CHAPTER VI

BACTERIA, FUNGI, AND UNICELLULAR ALGAE

MARINE BACTERIA AND FUNGI IN THE GULF OF MEXICO[1]

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Although the marine environment around the West Indies was one of the first to be examined by a bacteriologist (Fischer 1886) and has since been quite extensively studied (Drew 1912; Bavendamm 1932), there are very few published reports on bacteria and fungi in the nearby Gulf of Mexico. The author has been actively interested in the Gulf coast area since 1940, but the semiconfidential nature of the research projects has contraindicated the publication of the results. This paper summarizes personal observations in the region along with published reports that have a direct bearing upon microbiological conditions in the Gulf of Mexico where observations have been confined almost exclusively to regions near shore. The rather extensive but scattered literature on marine microbiology has been reviewed by Issatchenko (1914), Bavendamm (1932), Benecke (1933), ZoBell and Upham (1944), and ZoBell (1946a, 1947). Also noteworthy is the comprehensive article by Williams (1951) on the occurrence, importance, and characteristics of bacteria in the sea.

Waters of the littoral zone in the Gulf of Mexico are veritable bacterial gardens. At scattered stations from Tortugas to Aransas Pass, where water samples have been examined, bacterial populations ranging from thousands to many million per ml. have been observed. Large numbers of living bacteria have also been found in bottom sediments. The methods employed by various investigators for collecting and analyzing samples of water and marine sediments for numbers and kinds of bacteria have been summarized by ZoBell (1946a).

The abundance of bacteria in shallow Gulf waters, which greatly exceeds the abundance of bacteria in the open ocean, is believed to be attributable primarily to the higher content in the former of organic matter and suspended solids, both of which promote the growth of bacteria. The influx of fresh water with its load of organic nutrients from land drainage is also a contributing factor along the littoral zone. Here there is a commingling of both fresh-water and marine microorganisms and numerous transitional stages of both kinds. The observations of Berkeley (1919), Korinek (1926), Lipman (1926), Burke and Baird (1931), ZoBell and Feltham (1933), Burke (1934), and others indicate that ordinarily bacteria from fresh-water or terrestrial sources do not survive very long in sea water, but if the transition to the salt-water environment is gradual, as in brackish water of increasing salinity, a good many fresh-water forms may become acclimated to the marine environment (ZoBell and Michener 1938).

The bacterial flora of the Gulf coast region is characterized by exceptional biochemical versatility, cultures having been isolated that catalyze the transformation of virtually all types of organic matter and a good many inorganic substances. In the latter category are autotrophic bacteria of various kinds that oxidize hydrogen sulfide either in darkness or under the influence of sunlight (van Niel 1931, 1944). Autotrophs which oxidize ammonia to nitrite appear to be more common in surface water and sediment than those which oxidize nitrite to nitrate (Carey 1938). Methane oxidizers (Hutton and ZoBell 1949) were found in the topmost portions of mud samples from the Gulf coast region, and sulfate-reducing bacteria which oxidize molecular hydrogen as the sole source of energy were found in numerous samples from considerable depth (Sisler and ZoBell 1950).

Besides modifying inorganic substances, autotrophic bacteria are primary producers of organic matter. While some obtain their energy from sunlight in the manner of other photosynthetic plants, most autotrophic bacteria obtain their energy for the reduction of carbon dioxide from the oxidation of substances such as hydrogen sulfide, hydrogen, methane, ammonia, or nitrite.

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Quantitative data on the relative amounts of organic matter synthesized by autotrophic bacteria are not available, but judging from the abundance of such bacteria and the quantities of ammonia, hydrogen, methane, or other substance believed to be oxidized, organic production from this source may be appreciable.

The chief function, however, of bacteria in the marine environment is in the mineralization or modification of organic matter (Waksman 1934). Among the organic materials found to be attacked by marine micro-organisms are sugars, starches, celluloses (Bavendamm 1932; Waksman et al., 1933), pectins, glucosides, fatty acids (Thayer 1931), triglycerides, alcohols, sterols, proteins, amino acids, chitins (Hock 1940), lignins, agar (Stanier 1941; Humm 1946), and hydrocarbons (ZoBell 1950a). These organic substances are attacked by both aerobic and anaerobic bacteria.

From Gulf of Mexico mud, Campbell and Williams (1951) isolated 20 strains of aerobic chitin-decomposing bacteria, including species of *Achromobacter*, *Flavobacterium*, *Micrococcus*, and *Pseudomonas*. Several of the cultures were actively proteolytic and/or lipolytic.

Mixed cultures from marine mud tend to decompose the organic remains of plants and animals (Waksman 1934) in aerobic environments with the formation of carbon dioxide, ammonia, sulfate, phosphate, and other oxidation products at a rate which is primarily a function of the temperature. In the absence of free oxygen the rate at which organic matter is modified by bacteria may be much slower, and, while there may be much mineralization of organic substances, in anaerobic environments certain constituents may be reduced or hydrogenated to form the mother substance of petroleum (ZoBell 1950b).

The action of heterotrophic bacteria is not confined to the decomposition of particulate organic materials. Dissolved organic matter is also utilized, it having been shown by ZoBell and Grant (1943) that under static conditions bacteria may reduce the organic content of sea water to less than 0.1 mgm./L. According to Waksman and Carey (1935), roughly 60 percent of the organic carbon is oxidized by aerobes to carbon dioxide and the remaining 40 percent is assimilated for conversion into bacterial protoplasm. The latter, being particulate, becomes available as a source of food for protozoa, copepods, filter feeders, detritus feeders, and grazing animals in general.

Krizencky and Podhradsky (1927) regard the conversion of dissolved organic matter into particulate matter utilizable by animals as one of the most important functions of bacteria in aquatic environments. The importance of bacteria as food for animals has been emphasized by the work of Baier (1935), MacGinitie (1935), Voroschilova and Dianova (1937), Mare (1942), and ZoBell and Feltham (1938). The latter workers (1942) estimated that around 10 grams (dry weight) of bacterial organic matter is produced per day per cubic foot of mud in a shallow marine mud flat. In summarizing the ecological function of bacteria on sand beaches, Pearse et al. (1942) point out that besides serving as food for small animals, bacteria are important scavengers, and they produce plant nutrients, including ammonia, nitrite, nitrate, and phosphate. From thousands to millions of living bacteria were found in beach sands at Beaufort, North Carolina.

Large numbers of bacteria were found by Williams et al. (1952), to be associated with the bay shrimp, *Penaeus setiferus*, taken from Aransas Bay and from the Gulf in the region of Galveston. Species of *Achromobacter*, *Bacillus*, *Micrococcus*, *Pseudomonas*, *Alcaligenes*, and *Flavobacterium* predominated in the order named. Most of the attached bacteria were carried by the cephlothorax portion of the shrimp. The optimum temperature for the growth of the bacteria was around 25° C., but most of the 1,200 cultures examined grew slowly at 4° C. Neither coliforms nor enterococci were detected by Williams and Rees (1952) in the intestinal tract of shrimp, suggesting that such bacteria have sanitary significance.

Another important function of bacteria is as symbionts in the alimentary canal of most marine animals where they aid in the digestion of chitin, cellulose, pectin, lignin, and other organic complexes. Similarly, certain shipworms and wood borers are believed to depend upon commensal bacteria which help to digest cellulose and lignin.

On the other hand, a small percentage of the microbial flora is pathogenic for plants or animals. Fish, Crustacea, shellfish, and other marine animals in nearly all stages of development may be susceptible to microbial infections; the pertinent literature on this subject has been annotated by ZoBell (1946a). Seaweeds, diatoms, dinoflagellates, and other marine plants may be extensively parasitized by pathogenic bacteria, actinomyces, yeasts, and mold fungi. The wasting disease of eelgrass, which threatened the extermination of *Zostera marina* along the Atlantic seacoast a few years ago, is believed to be due to infection by *Labyrinthula* species (Renn 1936), although *Halophiobolus* species may also be involved (Barghoorn and Linder, 1944).

By vitiating the water in local environments or in the wake of periods of intense organic productivity, bacteria may have far-reaching adverse effects on the plant and animal populations. Among the ways in which bacteria contribute to the vitiation of aquatic environments are by depleting dissolved oxygen, by producing hydrogen sulfide, by forming toxic amines, or by changing the pH of the water. So-called stagnant water basins are rendered uninhabitable primarily by the activities of bacteria, and extensive areas in the open ocean may become temporarily lethal for plants or animals. For example, Copenhagen (1934) described an area approximately 25 by 200 miles in the Atlantic Ocean off Walvis Bay, South Africa, where hydrogen sulfide is liberated periodically by bacterial activity in quantities sufficient to kill both flora and fauna. The bacterial vitiation of water is believed by the writer to be an important feature of the "red tide." Extensive populations of purple sulfur bacteria, observed by Gietzen (1931) growing associated with decomposing algae along the Holstein coast, imparted a distinctly red coloration to the sea.

Marine bacteria also contribute to the biofouling of man-made structures. The attachment and growth of barnacles, bryozoans, tunicates, mussels, clams, algae, and other fouling organisms on ships' bottoms or other submerged surfaces may be promoted by bacteria in various ways (ZoBell and Allen 1935). Likewise, micro-organisms may contribute either directly or indirectly to the deterioration of pilings, planks, and other wooden structures in sea water. Lines, ropes, nets, seines, sailcloth, and other cordage or textile products readily rot in sea water unless they are treated to preserve them from microbial decomposition (Atkins and Warren 1941). Unprotected steel and iron structures are also susceptible to attack by bacteria which oxidize ferrous iron, produce acids, form hydrogen sulfide, create reducing conditions, or depolarize hydrogen films resulting from the reaction between water and iron. Acid production in microspheres from the bacterial oxidation of organic matter or sulfur may result in the corrosion of concrete. Even rubber and bituminous coating materials may be attacked by marine micro-organisms (ZoBell 1950a).

Bacteria are important chemical and geological agents in marine bottom deposits where they promote many processes involving organic compounds, inorganic constituents, and physicochemical conditions that affect the modification or diagenesis of sediments. One of the first geochemical processes to be studied by microbiologists was calcium carbonate precipitation which Drew (1911a, b) attributed to the activities of denitrifying bacteria found in great abundance in shallow subtropical seas in the vicinity of Jamaica and Tortugas. He (1912) reported that marine mud near the Bahamas contained an average of 160 million bacteria per ml. with *Bacillus calcis* predominating. Working in the same region, Kellerman and Smith (1914) confirmed Drew's hypothesis on the precipitation of calcium carbonate by bacteria which raise the pH by reducing nitrate, by producing ammonia, or by utilizing organic acids.

After finding rather sparse bacterial populations in the open sea around Tortugas, Lipman (1929) questioned whether bacteria contribute significantly to calcium carbonate precipitation. This view was rendered untenable, however, by the extensive observations in the Bahamas of Bavendamm (1932) who concluded that calcium carbonate precipitation in tropical seas is primarily a microbiological process. Similar conclusions were reached by Gee (1932) who investigated bacterial activity in the Florida Keys. Micro-organisms found there by Gee and Feltham (1932) promoted the precipitation of calcium carbonate by producing ammonia and otherwise increasing the pH.

The pH of marine sediments may be increased by micro-organisms which (1) form ammonia, (2) reduce nitrate or nitrite, (3) reduce sulfate, (4) oxidize or decarboxylate organic acids, or (5) utilize CO_2. On the other hand, the (1) production of CO_2 or organic acids, (2) oxidation of hydrogen sulfide or sulfur, (3) formation of nitrate, (4) assimilation of ammonia, or (5) the liberation of phosphate from organic compounds are microbial processes that tend to decrease the pH of their environment. Reactions ranging from pH 6.8 to 8.7 in Gulf coast sediments are believed to be attributable, at least in part, to microbial activities. Similarly, bacteria and allied microorganisms are believed to be the principal dynamic agencies that create conditions in marine sediments sometimes as reducing as $E_h - 460$ millivolts (ZoBell 1946b).

The general tendency is for micro-organisms to mineralize the organic remains of plants and animals in marine sediments. In highly reducing environments, however, the microbial decomposition of organic matter may result in residues relatively richer in hydrogen and correspondingly poorer in oxygen, nitrogen, sulfur, and phosphorus. This results in the accumulation of organic complexes that are more petroleum-like than their predecessors (ZoBell 1950b). The microbial formation of methane is a common property of recent marine sediments, and there is pretty good evidence that bacteria also produce higher hydrocarbons. While there is no reason to believe that bacteria produce petroleum, they may contribute in many ways to its formation. The high organic productivity and rapid rate of sedimentation in Gulf coast waters suggest this region as a potential source bed of petroleum.

Petroleum hydrocarbons may be modified in recent sediments by micro-organisms. Both aerobic and anaerobic bacteria which attack petroleum hydrocarbons were detected in nearly all 1-gram samples of surface mud collected from shallow water along the coasts of Louisiana and Texas. From hundreds to millions of such micro-organisms per gram of mud were demonstrated by the minimum dilution method.

Sulfate-reducing bacteria were also found in abundance, some at core depths exceeding a hundred feet. Sulfate reducers form hydrogen sulfide, and they may account for the formation of sulfur. The recovery of sulfate reducers having unique tolerance for temperature, salinity, and hydrostatic pressure from oil and sulfur wells suggests that they may be indigenous species in ancient marine sediments (ZoBell and Rittenberg 1948). A large percentage of the sulfate reducers isolated from Gulf coast sediments can utilize molecular hydrogen (Sisler and ZoBell 1950).

Several other physiological types of bacteria, that may function as geochemical agents, have been found in marine sediments, but their importance can be assessed only after they have been more thoroughly studied.

Marine fungi, including yeasts and molds, are found almost exclusively in water and the topmost layers of sediment. Being heterotrophs, such fungi are closely associated with organic substances. Both yeasts and molds commonly occur growing either saprophytically or parasitically on marine plants and animals. According to Sparrow (1936), who isolated 18 new species of mold fungi from the Woods Hole region, marine fungi have been even less completely studied than marine bacteria. Barghoorn and Linder (1944) were impressed by the diversity of fungi found in the sea. A good many of the fungi species isolated from the sea are quite unlike any known terrestrial species. They grew better in sea water than in corresponding fresh water media, and some species developed in media containing three times as much salt as normal sea water.

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DINOFLAGELLATES OF THE GULF OF MEXICO

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Dinoflagellates are important in the natural economy of the Gulf of Mexico as they are in all waters of the world. In marine phytoplankton they are usually outnumbered by diatoms, but they are second in importance to the diatoms as fundamental synthesizers of organic material in the sea. On the other hand, to the dinoflagellates belong most of the organisms which cause "red water," mass mortality of marine organisms, and paralytic shellfish poisoning. A thorough knowledge of the dinoflagellates is necessary to a clear understanding of the basic biology of the Gulf of Mexico.

Despite the importance of these organisms, the Gulf of Mexico is almost a terra incognita in respect to our knowledge of the dinoflagellate plankton. Very few oceanographic expeditions have included the Gulf in their itinerary, and those that visited the Gulf have not reported on any dinoflagellate collections.

Many species of dinoflagellates have a worldwide distribution, especially the offshore forms. Many of these can be expected in the Gulf. It is very likely that the pelagic species of the Gulf will be found to be similar to those of the tropical Atlantic, although the general composition of the flora may be different. The inshore, or neritic, plankton may well contain species peculiar to or at least characteristic of the Gulf of Mexico or of certain areas of the coast line. The dinoflagellate fauna of the open Gulf is very likely quite similar to that of the Caribbean and the tropical Atlantic.

As far as the dinoflagellates are concerned, there are three general habitats in the Gulf of Mexico: the offshore waters, the neritic waters, and the sandy beaches.

The offshore waters of the Gulf are clear and blue, characteristic of tropical waters the world over. Surface temperatures are high, the concentration of nutrients is low, and the salinity high throughout the year. The quantity of plankton in these waters (the standing crop) is low (Riley 1938), but the number of species is probably relatively high. The temperature of this water drops markedly in the northern part of the Gulf for a few weeks during the winter, but as far as we know there is no seasonal change in the dinoflagellate fauna during this period.

The neritic waters may be considered to include the shallow periphery of the open Gulf in which the water is often of very high temperature, with variable salinity and nutrient content and in which wind mixing creates high turbidity, particularly in the winter when the density of the water is uniform from surface to bottom. The bays, bayous, and lagoons are also within this zone. These include mangrove swamps and other brackish water areas. Tidal effects are strong in the neritic zone, and the physical and chemical conditions of the water vary greatly throughout the year and, in some cases, within a daily tidal cycle. As a general rule, the species of dinoflagellates found in the neritic zone are distinct from those in open waters. However, the invasion of the coastal area with open Gulf water frequently obscures the zonation.

Sandy beaches in the intertidal zone constitute the third type of environment for the Gulf dinoflagellates. Certain specialized species belonging chiefly to the genus *Amphidinium* thrive in this situation in some parts of the world (Herdman 1924) causing discoloration of the sand and luminescence. When they are abundant, each kick of the heel at night on a wet, sandy beach will cause a flash of light. There are apparently no reports of such "dinoflagellate sand" for the Gulf coast, but a careful investigation of this zone might reveal a rich fauna.

Interest in the dinoflagellates of the Gulf, particularly along the west coast of Florida, was stimulated by the disastrous outbreaks of red tide which occurred in that area in 1946 and 1947 (Galtsoff, 1948; Gunter et al., 1948; Gunter, Smith, and Williams, 1947; Smith 1949). This red water was caused by a previously undescribed species, *Gymnodinium brevis* Davis (1948). The study of the causes of these outbreaks was hampered by the lack of previous work in the area. As a consequence, the Marine Laboratory of the University of Miami and the Fish and Wildlife Service of the United States Department of the Interior initiated a study of the local plankton in order to gain some information regarding the causes of such plankton blooms. In the course of these studies some insight was gained of the normal dinoflagellate plankton along the west coast of Florida.

Davis (1950) reported upon a number of plankton samples collected there in 1947 and 1948. He listed 15 species of dinoflagellates.

He stated that the plankton of the west coast of Florida is markedly different from that of the east coast of Florida. Species found only on the west coast included the dinoflagellates, *G. brevis* and *Noctiluca scintillans* Macartney, which were found both inshore and offshore. In addition, a number of plankters were found only in the open waters of the Gulf. These included *Ceratocorys horrida* Stein.

Some species were found only in open waters but on both coasts. This group consisted of *Ceratium candelabrum* (Ehr.) Stein, *Pyrocystis fusiformis* W. Thomson, and *P. noctiluca* Murray. Occasionally, the open water species were found inshore. Davis interpreted this as indicating an admixture of open water with the inshore water. Davis and Williams (1950) listed seven species from brackish water in mangrove areas of southern Florida.

King (1950) listed 19 species of dinoflagellates from the west coast of Florida in a series of samples extending from inshore bays to a distance of 120 miles offshore and collected over a period of 10 months in 1949. About 10 of these species were not listed by Davis or Davis and Williams.

Additional species have been found by John Howell, biologist, Fish and Wildlife Service (unpublished data), along the west coast of Florida. *Ceratium pentagonum* Gourret occurred only at stations more than 30 miles offshore. A species of *Pyrocystis* (*Gymnodinium*) was present only offshore except in one sample. In a study of samples collected throughout the year Howell found the most commonly occurring species of dinoflagellates to be *Ceratium furca* (Ehr.) Dujardin and *C. tripos* (O. F. Muller) Nitzsch. Next in order of occurrence were *C. macroceros* (Ehr.) Vanhoffen, *C. fusus* (Ehr.) Dujardin, *C. trichoceros* (Ehr.) Kofoid, *C. massilliense* (Gour.) Jörgensen *Peridinium depressum* Bailey, and *Dinophysis caudata* Saville-Kent. All of these appear to occur inshore as well as in the offshore waters of the Gulf. However, a more intensive study of the distribution of dinoflagellates along the coast may bring out more zonation than is at present apparent. The situation is complicated by the fact that typical open Gulf water with high salinity, low nutrient content, etc., sometimes extends up to the beach and, indeed, is carried into the bays by tidal action.

Howell found 11 species not reported by Davis or King. In addition to those listed above, there were 4 species of *Ceratium: C. carriense* Gourret, *C. horridum* Gran., *C. falcatum* (Kof.) Jörgensen, *C. praelongum* (Lem.) Kofoid. The last-named was found only once and is typical of a large number of very rare species which may be expected to be found occasionally in the open Gulf waters if any extensive investigation of these waters is made.

Other rare species found by Howell were *Pyrocystis hamulus* Cleve, *Pyrophacus horologicum* Stein, *Amphisolenia* sp., *Goniodoma* sp., and *Ornithocercus quadratus* Schütt. In a laboratory culture of Florida west coast water *Oxyrrhis marina* Dujardin flourished, and a large population developed.

Despite the richness of the dinoflagellate fauna in the Gulf, the actual concentration in terms of populations is normally very low. The concentration of dinoflagellates in numbers of cells per liter of sea water is usually less than 50 in the waters along the west coast of Florida. Yet, under unusual conditions which are still not clearly understood, a particular species may increase to enormous concentrations and cause serious disruption of the normal biological balance in the area involved.

Thus, in the Florida red tide of 1946 and 1947 the concentrations of *Gymnodinium brevis* Davis reached 60 million cells per liter (Davis 1948). These enormous concentrations cause the water to turn color, usually a brownish red, producing what is commonly called "red water" or "red tide."[1] Such concentrations of dinoflaggellates are frequently accompanied by the death of fish

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[1] Red tide in the Gulf of Mexico waters is discussed in an article by R. Lasker and F. G. Walton Smith pp. 173-176.

and other marine animals. There is every reason to believe that many species of dinoflagellates elaborate an extremely potent toxin either normally or under the conditions of population crowding. The two blooms cited above were associated with serious "fish kills" and death of much of the marine life in the area.

The presence of even normal numbers of dinoflagellates in the water may cause shellfish to become unfit for human consumption. Thus, regularly during the summer months the California sea mussel (*Mytilus californianus*) is likely to be lethal to humans when *Gonyaulax catenella* Whedon & Kofoid is abundant in the coastal water (Sommer et al., 1937), and the clams in certain areas of the Bay of Fundy are regularly toxic when *Gonyaulax tamarensis* Lebour occurs in the plankton (Medcof et al., 1947). Paralytic shellfish poisoning caused by eating such toxic shellfish has not been reported from the Gulf of Mexico. Connell and Cross (1950) found a dinoflagellate resembling *Gonyaulax catenella* associated with the death of fish in Offatts Bayou, an inlet of Galveston Bay, in 1949. Unfortunately, no specific identification of this organism was made. There is also strong evidence that the fish kills which regularly occur in Offatts Bayou are generally caused by the production of hydrogen sulfide or to suffocation due to stagnant conditions at the inner end of the inlet (Gunter 1942, 1951) rather than by a dinoflagellate bloom.

Toxic red water such as occurs regularly in the pearl oyster beds in Japan (Mitsukuri 1904) could be disastrous to the vast oyster industry in the Gulf, but apparently the Gulf oysters have been spared any such visitation so far.

Reports of red water on Campeche Banks, off Yucatán, are made occasionally by fishermen in that area, but to date it has not been possible to ascertain the causative agent. It is quite possible that a dinoflagellate is involved.

One of the great difficulties in dinoflagellate research is the fragility of the naked forms. Many of these are almost impossible to preserve but must be studied alive under the microscope. This feature might not be serious if the organisms were easily cultured, but they are notoriously difficult to grow in the laboratory. The classical monograph of the unarmored dinoflagellates by Kofoid and Swezy (1921) was based largely on examination of living specimens which regularly dissolved before the eyes of the workers as they studied them. The Florida red tide was caused by such a naked form, *G. brevis*, which does not preserve in formalin. Special fixatives such as Bouin's solution and Schaudinn's solution do preserve some of these species but not without distortion.

However, a rich fauna of unarmored forms is not normally present inshore at Sarasota, Florida, where the workers of the Fish and Wildlife Service laboratory in their search for *G. brevis* have examined living material for 2 years and failed to reveal any *G. brevis*. They found only three other species of unarmored dinoflagellates. More work in other areas must be conducted before this problem can be solved.

The difficulty in making specific identification of dinoflagellates has lead to a paucity of records of these interesting and important organisms. Painstaking microscopic work on the part of a specialist is necessary for the differentiation of many species, even of the thecate forms which preserve well.

In these species, an analysis of the plate pattern is necessary for identification. Few general planktologists have either the time or training to pursue this kind of work which involves difficult micro-orientation and dissection. Concentrated study by a number of specialists for a considerable period of time will be necessary before the dinoflagellate plankton of the Gulf will be adequately revealed to science.

Since most of the pelagic tropical species of dinoflagellates are worldwide in distribution, published works for other areas can be used for a study of the Gulf fauna. The most important of these are listed in the bibliography. Lebour's (1925) work is designed for northern seas but includes many tropical species. It is a very useful treatise, especially for a beginner who needs orientation. Kofoid and Swezy's (1921) monograph is a classic on the naked forms but must be augmented by later papers. Kofoid and Skogsberg's (1928) Dinophysoidae is another classic and covers that group in a comprehensive manner. The Heterodiniidae has been monographed by Kofoid and Adamson (1933). Most of the Peridiniidae are in need of monographic treatment. It is very difficult to identify the smaller species with present literature. For the Ceratia Jorgensen's (1911) monograph and Graham and

Bronikovsky's (1944) treatise on *Carnegie* Ceratia are quite useful. The most comprehensive systematic treatment of the dinoflagellates as a group is Schiller's Dinoflagellata in Rabenhorst's Cryptogamen-Flora (1931–37). The reports of the larger world expeditions complete the general literature on dinoflagellate taxonomy. Such references are included in the bibliography.

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PRESENT STATUS OF DIATOM STUDIES IN THE GULF OF MEXICO[1]

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Very little concerted work has been done on the diatoms of the Gulf of Mexico region to date. Considering its size and diversity of habitat, the Gulf is a virtually untouched area in this regard. The few studies made have been of a somewhat casual, quite limited, and localized nature leaving almost the entire shoreline and open water area of the Gulf completely unexplored.

Previous records are confined mainly to the southwest corner of the Gulf (Campeche Bay), Mobile Bay on the north, the west coast of Florida (Tampa and Pensacola Bays), the Dry Tortugas, and a few in the West Indies, with fragmentary, unpublished records from a few other places. Few, or almost none of these (see bibliography), are well-defined floristic studies. A number of works on diatoms of Honduras and Caribbean waters, not within the Gulf region but closely allied to it in character of flora, add useful supplementary records.

Most of the previous efforts have been concerned with mere identification of species with very little data as to precise location, date of occurrence, and habitat. Many of the early listings are included in Schmidt's Atlas der Diatomaceenkunde (1876) with references only to the locality but without any further information. Despite the dearth of published records and the very limited territory explored the writer was able to compile from several sources a list (unpublished) comprising some 60 genera and about 500 species and varieties. The list is incomplete, however, and gives no assurance of what diatoms one may expect to find in the Gulf, because virtually no work has been done so far on the pelagic species, their succession and seasonal fluctuations. The diatom flora of many shallow water indentations of the shoreline, of swamps and reefs will also require further studies.

LITERATURE

In the appended bibliography are given only those papers which apply specifically to the Gulf or Caribbean waters and such few general works which include the forms found there. For reliable description of the species concerned it is necessary to consult such useful works as A. Schmidt's Atlas der Diatomaceenkunde (1876), H. Van Heurck's Synopsis des Diatomées de Belgique (1880–85); and H. and M. Peragallo's Diatomées Marines de France (1897–1908). Many of the papers dealing specifically with Gulf diatoms are merely lists of species or brief unillustrated accounts which cannot be used for identification.

The distribution of many diatoms is so widespread that it is sometimes necessary, and quite satisfactory, to rely for their identification on literature pertaining to areas entirely remote from the one in question. This is true not only of the free-floating species, but also of many bottom-dwelling and attached forms, such as, for instance, *Melosira sulcata* and *Actinoptychus undulatus*, which, despite a sedentary existence, are widely dispersed.

The standard plankton works of Gran, Nordisches Plankton (1905), and Marie Lebour's Plankton Diatoms of Northern Seas (1930), will be found applicable to a goodly number of tropical forms, especially the *Rhizosolenias* and *Chaetoceros* species, and other typical plankton diatoms although there may be some species in the Gulf waters which will not be found in these publications.

CAMPECHE BAY

Mann (1925) called attention to the remarkable correspondence between the diatom flora of the Campeche Bay in the Gulf of Mexico to that of the waters around the Philippine Islands. The list included by him in the introduction to his paper contains 78 forms common to both places

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[1] Published with the permission of the Secretary of the Smithsonian Institution

including 28 not found elsewhere. Both floras are characterized also by a number of remarkable species of *Campylodiscus.* As an explanation, Mann implies the possibility of parallel development and discounts the idea of transfer or dispersal between the two localities. Other workers take exceptions to the whole idea of attaching any significance to the common appearance of diatom species in the two widely separated areas. At least, it is an interesting observation and one not to be neglected.

Among the Campeche Bay diatoms, mostly registered in Schmidt's Atlas (1876–) are many species and varieties bearing the name *campechiana*, such as *Amphora crassa* Greg. var. *campechiana* Grun., *A. grevilleana* Greg. var. *campechiana* Grun., *Campylodiscus campechianus* Deby, *Cocconeis campechiana* Cleve, *Cosinodiscus gemifer* Ehr. var. *campechianus* Ratt., *C. marginulatus* Ratt. var. *campechiana* Grun., *Endictya campechiana* Grun., *Glyphodesmis campechiana* Boyer, *Navicula campechiana* Grun., *Nitzchia campechiana* Grun., *Stephanopyxis campechiana* Grun., *Surirella campechiana* Hust., *Triceratium campechianum* (Grun.?), and others, indicating a very diverse and novel flora. Yet we have little information as to the exact source and extent of the material from this sizeable area, and it is likely that more thorough and careful survey may add new findings to this apparently most interesting locality.

If the great diversity of the Campeche Bay diatom flora and the yield of new forms is any indication of what might be expected from examination of other places in the long stretches of unexplored shore line of the Gulf, interesting prospects are in order. It must be remembered, however, that the yield of new forms from Campeche Bay came mostly many years ago when fewer species were known from other places.

MOBILE BAY

Probably one of the more intensively studied areas of the Gulf coast thus far is Mobile Bay. A list of diatoms from this area published by Cunningham (1889), one of the few diatom students local to the Gulf area, includes 37 genera and 137 species, but is probably far from complete. Cox (1901) who identified the diatoms in Cunningham's collection, furnished a useful but clearly incomplete list of 29 genera and 62 species. This material obtained from George H. Taylor, Wm. McNeil, and his own collecting, includes typically fresh water, brackish, and marine forms. Since Cox specifically says that all the specimens are from Mobile Bay it is obvious that fresh water species in this collection were brought in by streams. This list is also correlated with records of George H. Taylor from Tampa Bay.

One form from salt marshes at Mobile found in Cunningham's material and named by Grunow is sufficiently remarkable and well known to deserve particular mention. It is *Terpsinöe intermedia* Grun., a diatom of abnormal structure with quite symmetrical adjutment on the central, valve face (see Schmidt's Atlas, 1876, plates 198–200). The species is closely related to *T. musica* Ehr., typical of the Gulf coast. It is evidently plentiful in its original locality near Mobile.

TORTUGAS AND WEST COAST OF FLORIDA

Extensive collections made by the writer at Tortugas and around Tampa Bay are in process of study, and some observations based on them are included in this summary. George H. Taylor made records from Tampa Bay as above cited. Mann prepared a list of diatoms of Pensacola Bay. The writer's report (unpublished) on plankton diatoms of the west Florida coast, off Tampa and Fort Myers, to E. Lowe Pierce of the University of Florida, includes 35 genera and 82 species and varieties. Some species of *Chaetoceros* and *Hemidiscus* included in this list were found in heavy concentrations, a fact which indicates that Gulf coastal waters are, at times, very productive.

From the studies mentioned above an inference may be drawn that mixed calcareous and organic muds of the west coast of Florida provide favorable environment and adequate supply of nutrients to support a generally rich and varied diatom flora which includes, conspicuously, forms like *Terpsinöe musica, Biddulphia rhombus, Isthmia capensis, Auliscus, Aulacodiscus, Navicula,* and others.

OTHER RECORDS

Diatom records made in connection with oil-pollution investigations conducted in Louisania by the biologists engaged by oil companies and by persons representing various conservation and fishery interests have not been published and are not generally available. They are probably rather limited since these investigators have not been prepared to give consistent attention to the studies of diatoms and were primarily concerned with other problems. Mention may be made here of the observation by Willis Hewatt of Texas Christian University (personal communication) that *Biddulphia mobilensis* periodically produces very heavy concentrations off the Louisiana coast near Grand Isle. This area, and probably also the coasts of Alabama to Texas, would seem to be optimum environment for this species.

DIATOM FLORAS OF GULF AND ADJACENT WATERS

At the present state of our knowledge there is no basis for correlating diatom floras of the Gulf and adjacent areas or for discussing their mutual effects. Currents that swing into the Gulf from the Caribbean on the southeast and out through the Florida Straits on the northeast must, of course, carry their complement of plankton diatoms; but, until more is known of both the Gulf diatom flora and that of the adjacent waters outside, no definite information can be given regarding the effect of one on the other. As has been said, practically nothing is known specifically of the Gulf diatom plankton or, for that matter, of that in adjacent tropical waters.

The mere presence of similar population constituents in the adjacent areas does not necessarily imply any direct relationship between them. It is quite possible that the greater sweep of the Gulf Stream tends to some extent to isolate the Gulf of Mexico from the adjacent seas despite the movement of some of the Atlantic and Caribbean waters through the Gulf.

With the bottom-living and attached species seemingly not so readily subject to dispersion, there is not enough difference of conditions, say, on the east and west coasts of Florida or the environs of Cuba, and there is so much correspondence in certain conspicuous species, such as *Terpsinöe musica*, *T. americana*, *Nitzschia paradoxa*, *Grammatophora marina*, *Biddulphia pentacrinus*, *Raphoneis surirella*, *Surirella reniformis*, and members of the genera *Coscinodiscus*, *Campylodiscus*, *Biddulphia*, *Navicula*, that in our present state of limited knowledge it is not feasible to give any general statements of significant relationship. It would seem that a very large variety of species find the waters both inside and outside the Gulf a suitable habitat, but it will take a great deal of more detailed collecting and comprehensive study to disclose any significant floristic differences or migrational influences within these areas.

ECOLOGY

The literature on the diatoms of the Gulf area contains practically nothing concerning their ecology and economic importance. The designation of species as fresh water, brackish, or marine is about the extent of ecological data. Yet, both subjects should be of great interest. One may expect that careful studies of many diverse habitats represented along the shorelines of the Gulf, and in its open waters could give valuable data regarding habitat characteristics, optimal range of the different species, and their seasonal occurrences.

The effects of the discharge of particulate matter by the Mississippi and other large rivers on the distribution and productivity of diatoms in the open waters constitutes another important problem.

Relation of the diatoms as a vital chain in the marine food cycle is also of great interest because of the extensive shrimp, oyster, and fishery industries of the area.

Such ecological studies of the diatoms correlated with their floristic survey may well contribute to general knowledge of the Gulf and will be helpful in understanding its specific problems.

PRODUCTIVITY

It has long been held that productivity of plankton diatoms in tropical and subtropical waters is in general lower than in colder regions. This, in the writer's experience, appears to be generally true, but the statement should be taken with some qualifications for there are instances in which, owing to a particular combination of local conditions, it does not hold. Even in tropical waters certain areas may contain heavy concentrations of diatoms. There is for instance evidence of occasional unaccountable surges of certain species, as *Hemidiscus*, *Biddulphia mobilensis* and *Isthmia capensis* about Tortugas and in other places for which the causative factors are not known. Because of the presence of very delicate, transparent and minute forms that pass through the meshes of the plankton net, the Gulf plankton may at times contain a greater number of individual diatoms and be more productive than meets the eye of the casual observer. Examples of such occurrences are given in the next section on silica relations. Although a phytoplankton tow in the very clear subtropical Gulf water will usually disillusion and disappoint the investigator used to northern collecting, he must be alert both in observation and method not to miss or lose the delicate and minute forms present.

The first adequate quantitative studies of diatom plankton productivity in the Gulf were made at Tortugas by Riley (1938). His work, based on Harvey's method of extraction of plankton pigments, and on measurements of oxygen changes in suspended clear and dark bottles (method of Marshall and Orr), gives indices of reliable value. It might be added that, especially with the phantom-like diatom plankton, these methods are dependable, while errors and uncertainties of sampling with quantitative plankton net and of cell counts would give deceptive results.

Comparing plankton productivity at Tortugas with that of Long Island Sound, Riley found that the amount of total plant pigment from Tortugas plankton was only one twenty-fifth that of the Long Island area. On the other hand, oxygen production in suspended bottles was one-third to one-half as much in the former as in the latter area. It would seem evident, he says, "that actual productivity is much greater than the standing crop would indicate." The results are subject to qualification with respect to a number of altering factors which are discussed in Riley's report.

The limited period covered by Riley's observations may or may not have been a favorable one for comparison, and further investigations of this character extended to other places in the Gulf and other times of the year, are clearly needed.

Another problem about which information to date is both meager and vague concerns the rate of turnover and renewal of the population, especially of the small diatom species such as members of the genera *Nitzschia*, *Synedra*, *Dimmerogramma*, *Grammatophora*, *Amphora*, *Raphoneis*. The estimation of the so-called "standing crop" of phytoplankton growth is a standard and fairly satisfactory practice, but an adequate evaluation of the amount of transformation of organic substance over a specified period of time is fraught with a complication due to the constant breakdown and renewal of population elements, in which the reproductive rate is rapid and the life span is short. Especially is this true where the plankton is very poor as it is frequently in the Gulf waters.

Knowledge of the general occurrence and succession of the Gulf flora is too meager to make any reliable statements as to the relative importance of the various diatoms for there are very many of the species mentioned, and perhaps others, that occur at times in large numbers. Just a few, however, that are definitely typical of the region, though by no means restricted to it might be cited: *Biddulphia mobiliensis* (Bail.) Grun., *Terpsinöe musica* Ehr., and *Hemidiscus hardmannianus* (Grev.) Mann. Further study will certainly add many others that periodically occur in abundance in different parts of the area.

SILICA RELATIONSHIPS

In the waters of tropical seas, poor in silica and other nutrients, the diatoms of wide or cosmopolitan distribution are smaller and have frailer shells than are to be found in the same species from waters of temperate and northern latitudes. The variety of species is not less in the tropics, nor is there necessarily a smaller number of individuals, but the size and robustness of their cells is diminished. Although this observation is applicable, in general, to species found both in tropical and in temperate seas, certain forms may be cited as notable examples, namely, *Synedra undulata* (tropical form often half the length of its northern counterpart), *Biddulphia pulchella* and *B. pentacrinus*, *Surirella reniformis*, *Grammatophora marina*, *Isthmia* sp., and others. On the contrary, some typically warmer water forms, like *Raphoneis surirella* do not appear to grow larger, heavier shells in richer waters of northerly latitudes.

The plankton diatoms of the waters containing minimum amount of dissolved silica are diaphanous, as for example, the *Chaetoceros*, large-celled *Hemidiscus* and *Coscinodiscus* species found in the Gulf plankton. These latter, and similar forms, may be both large and numerous, but their bodies are so watery and their shells so lightly silicified that they are very transparent and are easy to overlook.

Numerous minute-celled forms such as small *Nitzschia*, *Cocconeis*, *Dimmerogramma*, *Synedra*, *Grammatophora*, and *Amphora* species, common in the Gulf frequently are found in silica poor waters, while larger heavy-shelled forms (*Rhizosolenia, Coscinodiscus, Biddulphia* sp.) sometimes found in cooler, northern waters, are not present in the tropical or subtropical plankton unless reduced in size or weight of their silica shells. These observations are general and at present not based on extensive quantitative measurements which, however, are being planned by the author.

Further observations by the writer, although not quantitative, strongly suggest that wherever there is a substantial influent of silica-bearing water, the diatom growth is both more abundant, and the cells (and their shells) are of a more robust character. Such a condition was noticed, for instance, at Tortugas in close proximity to the crumbling walls of siliceous brick of old Fort Jefferson, washed on all sides by the shallow calcareous water. In the moat and in semienclosed pools adjacent to these walls a very heavy growth of *Tropidoneis lepidoptera* and other diatoms was noted. The more extensive result of such relations, however, is to be seen in areas influenced by the discharge of river systems that drain argillaceous soils, or in the inshore waters affected by the run-off from steeper siliceous terrain, such as found around the coast of Cuba, the west coast of Florida and the coast of Alabama. Waters of such constitution support heavy growths of robust shelled diatoms as *Terpsinöe musica, Biddulphia pulchella, Hydrosera triquetra, Lithodesmium,* and others.

The contrast of the rich diatom flora produced in such an environment with the frail and delicate plankton forms of the silica-poor calcareous waters about Tortugas, for example, appears to be a demonstration of a point long suspected by the writer that a plentiful supply of silica greatly enhances the growth of diatoms. Evidence from other regions and types of habitat, in the writer's experience, supports this contention. Where richer waters with a higher silica content occur in tropical regions owing to cold currents, upwelling, or run-off from siliceous soils, a heavy diatom productivity, with oftentimes more robust individuals is the result.

The relation of diatom growth to silica content of sea water is undoubtedly significant but not too well understood. The varied conditions of the Gulf of Mexico afford good opportunity for such study. The effects of phosphates, nitrates, and other nutritive elements should be examined coordinately although it does not appear from the present observations that they could be confused with the role of silica as a limiting factor.

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