jacq., sea-grape, *Maytenus phyllanthoides* Benth., and *Sophora tomentosa* L., necklace-pod. In addition to these, all found in the Tampa Bay region of central Florida, several other tropical associates of *Conocarpus* in the mangrove-hammock transition zone are found in the more tropical part of southern Florida and the Florida Keys. These are *Borrichia arborescens* (L.) DC., sea-oxeye, *Rhabdadenia biflora* (Jacq.) Muell. Arg., rubbervine, *Capparis flexuosa* L., *Achras emarginata* (L.) Little, wild dilly, *Jacquinia keyensis* Mez., Joe-wood, *Torrubia longifolia* (Heimerl.) Britt., blolly, *Erythalis fruticosa* L., *Acrostichum aureum* L., leather fern, and several cacti, *Acanthocereus floridanus* Small, dildoe, *Harrisia simpsonii* Small, prickly-apple, and *Opuntia dillenii* (Ker) Haw, prickly-pear. The loose bark of *Conocarpus* furnishes a foothold to several epiphytes including *Epidendrum tampense* Lindl., an orchid, and various species of *Tillandsia*, the air-pines.

Zonation in mangrove swamps appears to be correlated with water level and degree of salinity of the water and substrate and in some areas with tidal fluctuations. Each species, however, may be quite variable in relation to these factors. *Rhizophora* may form colonies well off shore on

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shoals or may occur as scattered plants in brackish or even fresh water well inland from the coast. Generally, it grows on shores or low islands where the substrate is covered by tidal water even at low tide. The *Avicennia* zone which commonly includes *Laguncularia* and various salt-marsh plants is flooded, at least in its outer part, by salt or brackish water at high tide. When *Laguncularia* forms a distinct community, it is usually inland from *Avicennia*. *Conocarpus* and its associates of the transition zone are seldom flooded. The mangroves grow on peat, muck, marl, sand, and rock. They are killed by severe frosts. Economically they have been of little importance except in certain areas where they have been used for fuel, pilings, and a source of tannin. It is contended by some that mangrove swamps protect shorelines, build up soil levels along the coast, extend shorelines, and form new islands, but it is doubtful that the mangroves play a very large part in land building.

Mangrove swamp in the Gulf region reaches its greatest development along the southwestern coast of Florida in the Ten Thousand Islands area. There mangroves of all three species, some more than 25 meters tall and 2 meters in circumference (Davis 1940), grow in the extensive strand and estuary swamps. Mangrove swamp to a depth of several miles covers the western and southern tip of peninsular Florida from Cape Romano to Cape Sable and thence eastward to Biscayne Bay. Mangroves also cover the numerous small keys in Florida Bay and fringe the larger Florida Keys south and west to the Marquesas. Northward along both sides of Florida less well developed mangrove swamp, perhaps better described as mangrove thicket, extends to the Cedar Keys area on the Gulf coast and Cape Canaveral or farther north on the Atlantic coast, mostly in lagoons, bays, and estuaries. As the mangroves become smaller and more scattered on the northern Gulf coast, salt marshes become more extensive. Killing frosts apparently are the deciding factor in the competition between the species comprising the two vegetation types. In Florida mangrove areas are estimated to total more than a thousand square miles (Davis 1940).

The botanically less known Gulf coasts of Cuba and Mexico are fringed in the appropriate habitats with mangrove swamp. According to Leopold (1950), mangroves extend northward along the Mexican Gulf coast to southern Tamaulipas. Along the northern shores of the Gulf from Cedar Keys in Florida to southern Tamaulipas typical mangrove swamp is absent, and mangrove species are represented only by the more hardy *Avicennia* which grows, where present, mostly as scattered shrubs with *Batis* and other salt-marsh associates.

Mangrove swamp is found throughout the tropics along low-lying shores and estuaries that are protected from direct wave action. Although it is best developed on mud and marl, it is present also on sand and even rock wherever crevices permit the seedling mangroves to gain a foothold (Crossland 1903). Oriental mangrove swamps are similar to those of the American and West African shores except that there are many more species of Oriental mangroves. Although few in number the American mangroves are widely distributed. *Rhizophora mangle*, *Avicennia nitida*, and *Laguncularia racemosa* are all found on the tropical coasts of West Africa as well as on both Pacific and Atlantic shores of tropical America. The floating seedlings or fruits of all three remain buoyant and alive in salt water for several months (Guppy 1917) and are thus well-adapted to long distance dispersal by ocean currents. Several of the plants associated with them on the Gulf coasts, such as *Caesalpinia crista*, *Sophora tomentosa*, and *Acrostichum aureum*, range even more widely in the tropics.

SALT MARSH

Salt marshes of temperate shores have received perhaps even more attention from botanists than mangrove swamps of tropical shores. Those along the Gulf coast have not been neglected. Penfound and Hathaway (1938) have made a very thorough study of marshes in southern Louisiana. Other botanists who have published on salt marshes of the northern Gulf shores are Mohr (1901), Lloyd and Tracy (1901), Cocks (1907), and Penfound and O'Neill (1934). Harshberger (1914), Harper (1927), and Davis (1940, 1943) have described salt marshes and salt flats along the Florida Gulf coast. The salt marshes along the Atlantic coast of North America are similar in many respects, and have been well described by Kearney (1900, 1901), Harshberger (1909), Johnson and York (1915), Conard (1935), and Chapman (1940a, 1940b).

Salt marshes are best developed along the more protected, temperate shores of the northern part of the Gulf of Mexico. There extensive marshes of salt-tolerating species of flowering plants cover the tidal shores of the estuaries, bays, and lagoons. According to Griffitts (1928) there are 5,600,000 acres of salt marshes in the South Atlantic and Gulf States, of which 3,381,500 are in Louisiana, 680,000 in Florida, 315,000 in Texas, 34,000 in Alabama, and 26,500 in Mississippi. Louisiana possesses almost one-half of the total salt-marsh acreage in the United States.

The dominant species in these marshes are *Spartina alterniflora* Loisel., smooth cordgrass, and *Juncus roemerianus* Scheele, black rush, each commonly forming extensive and exclusive colonies. Several other grasses or grasslike plants, however, are often found in association with them. These are *Distichlis spicata* (L.) Greene, saltgrass, *Spartina patens* (Ait.) Muhl., salt-meadow cordgrass, *Spartina spartinae* (Trin.) Merr., *Scirpus robustus* Pursh, salt-marsh bulrush, and *Fimbristylis castanea* (Michx.) Vahl, a sedge. Showy-flowered plants like *Limonium carolinianum* (Walt.) Britt., sea-rosemary, *Solidago sempervirens* L. var. *mexicana* (L.) Fern., seaside goldenrod, *Pluchea purpurascens* (Sw.) DC., salt-marsh fleabane, *Aster exilis* Ell., *A. subulatus* Michx., and *A. tenuifolius* L., the salt-marsh asters, and *Borrichia frutescens* (L.) DC., sea-oxeye, give some color to the marshes though they are seldom abundant.

On wet, saline flat areas which are near high tide-mark the vegetation is more open. There, sometimes with scattered and dwarfed specimens of *Avicennia nitida* L., black mangrove, and several plants, such as *Distichlis*, *Borrichia*, and *Limonium*, are found the peculiar halophytes with succulent stems or leaves, *Batis maritima* L., saltwort, *Salicornia virginica* L. and *S. bigelovii* Torr., glassworts, *Suaeda linearis* (Ell.) Moq., sea-blite, *Sesuvium portulacastrum* L., sea-purslane, *Philoxerus vermicularis* (L.) R. Br., beach-carpet, and *Bacopa monnieri* (L.) Pennell, marsh-hyssop. With these grow a few species with showier flowers: *Sabatia stellaris* Pursh, sea-pink, *Gerardia maritima* Raf., false-foxglove, and two vines, *Ipomoea sagittata* Cav. and *Cynanchum palustre* (Pursh) Heller. On slightly higher ground these herbs or small shrubs give way to a thicket of taller shrubs consisting mostly of *Iva frutescens* L., marsh-elder, *Baccharis halimifolia* L. and *B. angustifolia* Michx., groundselbushes.

Farther south along the Florida Gulf coast from Tampa Bay to Key West the salt marshes become much less extensive due to competition from the mangroves. Salt-marsh plants there generally form an understory in the *Avicennia* zone of the mangrove swamps or predominate in the transition zone between the mangroves and non-halophytic vegetation. Characteristic of this southern Florida coast, especially on Cape Sable, are the salt flats. These level expanses of hard-packed sand or marl or of limestone rock are flooded by high tides. They support a sparse vegetation of species listed above for the open salt marsh with the addition of several other common plants like *Monanthochlöe littoralis* Engelm., key grass, *Sporobolus virginicus* (L.) Kunth, drop-seed, *Borrichia arborescens* (L.) DC., sea-oxeye, *Flaveria linearis* Lag., *Conocarpus erecta* L., buttonwood, and its other woody associates listed under mangrove swamps.

In the marshlands of southeastern Louisiana Penfound and Hathaway (1938) found gradual changes in the flora from strictly salt-water to strictly fresh-water habitats. They noted that many marsh species have a wide range of tolerance for the salt factor and are found in brackish marshes as well as in salt-water or fresh-water marshes. Most of the salt-marsh species listed previously occur also in brackish water, and many fresh-water marsh plants are found in slightly brackish water. Some of these plants of brackish marshes are *Typha domingensis* Pers. and *T. latifolia* L., cattails, *Spartina cynosuroides* (L.) Roth, salt-reed grass, *Phragmites communis*, Trin., common reed, *Scirpus californicus* (C. A. Meyer) Britt. and *S. chilensis* Nees & Mey., bulrushes, *Sagittaria lancifolia* L., arrowhead, and *Alternanthera philoxeroides* (Mart.) Griseb., alligator-weed. The last-mentioned plant is often a pest in the bayous and ditches of southern Louisiana. Another bad pest of fresh waters, *Eichornia crassipes* (Mart.) Solms, water-hyacinth, although often floated downstream into salt water, will not tolerate salt, and soon dies in even slightly brackish water (Penfound and Earle 1948).

In southern Florida the transition from salt marsh or mangrove swamp to nonhalophytic types of vegetation is equally gradual or very abrupt. Where salt marsh is transitional between mangrove swamp and fresh-water prairie the brackish marsh zone is very wide. Dwarfed and scattered specimens of *Rhizophora mangle* L. grow inland along the rivers running from the Everglades and in the wet prairies where the water has little or no salt content. There it may be associated with *Cladium jamaicensis* Crantz, sawgrass, *Typha domingensis* Pers., cattail, *Sagittaria lancifolia* L., arrowhead, *Acrostichum danaeaefolium* Langsd. & Fisch., leather fern, and *Annona glabra* L., custard-apple. Similarly, where large rivers flow into the Gulf there are along the estuaries wide areas of brackish marshes transitional between the coastal salt marshes and fresh-water marshes and swamps. Where salt marsh abuts upon pineland, as in the Tampa Bay region, a difference of 30 centimeters in ground level brings an abrupt change in the physiognomy of the vegetation. The narrow zone of transition is often marked by a thicket of *Myrica cerifera* L., waxmyrtle, several species of *Baccharis*, groundselbushes, and *Sabal palmetto* (Walt.) Todd., cabbage palm.

There are no salt marshes on the Cuban Gulf coast. Many of the American salt-marsh species, however, grow mixed with tropical species in the mangrove swamps or on low-lying beaches. Although the coastal vegetation of Mexico is poorly known, the same relationship probably exists between salt-marsh plants and mangroves from southern Tamaulipas to Yucatán as on the southern Gulf coast of Florida and Cuba. The Yucatán coast possesses such salt-marsh or salt-flat plants as *Distichlis*, *Monanthochlöe*, *Spartina*, *Sporobolus*, *Fimbristylis*, *Philoxerus*, *Salicornia*, *Suaeda*, *Batis*, *Sesuvium*, *Baccharis*, and *Borrichia*, as well as the mangroves and many associated plants.

Salt-marsh plants live under most difficult conditions: high salt content in the soil solution, poor aeration resulting from the poor drainage, recurrent submersion and exposure, and full insolation. Only species with a wide range of tolerance to these conditions can survive. Marsh height, tidal submergence, and salinity of the soil solution appear to be the most important factors in producing zonation in salt marshes. *Spartina alterniflora* Loisel. withstands the deepest flooding. It is also, with *Distichlis spicata*, *Juncus roemerianus*, *Batis*, *Salicornia*, and the other succulent halophytes, apparently the most salt-resistant. Uphof (1941) has reviewed the literature on halophytes.

SAND-STRAND VEGETATION

The flowering plants of sandy shores are not strictly aquatic, yet they are too conspicuous and too abundant along Gulf coasts to omit from this treatment. Most thoroughly studied and described are the Florida beaches. Webber (1898), Millspaugh (1907), Harshberger (1914), Bowman (1918), Simpson (1920), Harper (1927), Davis (1940, 1942, 1943), and Kurz (1942) have described the beach vegetation of the Florida Gulf coast. Strand vegetation along the northern Gulf coast has been treated by Mohr (1901), Lloyd and Tracy (1901), Cocks (1907), Lowe (1921), and Penfound and O'Neill (1934). Except for the addition of more tropical species and the dropping out of more temperate species, the strand flora of Yucatán, Cuba, and other West Indian islands is very similar to that of southern Florida. This similarity is readily apparent from the descriptions of the beach vegetation of Yucatán (Bequaert 1933; Lundell 1934), Cuba (Uphof 1924; Seifriz 1943), Puerto Rico (Cook and Gleason 1928), and the Virgin Islands (Børgesen 1909; Raunkiaer, 1934). Beach and dune vegetation along the Atlantic Coast of North America is described by Kearney (1900, 1901), Harshberger (1900), and Conard (1935). General treatments of strand vegetation in other parts of the world can be found in Schimper (1891), Schimper and Faber (1935), and Warming (1909).

Sandy shores of the Gulf coast show as definite a zonation as salt marshes and mangrove swamps. Oosting (1945) attributes this zonation to the tolerance to salt spray of the various coastal dune plants. The community is definitely a halophytic one. Due to vigorous wave action few plants survive on the lower beach. The pioneers of wet or shifting saline sands are found on the upper beach and the fore dunes. In the Tampa Bay region of the Florida coast the most abundant strand species are *Sesuvium portulacastrum* L., sea-purslane, *Sporobolus virginicus* (L.) Kunth, drop-seed, *Atriplex arenaria* Nutt., beach orach, *Cakile edentula* (Bigel.) Hook., sea-rocket, *Heliotropium curassavicum* L., seaside heliotrope, *Philoxerus vermicularis* (L.) R. Br., beach-carpet, *Iva imbricata* Walt., beach-elder, *Uniola paniculata* L., sea-oats, *Euphorbia buxifolia* Lam. and *E. ammannioides* HBK., spurges, *Ipomoea pes-caprae* (L.) Sweet and *I. littoralis* (L.) Boiss., railroad vines, *Scaevola plumieri* Vahl, beach berry, *Andropogon glomeratus* (Walt.) BSP., bunchgrass, *Cenchrus pauciflorus* Benth., sandbur, *Croton punctatus* Jacq., silverleaf, *Oenothera humifusa* Nutt., seaside evening-primrose, and *Helianthus debilis* Nutt., dune sunflower.

Many of these species, especially the dominant, graceful sea-oats, *Uniola*, remain abundant in the back dunes and dune plateaus inland from the beach. Here, however, the conspicuous species are the larger plants like *Coccoloba uvifera* (L.) Jacq., the seagrape, which is the most characteristic shrub of sandy strands in the American tropics. Other woody species are *Yucca aloifolia* L., Spanish-bayonet, *Forestiera porulosa* (Michx.) Poir., Florida privet, *Chiococca alba* (L.) A. Hitchc., snowberry, *Ernodea littoralis* Sw., *Myrica cerifera* L., waxmyrtle, *Sabal palmetto* (Walt.) Todd., cabbage palm, *Suriana maritima* L., bay-cedar, *Lantana ovatifolia* Britt., shrub-verbena, *Sophora tomentosa* L., necklace-pod, *Dalbergia ecastophyllum* L., coin-vine, *Canavalia obtusifolia* (Lam.) DC., bay bean, *Zanthoxylum clava-herculis* L., toothache tree, *Rapanea guianensis* Aubl., myrsine, *Ardisia escallonioides* Schlecht. & Cham., marlberry, and *Eugenia axillaris* (Sw.) Willd., white stopper. Most of these beaches and dunes along the central Florida coast are on narrow barrier islands which are covered with strand vegetation on the Gulf side and mangrove thicket on the bay side. Between these two types of vegetation may be developed a grassy palm savannah with *Sabal* dominant or a dense coastal hammock composed of more luxuriant and crowded growth of the same species listed above for the back dunes.

Along the northern Gulf coast many of the tropical elements of the dunes and dune-plateau drop out. On the other hand, some of the temperate species are replaced by more tropical species on the Florida Keys and northwestern coast of Cuba. Among the more important additions to the strand flora there are *Tournefortia gnaphalodes* (Jacq.) R. Br., sea-lavender, *Casasia clusiifolia* (Jacq.) Urban, seven-year-apple, *Erithalis fruticosa* L., *Strumpfia maritima* Jacq., *Chrysobalanus icaco* L., coco-plum, and the less common, poisonous *Hippomane mancinella* L., manchineel. Most of the strand species are widely distributed throughout the tropics, and a few, like *Ipomoea pes-caprae* (L.) Sweet are circumtropical. One exotic tree from Oceanica, *Casuarina equisetifolia* Forst., Australian-pine or beefwood, has become widely naturalized on the sandy shores of peninsular Florida and the West Indies. On some of the Florida beaches it is the dominant tree.

Most of the abundant species of the Florida and Cuba beaches and dunes are listed from Yucatán, and the strand vegetation along the rest of the Mexican Gulf coast is probably similar to that of the southeastern shores of the Gulf. Little seems to have been published on the vegetation of the Texas coast, but there, too, the strand flora must be rather similar to that of the Florida coast in the same latitude.

CONCLUSION

The vegetation of the shallow waters and shores of the Gulf of Mexico includes four principal communities of flowering plants. Throughout the Gulf a characteristic strand flora grows on exposed sandy shores of the fringing barrier islands, the larger bays, and the headlands. Grass-like marine spermatophytes form submarine meadows or carpets in shallow, quiet waters, except along the extreme northern Gulf coast. Extensive salt marshes cover muddy, protected shores in lagoons, bays, and estuaries along the northern Gulf coasts. Protected shores in the central and southern Gulf region, however, support swamps or thickets dominated by mangroves, with salt-marsh plants restricted to small areas of open marsh, to open saline flats, or to the understory of the more open zones of the mangrove swamps.

Knowledge of the flora and vegetation of most of the Gulf shores is relatively meager. Only the coast from Louisiana to the Florida Keys has received considerable attention from botanists. The Cuban and Texan coasts have largely been neglected, and the Mexican coast, excluding Yucatán, has received almost no botanical attention. The whole Gulf perimeter should be subjected to an intensive, systematic survey by competent plant taxonomists and ecologists.

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BOTTOM COMMUNITIES OF THE GULF OF MEXICO

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The study of bottom communities, according to the quantitative approach of Petersen, has not been attempted in the Gulf of Mexico or its coastal bays. It is possible to assemble information, in a general way, about certain characteristic bottom aggregations such as coral reefs, sponge grounds, and oyster beds, but the necessary data for comparing these areas with similar situations elsewhere do not exist. This gap in our knowledge has been due in part to our fragmentary information concerning the qualitative composition of the flora and fauna of the area. As many of the contributors of the sections on various animal groups in this volume have shown, our knowledge of the fauna is still far from satisfactory. It is, on the other hand, not without advantage that we have lagged behind other countries in quantitative bottom studies, since we may profit by example. Leaders in this field in recent years have been Russian fishery biologists whose work on biological productivity, biomass, and bottom communities in general has been summarized up to 1947 by Zenkevich (1947). Discussion of the methods and principles of this work are available in English (Brotskaja and Zenkevich, 1939; Zenkevich and Brotzky, 1939). It must be pointed out that such concepts of "productivity," "production," and "biomass" should be used with caution and only after careful consideration of the life spans and metabolic rates of the components of the community.

An example of a study of sponge grounds, in some ways comparable to those off western Florida, will be found in the paper by Chambost (1928). Communities of bay bottoms, including many closely related species living under similar conditions to those encountered along the northern Gulf coast, have been recently described by de Oliveira (1948, 1950). The literature on North Atlantic bottom communities has been reviewed by Jones (1950) who also discusses the concept of marine communities in general.

There is a certain amount of published misinformation, most of it well intentioned, concerning the occurrence of organisms which are considered important community dominants in the Gulf of Mexico. Andree (1920, v. 2, pl. 7), for example, presents a map indicating the occurrence of pearl oysters from Panama northward to Texas and eastward to Alabama. Literally, this is true; small specimens of *Pinctada* are frequently cast adrift on sargassum and reach these coasts, but there are no pearling grounds in the northern Gulf. At the same time, however, reef building oysters are not indicated west of the Atlantic side of Florida, and there is no indication of the Gulf of Mexico sponge grounds. This is comparable to the gaps in Bartholomew's (1911) Atlas of Zoogeography and Orton's (1937) peculiar omission of oysters from the northern Gulf coast. The well-known map of coral reefs indicating reefs throughout the Gulf prepared many years ago by Joubin has appeared in many texts (including the standard Russian text on hydrography). From such information as this, Ekman (1935) originally classified the northern Gulf of Mexico as a tropical littoral region. In his new edition Ekman (1953) gives a more precise account, characterizing the northern part of the Gulf of Mexico as a "warm temperate" region, with species common to temperate eastern North America. A more detailed discussion of the biogeographical relationships of the northern Gulf of Mexico will be found in Hedgpeth (1953).

Of the various bottom communities in the Gulf of Mexico, several of them of prime economic importance, the most intensive work has been done on the oyster bottoms. Various surveys have been undertaken, mostly with the purpose of delineating the beds and determining the causes of decline. While most of the published surveys are out of date, they are useful in studying the changes, many of them the result of human interference with the environment, which have occurred subsequently. The results of the most recent and intensive surveys are not generally available, although two minor papers from one of them have appeared (Norris 1953; Puffer and Emerson 1953).

Most of the study of coral reefs has been faunistic or geological; some minor contributions to the ecology of Gulf of Mexico coral reefs are to be found in the publications of the Tortugas Laboratory. The sponge grounds have been even less adequately studied from the ecological standpoint, although investigations are now in progress.

Gunter's work in Louisiana and Texas

Important marine ecological work, chiefly with motile invertebrates and bottom-feeding fishes, has been done by Gunter in the past 20 years on the coast of Louisiana and Texas. The general results can be divided into the following main categories:

1. A description of the relative abundance and species mass of the larger motile vertebrates and invertebrates.
2. Description of seasonal cycles and movements from Gulf to estuarine waters and return, and seasonal variations in abundance, correlated with temperature change.
3. Distributions of organisms as related to salinity.

This work probably gives as complete a view of the motile and free-swimming fauna of the bays and shallow Gulf as there is for any coast of this continent. While it describes the motile part of the bottom community it does not add to knowledge of the in-fauna of the bottoms. Life history notes on the various important fish and Crustacea with some data on food consumption were gathered as a side issue.

The work in Louisiana was carried on for 2 years from 1931 to 1933. It consisted of the analysis of populations of bottom fishes over a salinity gradient from almost fresh water in the upper part of Barataria Bay to 3 miles offshore in the open Gulf of Mexico. It was during this initial work that Gunter became interested in relative numbers of species mass which he emphasized in later papers. In view of the impossibility of obtaining knowledge of total quantities of the species involved, the relative numbers data of the animals taken in the various environments seem to be about as quantitative as can be obtained. This was used in estimating the relative species mass. Any gear used gives a somewhat distorted view of the actual populations, and the various advantages and disadvantages of the trawl were considered. The results of this work were given in Gunter (1936, 1938a, b). The seasonal variations in abundance of the whole fish population and of various species alone are given. The seasonal cycle of movement in and out of the bays, giving somewhat regular arrivals and departures of some species, was described. The predominant family of fishes was found to be Sciaenidae, followed by Otolithidae and Engraulidae. Several abundant species of Sciaenidae were led by the croaker, *Micropogon undulatus*. Certain comparisons between the shallow water fish fauna of the Louisiana and Texas coasts were made later (Gunter 1945). This work was done under the auspices of Shrimp Investigations of the United States Bureau of Fisheries, and during this time large catches of shrimp were made. The data have not been published, but it can be said that the motile fauna living close to the bottom in the Louisiana bays and shallow Gulf consists chiefly of the fishes described by Gunter, the peneid shrimp, *Penaeus setiferus* and *Penaeus aztecus*, and the blue crab, *Callinectes sapidus*.

During the years 1941 to 1943 Gunter set up a series of stations covering a transect from almost pure fresh water (salinity 2.1 parts per thousand) to 5 miles offshore in the Gulf of Mexico and 5 miles down the Gulf beach. This was on the Texas coast and ran through Copano Bay and Aransas Bay and out into the Gulf, a distance of 40 nautical miles. Thirty-two stations were covered by trawl hauls, trammel nets, beach seines, and fine-mesh net hauls on the beach and shores. The original plan was to carry the work on for 2 years, but it was carried out for a year and a half, and only 1 full year without spotty collections was obtained. Even so, it covered bay and estuarine waters and the connecting sea as extensively as has been done in this country.

Gunter (1945, 1950) was considerably impressed with the fact that the bays serve as nursery grounds for large numbers of organisms. For instance, many fishes such as the croaker, *Micropogon undulatus*, the redfish, *Sciaenops ocellata*, the mullet, *Mugil cephalus*, and several others spawn in the Gulf and grow up in the bays. The same holds true for the blue crab, *Callinectes* *sapidus*, and the two shrimp, *Penaeus setiferus* and *P. aztecus*, all important components of the fauna. This system of bay waters forms a rim along the whole northern Gulf coast. Although certain species such as the cyprinodont fishes, the common oyster, and the various species of palaemonid shrimp remain in the bays and are found nowhere else, the bays are not faunistically isolated from the shallow Gulf, despite narrow connections through the passes, but form a system with it. The dominant life of the region has perforce become adapted to this estuarine-sea water system and moves back and forth within it during the life cycle.

Gunter also emphasized the importance of two gradients connected or correlated with salinity. One, an ostensible relation between salinity and size, depends on the fact that most motile animals move out from shallower waters as they grow larger and go toward or to the sea. This migration is accelerated by the onset of cool weather in the fall when large movements from the bays to the Gulf take place amounting almost to a general exodus for some species.

The other gradient is a decline in the number of species as the salinity falls. As he pointed out, the bay fauna is marine, and although practically all species can live in high salinities they only tolerate varying degrees of low salinity, and thus the numbers of species present become less as the salinity falls along the gradient. The difference in numbers of species in the Gulf and Copano Bay is particularly striking in winter. At that season the fresher, shallower, and thus cooler waters of Copano Bay are dominated by only four or five motile species. The importance of these general phenomena to paleoecological studies was specially mentioned (Gunter 1947).

Since ecological studies by Gunter did not include the sessile, poorly motile or burrowing forms in the area they are incomplete. Nevertheless, they go a long way toward describing the communities of the shallow Gulf. Readers interested in details should consult the original papers. As for the deeper water communities, virtually nothing is known except the results of sporadic dredging stations by the *Blake* and *Albatross* more than 50 years ago. There has been no attempt to list the findings of these dredgings by stations, a difficult task of reassembling in view of the scattered publication of reports on the various animal groups. Hence, our knowledge of the deep-water life of the Gulf of Mexico is still that of Agassiz' Three Cruises of the *Blake*.

Investigations of recent facies

A relatively new development is the study of assemblages of living (and dead) organisms as potential fossil assemblages. In such studies, groupings or facies correlated with environmental conditions are emphasized. Such facies may be the same as a natural community (especially that of the oyster reefs), or they may have no particular relationship to the communities in which they occur especially if they include such remains as mollusk shells and coral fragments carried there by physical forces. In his study of molluscan-foraminiferan assemblages in San Antonio and Aransas Bays, Texas, Ladd (1951) recognizes a series of facies roughly corresponding to the salinity gradient: bay head, inter-reef, reef, polyhaline bay, passes, open gulf (near- and offshore), beaches, and highly saline lagoon. A similar series, based exclusively on foraminifera is recognized in the same region by Parker, Phleger, and Peirson (1953); river, marsh, bay, beach and open gulf. The distribution of various foraminifera along several transects in the northern Gulf from Florida to Texas in relation to sedimentary facies is discussed by Lowman (1949).

Community terminology

The matter of terminology and classification of marine communities, in general, is not settled. The ambitious attempt of Clements and Shelford (1939) to classify the biota of the North Atlantic into various biomes and their component associations has served principally to emphasize that the criteria of terrestrial biomes have but limited application to the marine environment. The term biome was accepted somewhat uncritically by Jones (1950) who classified the North Atlantic bottom communities into various hard and soft bottom "biomes." It is suggested in the recent monumental treatise of Allee et al. (1949), that self-sustaining communities within the sea are difficult to recognize, and that biomes, as defined on land, do not exist: "The major marine community despite its great regional biotic variation, is so lacking in effective barriers to dispersal, is so much subject to slow continuous circulation of its medium and exhibits so much interdependence of its components from region to region and area to area, that it may be regarded as a single biome type." This is probably an extreme view, but in view of our ignorance concerning the bottom communities of the Gulf of Mexico, we cannot examine this question in detail here.

It is necessary to emphasize, however, that the complex character of marine communities cannot be simplified by terminology. The dual character of that community which includes the various species of shrimp is an example. Both estuarine and neritic bottom communities are part of this complex which may be best regarded as elements in a major ecosystem transgressing the various environments in both space and time (Hedgpeth 1953). For the purposes of discussion, several "major bottom communities" are recognized (fig. 51). The four major communities recognized are: the oyster bottoms, the shrimp grounds, the coral reefs and patches, and the sponge grounds. The sponge grounds occupy roughly the same area as the coral patches west of Florida and may, on further study, be considered a subcommunity of the coral grounds. Segregating these by physiographic or environmental requirements, we have in the euryhaline-bay environment the oyster community (and other communities); the shrimping grounds fall in the estuarine and neritic environment; while the coral and sponge communities are stenohaline-neritic. These are also working labels, simply describing as briefly as possible the conditions in which the communities are found.

THE OYSTER COMMUNITY

Foremost among the communities of bay waters is the oyster community. This is not a continuous

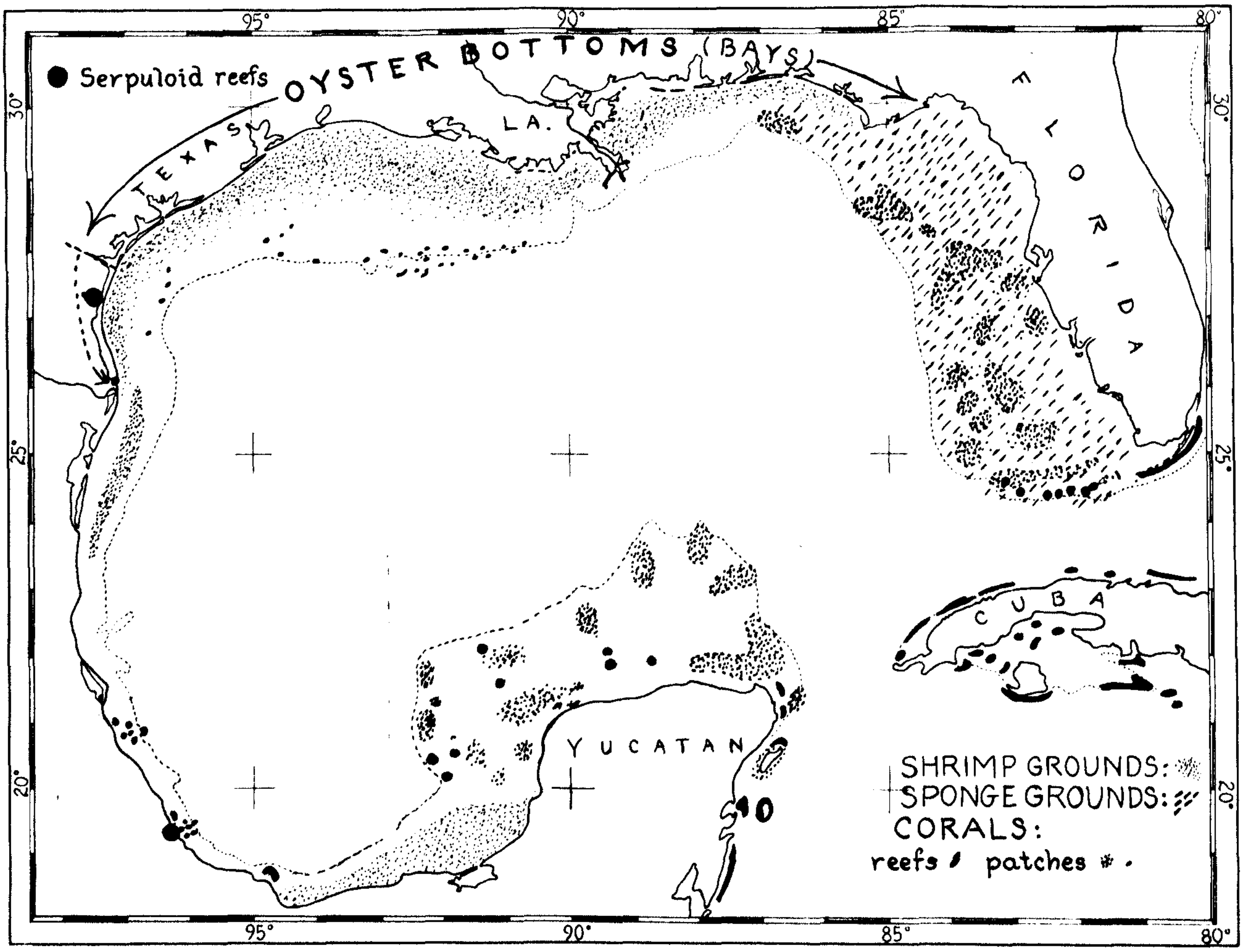

FIGURE 51.—Approximate location of major bottom communities in the Gulf of Mexico.

aggregation of oysters covering entire bay bottoms but an arrangement of ridges and patches of oysters and dead shells, "fragmented faciations of the *Macoma-Mya* biome," in the language of Clements and Shelford (1939). Since *Mya* is absent from Gulf waters and *Macoma* sparsely scattered, this terminology has little meaning. To think of oyster reefs as isolated patches in extensive clam beds is to overlook the influence of oysters in changing the bottom of the bays and the conditions of life for the clams. The clam beds, where they may occur, might better be considered as fragmented by the oyster reefs.

The formation of oyster reefs was studied by Grave (1905) who proposed a theory of the formation of oyster reefs transversely across bays. This theory still remains the best explanation for this characteristic placing of oyster reefs. See figure 52 for a sampling of typical examples, including some studied by Grave.[1] As may be seen from the figure, not all reefs are transverse; some are parallel to the main currents.

The typical oyster reef on the Gulf coast is, in cross section, a low mound with a high center, or "hogback," which is occupied by loose dead shells with the live oysters on the sloping shoulders. These reefs occur on muddy bottoms widely distributed in bays of lower salinities and more or less restricted to the upper ends of those bays which are subject to the invasion of higher salinities through the passes from the Gulf during periods of low rainfall and decreased run-off. A natural reef is usually oval or spindle-shaped or is a narrow bar extending from the shore. Although reefs in Texas have been badly cut up in recent years by artificial channels and mudshell dredging so that the original pattern is now obscured, the usual location of the reefs is such that their long axes are at right angles to the prevailing currents of the bays. Many of these reefs can be studied in the various coastal charts, and details of the more important oyster reefs of the Gulf waters will be found in the old survey papers of Cary (1906), Galtsoff (1931), Moore (1899, 1907, 1913a, 1913b), Moore and Danglade (1915). Ecological accounts will be found in Pearse and Wharton (1938), Archer (1947, 1948a, 1948b), Puffer and Emerson (1953, pp. 164–173).

[1] The biology of the oyster of the Gulf coast and the oyster reefs of the Gulf of Mexico are discussed in detail in chapter XV of this book in articles by Philip A. Butler, p. 479, and W. Armstrong Price, p. 491.

Gulf coast oyster communities differ from those of Chesapeake Bay and more northern waters in lacking predacious starfish, and the Atlantic oyster drill, *Urosalpinx*, is replaced in the lower bays of the Gulf by *Thais*. Other than this, the communities are essentially like those of the Atlantic coast. One of the peculiarities of distribution within the oyster community or biocoenosis is the apparent absence of the commensal (or at times parasitic) crab, *Pinnotheres ostreum*, from the northeastern part of the Gulf, although it has been reported from Cameron, Louisiana, and is not rare in Matagorda and Mesquite Bays in Texas.

There are some examples of marginal oyster communities which are worthy of notice. In parts of coastal Louisiana, especially in the vicinity of Atchafalaya Bay and Marsh Island, oyster reefs in the bays have been reduced by invasion of fresh water, and salinity conditions suitable for the development of reefs are found in the Gulf itself. At the other extreme, a small oyster community persists near Port Isabel where salinities are nearly oceanic most of the year, and the epifauna is characteristically marine (Hedgpeth 1953).

Since the reefs south of Marsh Island were mapped in 1906 by Cary, there seems to have been little change in their extent, and they remain the only extensive oyster reefs known in the Gulf of Mexico proper. From time to time there have been rumors of large reefs in offshore waters, but these rumors seem to be kin to those of fabulous lost mines which can never be found.

Clam beds have been reported for various places, but none have been studied. The low-salinity *Rangia* forms extensive beds in Louisiana and brackish lakes of Texas as far south as Green Lake. Extensive worm communities probably exist, in view of the great shrimp populations, but none have been studied in detail. We have only recently begun to learn which species of worms occur (Hartman 1951). Beds of *Spiochaetopterus* have been observed in Louisiana. The only study of clam beds is that of Spaulding (1906) who worked out the distribution of clams and scallops in the Chandeleur Islands (fig. 53).

Investigations of bottom communities in Texas and Louisiana are now being conducted as part of a study of the nearshore Recent sediments. This project is sponsored by the American Petroleum Institute (Shepard and Moody, 1952). The

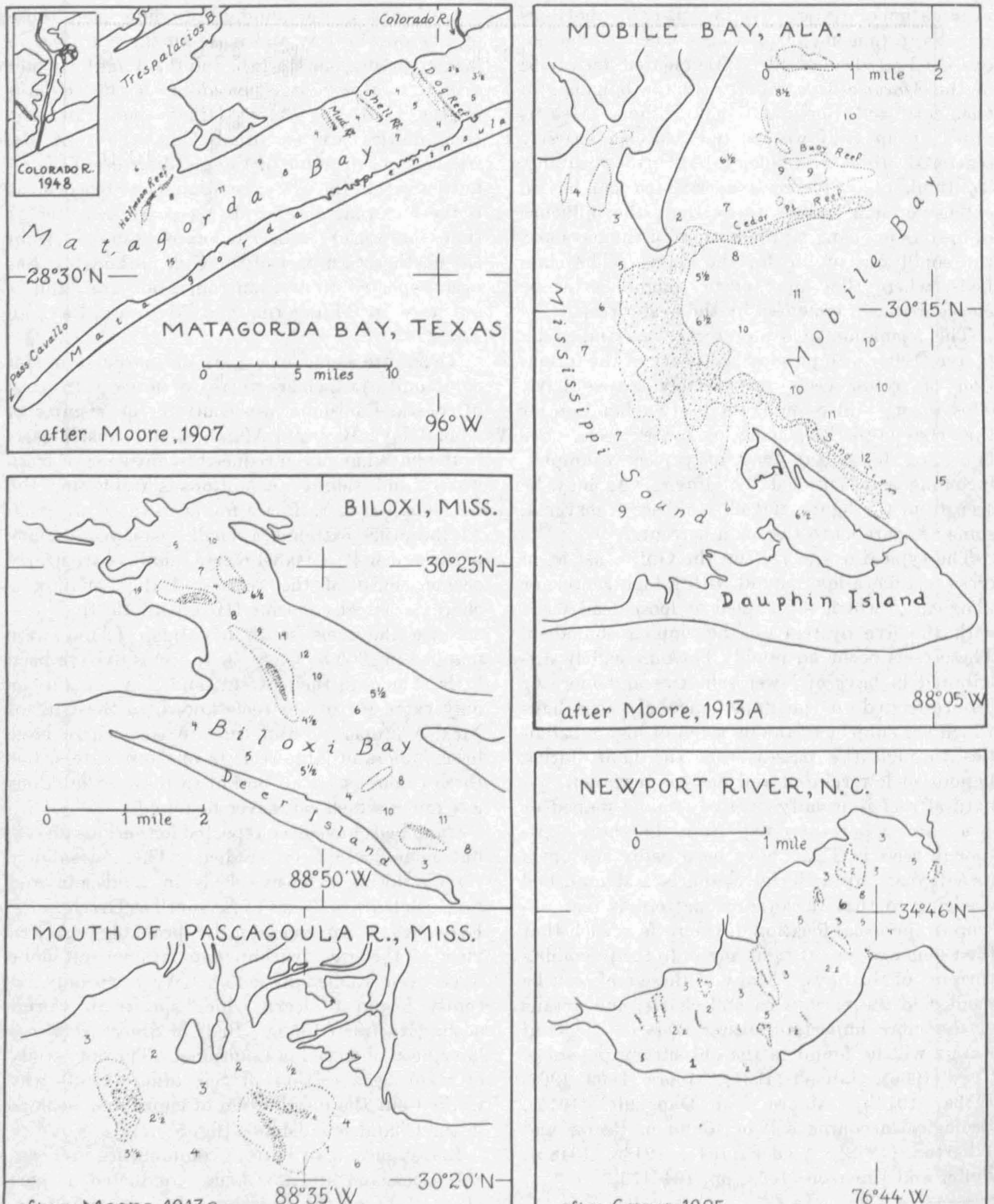

FIGURE 52.—Characteristic Gulf coast oyster reefs from various survey reports as indicated, together with those of Newport River, North Carolina.

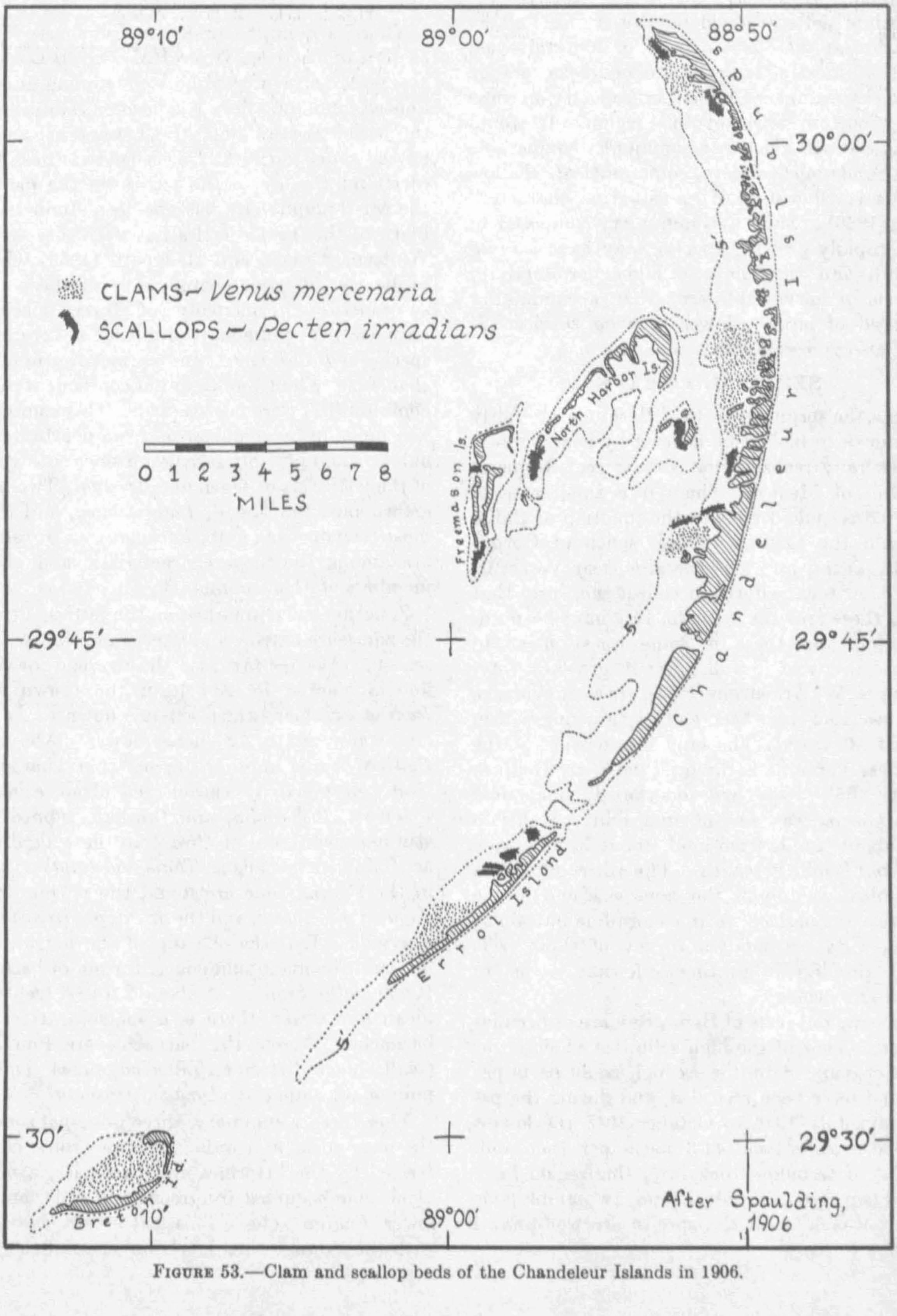

FIGURE 53.—Clam and scallop beds of the Chandeleur Islands in 1906.

preliminary results of the work east of the Mississippi delta (carried out by R. H. Parker) indicate that there is a density of 100 individual mollusks (mostly *Mulinia lateralis*) per orange peel bucket sample of 100 cu. in. capacity on some muddy bottom areas in this region. It would appear that we have here a community comparable to the *Syndosmya* (=*Abra*) community of "shallow and protected waters of an estuarine character" (Jones 1950). Such a community, composed of small, rapidly growing species, may have a rapid overturn and thus have a higher productivity in terms of harvestable crop than a community composed of larger, slower growing species. It would also be less stable.

SERPULOID REEFS

While the serpuloid reefs of Bermuda are fairly well-known to biologists, at least by hearsay, it is not generally realized that similar reefs occur in the Gulf of Mexico. There is a small area of scattered serpuloid reefs at the junction of Baffin Bay and the Laguna Madre, south of Corpus Christi, Texas, and a larger area near Veracruz, Mexico. Recent efforts to collect the worm that caused these growths in Baffin Bay have been unsuccessful, and there is some question as to whether this reef is still actively growing. According to W. Armstrong Price, there is evidence that these reefs had been actively growing within the last 80 years. The only information of the reefs near Veracruz is the brief paper by Heilprin (1890). Two reefs are mentioned; one, near Punta Gorda, was, at the time, lying parallel to shore about ⅛ mile from land, about 3/16 mile wide and about ⅝ mile in length. The other, off Punta de Hornos, was about the same size and in the same relative position to the shore line but about half as wide. A modern survey of these reefs should provide interesting information as to growth and ecology.

The serpuloid reefs of Baffin Bay are of peculiar interest in view of the high salinities which occur in this region. Salinities as high as 80 parts per thousand have been recorded, and during the period from July 1946 to October 1948 the lowest recorded salinity was 41.6 parts per thousand. Samples of serpuloid rock from this region have yielded two species of polychaetes, two amphipods and a barnacle. All the species are well-known estuarine forms.

THE JETTY COMMUNITY

There are no naturally rocky shores in the eastern or northern Gulf of Mexico, hence, there are no extensive hard-bottom communities. A limited fauna and flora has become established on the various jetties along the Texas coast and also on the short jetties at Calcasieu Pass near Cameron, but the life of the jetties on the passes of the Mississippi Delta has not been studied. The biota of the Texas jetties has been discussed by Whitten, Rosene, and Hedgpeth (1950) who describe the intertidal community of these jetties as consisting principally of three species of barnacles, a pulmonate limpet, a littorine, a species of *Brachidontes*, and various less numerous elements. Plants, an essential component of such communities, were not studied. This community was built up by colonization from nearby bottom habitats and possibly sargassum since construction of the jetties six or seven decades ago. Two motile arthropods, the isopod, *Ligia exotica*, and the almost cosmopolitan crab, *Pachygrapsus transversus*, are among the most characteristic and obvious members of this community.

Zonation is well-marked on the jetties, although the zones are narrow and vary somewhat with the season. At Port Aransas the average low-water line is marked by a belt of the brown algae, *Padina vickersae*, which extends down to extreme low water, 8 to 12 inches lower. Above the *Padina* belt is another narrow zone characteristically occupied by various red algae, especially *Gelidium*, *Bryocladia*, and the like, topped by a still narrower band of *Ulva*. In these algal zones are found such snails as *Thais* and *Cantharus*, and in the *Padina* zone are found the purple urchin, *Arbacia punctulata*, and the anemone, *Bunodosoma cavernata*. Between the top of the narrow *Ulva* belt and the maximum concentration of barnacles (*Chthamalus fragilis*) at about 2.5 to 3 feet above mean low water, there is a sparse scattering of barnacles. Above the barnacles are found the small, black littorine, *Littorina ziczac*, and the pulmonate limpet, *Siphonaria pectinata*.

There are, in summary, three principal zones on the jetty rocks and walls: an upper zone, characterized by the littorines and barnacles, a middle algal zone occupied by greens and reds, and the lower *Padina* zone. This pattern is associated with the average tidal levels for most of the year.

During the periods of lower mean sea level in January and February, the lowermost zone, below the brown algae, is exposed. This zone consists of hydroids, Bryozoa, and encrusting sponges. Inshore, near land and on concrete pilings at Port Aransas, the middle zone is also occupied by oysters. Mussels do not occur at Port Aransas but are found at Freeport and Galveston on the jetties.

Although not occurring in the Gulf of Mexico proper, the zonation in the Florida Keys and at Beaufort described by the Stephensons (1949, 1950, 1952) have aspects in common with that at Port Aransas. The most conspicuous difference is the generally lower arrangement of the entire zonal pattern at Port Aransas in relation to tide zero, a phenomenon apparently associated with the pronounced seasonal differences in sea level on the Texas coast (fig. 54) and the higher level of the tide zero in relation to the tidal cycle.

There is a tendency toward the formation of sub-zones in Texas and Florida which may be induced by irregular tidal cycles; this complex pattern seems much less developed at Beaufort, where the tidal cycle is more regular (Hedgpeth 1953, pp. 188–194).

SAND BEACH COMMUNITIES

The communities of the sand beaches are evidently similar to those of the Beaufort area which were studied by Pearse, Humm, and Wharton (1942) since many of the same species, or closely related species, occur on the sandy beaches of Texas and Louisiana. LaFleur (1940) briefly described the biota of sand beaches of Grand Isle. Neither of these are studies of communities, in the strict sense of the term. The most noticeable bottom community of the sandy beach is that of *Donax* which occurs in large beds, moving up and down with the tides. Immediately offshore there are evidently large communities composed of such bivalves as *Dinocardium robustum*, *Arca* and *Anadara*, *Dosinia* and *Tellina*, predaceous gastropods, and such echinoderms as *Mellita* and *Astropecten*. This assemblage appears to be a counterpart of the sandy-bottom *Tellina* community of European waters.

The characteristic inhabitant of the sand beach is the ghost crab, *Ocypode albicans*, which seeks refuge during daylight hours in burrows well above high tide lines. Beyond this region, at Port Isabel and in southern Florida, there occurs the larger land crab, *Cardisoma guanhumi*. Occasional individuals are found at Port Aransas, but established colonies of them are unknown north of Port Isabel except at Grand Isle (Behre 1950). Lower down on the beach, associated with the windrows of algae (sargassum in spring and summer and various reds in winter) are the amphipods, *Orchestia grillus*, *O. platensis*, and *Talorchestia longicornis*.

Intensive study of the animal life of this most characteristic of Gulf coast environments has hardly begun. Caspers (1951), in a study of the arthropods of the Bulgarian coast, characterized the community of the sandy beaches as the "*Orchestia* variation of the *Pachygrapsus* biocoenosis." From the vantage point of the Texas coast where *Pachygrapsus* seems most abundant on the jetties and the sand constitutes the major part of the environment, we might say that *Pachygrapsus* is a "variation" of the "*Orchestia* (or *Ocypode*) biocoenosis."

THE SHRIMP GROUND COMMUNITY

Offshore in the muddy bottoms between the foot of the sandy beach and the 10- to 15-fathom line there occurs a large community which we recognize principally as that from which white shrimp, *Penaeus setiferus*, are taken in commercial quantities. Several sedentary invertebrates are characteristic of these bottoms. The most conspicuous of these is the sea pansy, *Renilla mülleri*, which must pave the bottom in some localities. A gorgonian, *Leptogorgia setacea*, also flourishes in this region. Other characteristic members of this shrimp ground community include tube building worms of the family Onuphidae, crabs of the genera *Hepatus*, *Calappa*, and *Persephone*, the anemone, *Paranthus rapiformis*, and certain gastropods, e. g., *Busycon*, *Murex*, *Dolium*, and *Fasciolaria*. In the larger abandoned shells of these snails there occurs the large red hermit crab, *Petrochirus bahamensis*. Usually the shells bear one or more anemones, *Calliactis tricolor*, and inside, living commensally with the hermit crab, is the porcelain crab, *Porcellana sayana*. Also common, but perhaps occurring in irregular colonies, is the stomatopod, *Squilla empusa*.

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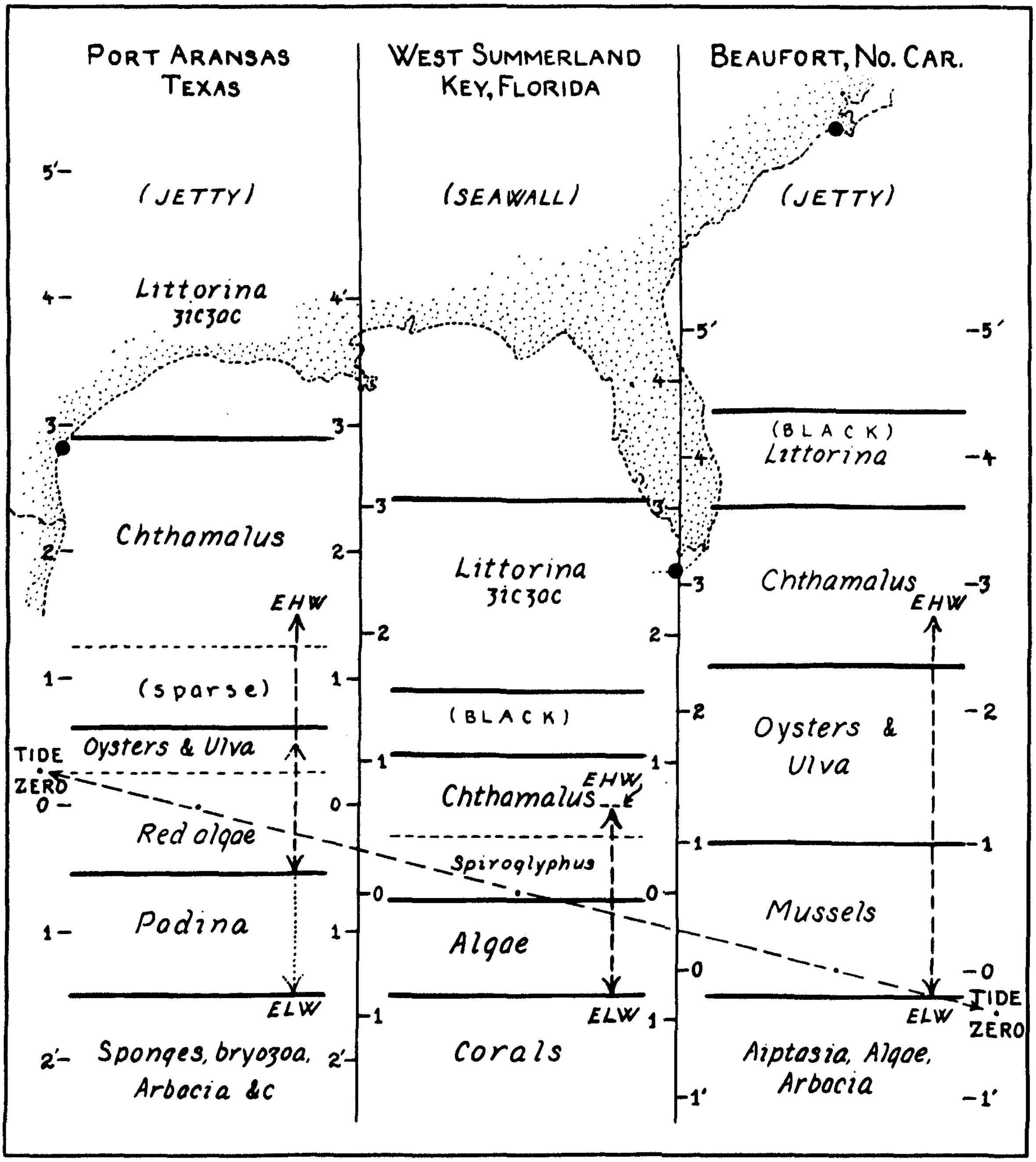

FIGURE 54.—Pattern of distribution of organisms on jetties and sea wall in Port Aransas, Texas, West Summerland Key, Florida, and Beaufort, North Carolina.

The preceding description applies principally to the grounds frequented by the commercial shrimp, *Penaeus setiferus*. The recent change in the shrimp fishery toward exploitation of the populations of the brown or grooved shrimp, *P. aztecus*, has revealed some differences in the constitution of the bottom communities frequented by *P. aztecus*. *Renilla* is no longer characteristic, but one of the *Astropectens* is abundant, and two bivalves, *Pitaria cordata* and *Chione clenchi*, are much more abundant than they are closer inshore on the *P. setiferus* grounds. The principal region occupied by the pink shrimp, *P. duorarum*, is near Key West across the Strait from Campeche Bank (fig. 51), the fauna of which is predominantly tropical in character.

The communities which support penaeid shrimp appear to have no counterpart in European waters, but similar communities evidently occur in waters of southeastern Asia and along the western coast of Central America. It is worthy of note that the commercial fishery of shrimp is one of the few major fisheries drawing upon an annual (or perhaps biennial) production and is thus more dependent on the short term production of bottom fauna and short-term secular changes in the environment than are the fisheries which exploit organisms that have required several years to reach marketable size.

THE CORAL AND SPONGE COMMUNITIES

These are tropical, stenohaline communities, rich in number of species and difficult to characterize except in terms of their dominant members. The reef-building coral is a true community dominant, shaping the community and altering the environment. The small reefs or patches along the Texas and Louisiana coast are peculiar northern fragments of the West Indian reefs. Their position is governed primarily by the occurrence of small elevations along the edge of the continental shelf which rise to within 10 to 25 fathoms of the surface rather than by temperature or sedimentation conditions. These elevations may indicate dome structures. It can be inferred from the presence of these living reefs that the mean temperatures do not fall below 20° C. along the summits of these structures. There are rare records of tropical reef animals, especially decapod Crustacea, along the Texas coast indicating that these reefs have the usual West Indian tropical fauna and that a certain amount of straying, especially during the summer months, occurs. More information concerning the sponge and coral communities of western Florida will be found in other parts of this volume.

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