CHAPTER XV

MOLLUSKS

MOLLUSKS[1]

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The Gulf of Mexico is, chronologically speaking, probably the least known body of water adjoining the United States, and the mollusks of its shores are as yet only imperfectly known. This is particularly the case with the area between Cedar Keys on the Florida coast, and Sabine Pass on the Louisiana-Texas border, and with the part of the coast line stretching between the mouth of the Rio Grande and the vicinity of Veracruz.

The littoral fauna of the Gulf of Mexico may be divided into two elements that inhabit different geographical areas. There is first the tropical element found on the Florida Keys and north on the Gulf side of Florida to about Tampa Bay, the northwest coast of Cuba, and the Mexican coast from Cabo Catoche on Yucatán north to the vicinity of Corpus Christi, Texas (and possibly to near Matagorda Bay). This area forms the southern limit of the Gulf of Mexico and is the only part of the Gulf area in which living, fringing reef corals are found. Joubin's (1912) representation of coral reefs in Tampa Bay is obviously an error.

North of this tropical Caribbean area the fauna takes on a more temperate character, showing an obvious relationship with that of the zoogeographical province generally known as the Carolinian. The physiography of this area is also in general different from that of the more southerly shores. It is a region characterized mainly by sandy beaches either on the mainland or on low coastal or barrier islands that are separated from the mainland by shallow lagoons or bays with passes or inlets between the individual islands. No coral reefs are found in this area, although there are submerged coral banks off the coast as far north as northern Florida.

The mollusks of the deeper waters of the Gulf show, mainly, a relationship with the West Indian fauna but have also some affinities with those of the deeper waters off the southern Atlantic coast of the United States.

[1] Published by permission of the Secretary of the Smithsonian Institution
[2] I would like to acknowledge the helpful suggestions received from Prof. T. E. Pulley of the University of Houston.

PAST WORK DONE IN THIS AREA

GENERAL

The first publication that gave a list of the mollusks found along the entire Gulf coast and discussed their geographical ranges was Dall's (1889) catalog, reprinted, with additions, in 1903. Dall divided the southeastern coast into 10 geographical districts. Three of these districts covered the area included in this report: Florida Keys, from the Keys north to Charlotte Harbor, West Florida, from Charlotte Harbor to the Mississippi Delta, and the deeper waters of the Gulf east of longitude 90°, and Texas, from the Mississippi Delta to the Rio Grande, and the deep waters south to Yucatán. The broad extent of the Texas district has led to the inclusion, in later lists, of many species as being found in Texas that have not as yet been recorded from the waters of that State. This is true, for instance, of Johnson's (1934) list mentioned later.

Maury (1920, 1922) published a catalog of the recent mollusks of the Gulf of Mexico in which were included some Tertiary species. Johnson's (1934) List of the Marine Mollusca of the Atlantic Coast from Labrador to Texas came out posthumously. This check list, though not always, indicates those species found along the shores of the Gulf of Mexico.

FLORIDA

The west coast of Florida is better known from a malacological standpoint than any other section of the area under discussion. Numerous catalogs and annotated lists covering this area were published in the seventies and eighties: Calkins (1878, 1880), Dall (1884), Simpson (1887, 1889). Melvill (1881) gave a list of the mollusks of Key

West, enumerating 123 species. In more recent years several papers have been published dealing with the mollusks of Sanibel Island, near the mouth of the Caloosahatchee River, in Lee County; Clench (1923, 1925) listed 89 species, while Haas (1940) gave ecological notes on many of the species found here. In the last few decades some collecting has been done along the northwestern coast (Lyman 1942; Schwengel and McGinty 1942). The most complete work on the mollusks of western Florida is that by Louise Perry, Marine Shells of the Southwest Coast of Florida, 1940, in which she describes 346 species most of which are illustrated.

ALABAMA-LOUISIANA

The published records for this area are fewer than for the Gulf coast of Florida or for Texas. The first faunal list I have been able to find is that by Vanatta (1904) who published a list of mollusks from Horn Island, Mississippi. Cary (1906) enumerated 73 species from various places along the Louisiana coast from Cameron in the western part to the Chandeleur Islands in the east. Whereas in Cary's list the proportion of gastropods to pelecypods is 32 to 38, in the Horn Island list the proportion is 3 to 32. This seems to suggest that the shells of Horn Island were gathered almost exclusively along the outer beach and that further search on the lagoon side of the island would bring to light further species. In 1929, Clench listed 23 species from various localities in southern Louisiana in the Mississippi Delta region. Burkenroad (1933) enumerated 9 species of pteropods from the waters of Louisiana. The most recent list of Louisiana shells (Harry 1942) gives 93 species from the vicinity of Grand Isle and Barataria Bay. This report, the result of 12 years collecting by members of the staff of the Louisiana State University Marine Laboratory staff there, shows how impoverished the fauna is in this part of the Gulf in comparison with that of the regions farther south on both sides of the Gulf.

TEXAS

The first enumeration of the mollusks of this part of the Gulf, and indeed of any part of the area covered by this report, was that published by Ferdinand Roemer in his work on Texas (Roemer 1849). Out of 54 species he listed from the island of Galveston 7 were new species described by R. A. Philippi. Singley (1893) gave an extensive list of the marine mollusks of the Texas coast, listing 342 species. This contribution, being based in part on Dall's (1889) catalogue, contained many species for which no records from the waters of Texas proper are known. Mitchell (1894) published, privately, a list of Texas marine shells enumerating 81 species. The list was based on his own collecting and dealt mainly with the mollusks of the Matagorda-Corpus Christi Bay area. Strecker's (1935) list of Texas marine shells appeared posthumously; it contained 188 species, a number of which were not in Singley's list. As an appendix Strecker gave a list of 176 species said by Dall to come from the Texas district but for which Strecker had no specific localities. Stenzel (1940) published a list of 56 species from Point Isabel, Texas. A considerable amount of ecological work is being carried on at the present time by workers at the Institute of Marine Science at Aransas Pass (Hedgpeth, 1950; Whitten et al., 1950) as well as at the laboratory of the Texas Game, and Fish Commission at Rockport. Recently, Pulley (1949 and 1952) published on the mollusks of the Texas coast. His 1952 paper is a comprehensive one, in which he has included, with appropriate comments, those species previously recorded from Texas, but not known to occur there.

MEXICO

Only a few papers have been published on the mollusks of the east coast of Mexico. Baker (1891) listed 216 species from Veracruz, Silam, Progreso, and Campeche (the last three localities are on the peninsula of Yucatán), and Hinkley (1907) enumerated 47 marine shells from the vicinity of Tampico.

CUBA

The older works on Cuban shells, such as those by d'Orbigny and Arango, gave no specific localities for the marine mollusks. In the Catalogo de los Moluscos de Cuba, Aguayo and Jaume (1947–52) published some records from the northwest coast of Cuba. Henderson's (1916) book contains, also, a good picture of the northwestern coast of Cuba, although he gives no list of mollusks. Little collecting seems to have been carried out along the part of the Cuban coast between Habana and Cabo San Antonio, a region that should be very rich in mollusks.

DEEPER WATERS

The first work on the fauna of the deeper waters of the Gulf of Mexico was carried out in 1878 by the United States Coast Survey steamer *Blake* under the direction of Professor Alexander Agassiz. The mollusks gathered during this cruise were reported on by Dall (1886–89). Subsequently, the steamer *Albatross* of the United States Fish Commission made numerous stations in the eastern part of the Gulf, the results of which have been referred to in various scattered papers. More recently, the Fish and Wildlife Service vessels *Pelican* and *Oregon* have been carrying out investigations in the Gulf of Mexico in the course of which they have gathered many interesting mollusks which have been only partly reported on. The commercial shrimp fishermen have been initiated by the amateur shell collectors into the practice of saving the mollusks brought up in their nets, and in this way they are contributing many interesting finds. A preliminary report on some of these mollusks has recently been published by Rehder and Abbott (1951).

ECOLOGY

Under this heading are listed what seem to be the most important biotopes present in the littoral zone of the Gulf of Mexico. No attempt has been made to go into a detailed description of the various facies, zones, and associations.

Some of the species listed as occurring in one province or in one kind of habitat may, of course, be found also in other areas. It should likewise be pointed out that because of the lack of careful collecting along much of the coast line of the Gulf the extent and exact position of the transition areas between the Caribbean and Carolinian provinces is at the present time still largely a matter of speculation. This is especially true of the fauna of the moderate depths between the shore and the deeper waters.

CARIBBEAN PROVINCE

This zoogeographical area includes the northwest coast of Cuba from Cabo San Antonio to Habana, the west coast of Florida from the Dry Tortugas and Key West north to probably Tampa Bay (the northern limit of this province is somewhat doubtful here but lies somewhere between Sanibel Island and Cedar Keys), and the coast of Mexico from Cabo Catoche to the vicinity of Port Isabel, Texas, and possibly beyond to Corpus Christi Bay.

As is to be expected, the mollusks of this area show an obvious relationship with those of the West Indies and the entire Caribbean region.

The list of species has of necessity been taken largely from our knowledge of the Floridian molluscan fauna. An interesting and more extended discussion of these associations can be found in a report by Bartsch (1937).

1. Coral reefs, rocky outcrops, and jetties:

Here we find a rich fauna of which I list only a few species.

Acanthopleura granulata Gmelin.
Acmaea pustulata Helbling.
Fissurella cayenensis Lamarck.
Astraea americana Gmelin.
Nerita peloronta Linné.
Nerita versicolor Gmelin.
Nerita tessellata Gmelin.
Littorina ziczac Gmelin.
Tectarius muricatus Linné.
Cerithium literatum Born.
Batillaria minima Gmelin.
Thais rustica Lamarck.
Cantharus tinctus Conrad.
Conus mus Hwass.
Siphonaria pectinata Gmelin.
Arca zebra Swainson.
Barbatia barbata Linné.
Brachidontes exustus Linné.
Lima scabra Born.
Isognomon alatum Gmelin.

2. Shallow water sandy stretches, shallow grassy bays, muddy flats:

Here the sand-burrowing mollusks are at home, and hence we find more pelecypods than in the preceding habitat.

Cerithium variabile C. B. Adams.
Epitonium lamellosum Lamarck.
Sinum perspectivum Say.
Natica canrena Linné.
Busycon contrarium Conrad.
Melongena corona Gmelin.
Oliva sayana Ravenel.
Olivella floralia Duclos.
Marginella apicina Menke.
Conus pealei Green.
Terebra dislocata Say.
Aplysia willcoxi Heilprin.
Cardita floridana Conrad.
Anodontia alba Link.
Lucina floridana Conrad.
Trachycardium egmontianum Shuttleworth.
Dosinia elegans Conrad.

Macrocallista maculata Linné.
Chione cancellata Linné.
Donax variabilis Say.

3. Brackish water estuaries:

This habitat is found all along the shores of the Gulf of Mexico. The mollusks listed here are found both on sandy and muddy bottom as well as on rocky substrata and on objects such as jetties and pilings.

Neritina reclivata Say.
Batillaria minima Gmelin.
Cerithidea scalariformis Say.
Congeria leucophaeata Conrad.
Cyrenoida floridana Dall.

4. Mangrove flats:

A few species are found predominantly in this habitat.

Littorina angulifera Lamarck.
Cypraea zebra Linné.
Isognomon alatum Gmelin.
Ostrea floridensis Sowerby.

CAROLINIAN PROVINCE

This area extends from Cape Hatteras, North Carolina, south to about Cape Canaveral on the east coast of Florida, and from about Tampa Bay on the Florida west coast northward and westward along the shore of the Gulf to about Corpus Christi Bay, Texas. Some elements of this fauna on the western side of the Gulf may go farther south into Mexico, while some tropical forms may reach the vicinity of Matagorda Bay.

The shores of this area have a rather uniform character, without coral reefs or mangrove vegetation. Instead we have mile on mile of sandy beaches, often along low coastal islands, behind which are lagoons, bays, and estuaries with varying degrees of salinity. Frequently we find oyster reefs on the lagoons and bays, but outside of these oyster banks the only solid substrata are mainly in the form of man-made structures such as jetties and pilings.

This province may conveniently be subdivided into the following ecological areas:

1. Outer sandy beaches and nearshore sandy areas:

Epitonium angulatum Say.
Polinices duplicata Say.
Sinum perspectivum Say.
Strombus pugilis alatus Gmelin.
Chicoreus fulvescens Sowerby.
Busycon spiratum plagosum Conrad.
Oliva sayana Ravenel.
Anadara campechiensis Gmelin.
Anadara brasiliana Lamarck.
Noetia ponderosa Say.
Trachycardium muricatum Linné.
Dinocardium robustum Humphrey.
Laevicardium mortoni Conrad.
Dosinia discus Reeve.
Macrocallista nimbosa Humphrey.
Tellina alternata Say.
Tellina versicolor DeKay.
Donax variabilis Say.
Tagelus gibbus Spengler.
Barnea costata Linné.

2. Bays and lagoons, moderate to high salinity, sandy or muddy bottom:

Cerithium variabile C. B. Adams.
Nassarius acuta Say.
Nassarius vibex Say.
Acteocina canaliculata Say.
Pecten gibbus amplicostatus Dall.
Volsella demissus granosissimus Sowerby.
Chione cancellata Linné.
Mercenaria mercenaria Linné.
Abra aequalis Say.
Mulinia lateralis Say.
Ensis minor Dall.

3. Bays and lagoons, brackish water:

Neritina reclivata Say.
Littorina irrorata Say.
Polymesoda carolinensis Bosc.
Rangia cuneata Gray.

4. Jetties and oyster reefs in bays:

Crepidula plana Say.
Thais floridana Conrad.
Anachis obesa C. B. Adams.
Brachidontes recurvus Rafinesque.
Crassostrea virginica Gmelin.

DEEPER WATERS OF THE GULF OF MEXICO

In these deeper waters we find many species that show a relationship with the tropical element of the Caribbean area. We have, for instance, *Terebra taurinum* Humphrey (*flammea* Lamarck) and *Sconsia striata* Lamarck which extend into the West Indies. Others are peculiar to the Gulf. The explorations that are now going on in the Gulf of Mexico and future dredgings will unquestionably bring to light many more new and interesting forms.

Gaza superba Dall. (W)
Murex beaui Fischer and Bernardi. (W)
Oocorys bartschi Rehder. (G)
Fusinus couei Petit. (G)
Scaphella junonia Shaw. (G)
Conus sozoni Bartsch. (G)
Polystira albida Perry. (W)
Polystira tellea Dall. (G)

Terebra taurinum Humphrey. (W)
Anadara baughmani Hertlein. (G)
Aequipecten glyptus Verrill. (C)
Amusium papyraceum Gabb. (W)
Pitar cordata Schwengel. (G)

(W) Also known from the West Indies.
(G) Known only or almost solely from the Gulf of Mexico.
(C) Found also in the Atlantic off the southeastern United States.

In this brief survey of our present-day knowledge of the mollusks of the Gulf of Mexico I have attempted to list some of the conspicuous species found in the various parts of the Gulf and have pointed out how little we actually know of the mollusks. There has lately, however, been an increase in interest in this region, and we can look forward to valuable contributions on this subject in the not too distant future.

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CEPHALOPODA OF THE GULF OF MEXICO[1]

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The taxonomy and biology of the cephalopods of the Gulf of Mexico have been neglected by workers in the field of malacology, and consequently, records and reports are very meager. LeSueur (1821) described the first species from this area when he gave the description of *Onykia carribaea*. De Blainville (1823) described several of the loliginid squids which are now known to occur in these waters, the fact which he failed, however, to record. Howell (1868) described *Loligo hemiptera*, a new squid from the Gulf. This species has since been shown by the author to be synonymous with *Lolliguncula brevis* (Blain.).

Verrill (1882), in his report on the cephalopods of the northeastern coast of the United States, lists five species, only, as occurring in the Gulf of Mexico region: *Sepioteuthis sepioidea* (Blain.), *Loligo gahi* Orbigny, *Lolliguncula brevis* (Blain.), *Sthenoteuthis pteropus* Verrill, and *S. bartrami* (LeSueur). Of these, *L. gahi* Orb., which occurs on the Pacific coast of South America and is not found in this area, has been a cause of much confusion ever since as it has been applied to the arrow squid, *Doryteuthis plei* (Blain.).

From 1882 to 1934 the cephalopods of the Gulf of Mexico were ignored due largely to the lack of specialists in this field. In 1934 Johnson's List of the Marine Mollusca of the Atlantic Coast from Labrador to Texas appeared. In it, Berry (1934), who wrote the cephalopod section, records 64 species within its range of which only 15 species are referred to Florida and the West Indies and only one specifically to the Gulf of Mexico.

Robson (1932) published an account of certain octopods sent him by van Hyning mostly from the Gulf coast of Florida, and this account was followed in 1937 by Adam's report on the *Mercator* collections and the description of a new species from Dry Tortugas, *Octopus mercatoris*, since considered by Pickford (1945) to be synonymous with *O. joubini* Robson.

The first major contribution to the knowledge of the cephalopods of the Gulf of Mexico was made by Pickford (1945) in her study of the littoral octopods of the western Atlantic. Three of the six octopods treated in this study are common to the Gulf of Mexico: *Octopus vulgaris* L., *O. briareus* Robson, and *O. joubini* Robson. The only other published records of Gulf of Mexico cephalopods are a record of *O. burryi* Voss from the upper Gulf and comments upon its distribution by Voss (1950, 1951b). Hedgpeth (1950) records *Loligo brasiliensis* Blain. from the Texas jetties, but this is erroneous, the species involved being *Lolliguncula brevis* (Blain.) which is also recorded in the paper.

Thus it is seen that the cephalopodan fauna of the Gulf of Mexico is comparatively untouched, and to date no survey or monograph upon them has been published such as has appeared for those of other areas such as the Mediterranean Sea or the Hawaiian Islands. According to some zoologists the lack of published records indicates that maybe this area is fairly devoid of specimens. However, an examination of the material, still unreported, from the *Atlantis* circumnavigation of Cuba in 1937–38 presents another picture. The large collection made by that vessel and recently examined by the author contains many new records for the Gulf of Mexico and several species which are new to science. Of the entire collection only a single specimen has been recorded in the literature (Pickford 1946).

Since the initiation by the United States Fish and Wildlife Service of the exploratory fishing by the *Oregon* an entirely new and rich cephalopodan fauna has unfolded in the Gulf of Mexico. The collections made by this vessel are rather large and at this date (September 1952) are in the process of being worked up by the author.

From the material so far examined it appears that there is a strong connection between the

[1] Contribution No. 124 from the Marine Laboratory, University of Miami.

cephalopodan fauna of the Mediterranean Sea and the Gulf of Mexico. The *Oregon* material, both benthic and pelagic, parallels very closely the material from the Mediterranean both in genera and species. Considering the sometimes rather long planktonic life of many of the larval forms and the sweep of the North Equatorial Current into the Caribbean and thence into the Gulf of Mexico, such distribution is not surprising. This close connection is best exemplified by the presence of *Pteroctopus tetracirrhus* (delle Chiaje), apparently quite common in the Gulf of Mexico, which was known previously only from the Mediterranean Sea and a single record from the Azores, and *Scaeurgus unicirrhus* Orbigny, a related genus, which is well known in the Mediterranean but not elsewhere in the Atlantic but was recently reported by Voss (1951a) as occurring along the southeast Florida coast and presumably in the Gulf of Mexico.

Pickford (1946) reported the presence of *Vampyroteuthis infernalis* Chun taken by the *Atlantis* in 1,480 meters from the Gulf of Mexico. This form has not been found in the Mediterranean presumably due to the shallowness of the sill at the Straits of Gibraltar, a factor which does not enter into the discussion of the Gulf of Mexico due to the greater depth of the Yucatán Channel. A discussion of the bathypelagic conditions of this species may be found in the above-mentioned paper.

The extent of the distribution of the Caribbean and Atlantic species into the Gulf of Mexico at the present time is unknown. In the appended list of species known to occur in the Gulf of Mexico those with asterisks have been reported only from the Gulf Stream in the vicinity of Miami or from the Florida Keys. Thus their presence in the Florida Current which sweeps through the southern portion of the Gulf of Mexico must be assumed, yet they have not been reported from the rather extensive hauls made by the *Oregon*. One species investigated by the author, *Sepioteuthis sepioidea* (Blain.), is known from both sides of the Gulf Stream from below its origin in the Lesser Antilles to Bermuda, but there is no record of its occurrence in the Gulf of Mexico proper. The cause of this rather peculiar distribution or limitation is not known.

So little is known concerning the life histories of the cephalopods, especially the octopods, in our area that only generalities can be drawn. From the literature and independent investigations it seems apparent that the octopods and decapods spawn during the spring, although there are indications that some spawning occurs throughout the year. In general, the octopods care for their spawn by brooding over the eggs which are attached either singly or in festoons beneath rocks or in old mollusk shells. Certain of the octopods, particularly those with large eggs (10–15 mm.), hatch out fully developed and immediately take up a benthic life. Others with small eggs hatch out as temporary members of the plankton and spend a certain interval of time, from a few days to several weeks or months, in a drifting state after which they settle to the bottom. The decapods, at least for the few examples known, attach their eggs to the bottom either to rocks, algae, or other objects, and leave them uncared for until hatching whence they become part of the temporary plankton; others attach their eggs to floating objects at or near the surface. Among many exceptions to these are *Vampyroteuthis infernalis* Chun which reportedly has free pelagic eggs and *Argonauta argo* L. in which the minute eggs are retained within the egg case by the female.

The length of life in cephalopods is uncertain and a matter of some dispute. Verrill (1882) suggests that *Loligo pealei* LeSueur reaches maturity in about 2 to 3 years. The actual span of life is uncertain but is believed to average, at least in the smaller species, about 2 to 4 years.

Cephalopods may be either free-swimming open ocean forms such as the Ommastrephidae, benthic such as the Octopodinae, bathypelagic as the Vampyroteuthidae and Spirulidae, or planktonic as in the Cranchiidae. In general, the Loliginidae, a group of great commercial importance in some areas of the world and found in large numbers in the Gulf of Mexico, are free-swimming forms found in coastal waters never far from land. The food of cephalopods consists mainly of crustaceans, bivalve mollusks, and small fish. In return, they furnish a considerable portion of the diet of many fishes. As many as 24 pairs of beaks of *Argonauta argo* L. have been taken by the author from the stomach of a single sailfish (*Istiophorus*). Springer (personal communication) records sucker disc marks the size of a half dollar on the skin of a young sperm whale taken in the Gulf of Mexico, and a single specimen of *Architeuthis* sp. badly mutilated by sharks was taken from the surface of the Gulf Stream off the Florida Keys. The specimen was measured by the author and estimated to be about 15 feet long when entire so that the presence of the giant squid in these waters is now confirmed.

The number of individual species of cephalopods found in the Gulf of Mexico is rather difficult to determine due to the previously mentioned lack of records. However, the completed results of the *Oregon* explorations will materially increase our present knowledge of this interesting fauna. The following list of species arranged in their taxonomic order includes species which have been taken from the plankton of the Gulf Stream off Miami and as such should be found in the portion of the Florida Current traversing the Gulf of Mexico. Certain others have been reported thus far only from the Lower Florida Keys. Both of these groups are marked with asterisks, and only those not so marked have been actually found in the Gulf of Mexico proper. Many more records could be added from the Caribbean area, but as the presence of these species in the Gulf of Mexico has not been proved they are not included in the present list.

SYSTEMATIC LIST

Order DECAPODA

Family SPIRULIDAE:
Spirula spirula L., 1758.

Family SEPIOLIDAE:
Rossia (Semirossia) tenera Verrill, 1880.
Rossia (Semirossia) equalis Voss, 1950.

Family LOLIGINIDAE:
Lolliguncula brevis (Blain.), 1823.
Loligo pealei LeSueur, 1821.
**Sepioteuthis sepioidea* (Blain.), 1823.
Doryteuthis plei (Blain.), 1823.

Family LYCOTEUTHIDAE:
Lycoteuthis diadema (Chun), 1900.

Family ENOPLOTEUTHIDAE:
Abraliopsis morisii (Verany), 1837.
**Thelidioteuthis alessandrinii* (Verany), 1851.
**Pyroteuthis margaritifera* (Rüppell), 1844.
**Pterygioteuthis giardi* Fischer, 1895.

Family ONYCHOTEUTHIDAE:
**Onykia carribaea* LeSueur, 1821.
Onychoteuthis banksii (Leach), 1817.

Family ARCHITEUTHIDAE:
Architeuthis sp.

Family OMMATOSTREPHIDAE:
Illex illecebrosus (LeSueur), 1821.
Sthenoteuthis bartrami (LeSueur), 1821.
Sthenoteuthis pteropus Steenstrup, 1856.

Family CHIROTEUTHIDAE:
Chiroteuthis lacertosa Verrill, 1881.

Family CRANCHIIDAE:
Cranchia scabra Leach, 1817.

Order OCTOPODA:

Family VAMPYROTEUTHIDAE:
Vampyroteuthis infernalis Chun, 1903.

Family STAUROTEUTHIDAE:
Grimpoteuthis umbellata (Fischer), 1883.

Family OPISTHOTEUTHIDAE:
Opisthoteuthis agassizii Verrill, 1883.

Family ARGONAUTIDAE:
**Argonauta argo* L., 1758.
**Argonauta hians* Solander, 1786.

Family TREMOCTOPODIDAE:
**Tremoctopus violaceus* delle Chiaje, 1830.

Family ALLOPOSIDAE:
Alloposus mollis Verrill, 1880.

Family OCTOPODIDAE:
Octopus briareus Robson, 1929.
O. vulgaris L., 1758.
O. joubini Robson, 1929.
O. burryi Voss, 1950.
Pteroctopus tetracirrhus (delle Chiaje), 1830.
**Scaeurgus unicirrhus* Orbigny, 1840.

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SUMMARY OF OUR KNOWLEDGE OF THE OYSTER IN THE GULF OF MEXICO

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The American oyster, *Crassostrea virginica*, in the Gulf of Mexico is characterized perhaps most of all by its versatility in adapting itself to different habitat niches. There are few places where at least a scattered growth of oysters is not found along the 3,600 miles of tidal shore line from Cape Sable in Florida to the Rio Grande in Texas. The distribution of this oyster population is more impressive if we consider its area. There are probably more than 1,400 square miles of water bottoms along the Gulf coast suitable for and more or less populated with oysters. In some areas the oyster communities consist of small isolated patches only a few yards in area which are elevated like islands in a "sea" of too soft mud. Where the bottom is more firm the communities may cover many acres, and reefs up to 25 miles in length are not unknown.

Oysters establish successful colonies in the range from a foot above mean low water to a depth of 30 to 40 feet in some of the deeper channels. Their occurrence is everywhere dependent on a suitable or rather a physically possible substratum. They compete with the tree oyster for space on the mangrove roots; they cover bridge footings and piles of old ballast rock, and have even been found 5 miles out in the open Gulf on an oil well rigging (Gunter 1951a).

In well-protected areas small clusters and single oysters become established on pure sand bottoms. On mud bottoms, too soft to support a reef, single oysters may grow until their own weight carries them below the surface. New spat settle on the edges of such oysters and grow until they, in turn, sink into the mud. Formations such as these with a living oyster attached to buried older generations may extend like poles 3 feet or more into the soft substratum. Oysters persist in isolated marsh ponds whose waters connect with the open sea only for short intervals in time of flood or storm. Scattered individuals attach to the roots of marsh grass fringing the bayous and bays or settle secondarily on mussels growing in the marsh. With natural cultch frequently at a premium oysters are found attached to crabs, turtles, and even on the shell of their worst enemy, the drill.

More typically, reefs build up on the sticky mud bottom found in most of the coastal bays and estuaries along the Gulf shore.[1] The foundations of some of these reefs have persisted since prehistoric times. Successive generations of oysters, attaching to the older oysters and dead shells, have created deposits many feet in thickness. The living population forms an infinitesimal percentage of the total mass on such reefs. In other areas, although the reef may have existed for innumerable years, the substratum of shell is relatively thin, comprising little more bulk than that of the living oysters. In these cases, the high population density of commensals, which excavate the valves, and perhaps chemical factors in the environment lead to the rapid disintegration and disappearance of the old shells.

A fundamental requirement in the ecology of the oyster is the mixture of salt water from the Gulf or ocean with the fresh water from land drainage. The characteristics of the growing oyster community, dependent in large measure on the salinity level resulting from the admixture of these waters, are governed not only by the average salinity levels but also by the extremes of seasonal fluctuation in the total salt content. The size of the population and of the individual oyster, appearance of the shell and quality of the meat, reproductive potential, commensals, predators, parasites, all of these and probably a host of other factors have an obligatory relation to the salinity level of the environment.

[1] The formation of oyster reefs in the Gulf of Mexico is discussed in detail by W. A. Price, p. 491.

The majority of Gulf oyster communities fall into one of four distinctive categories which I classify on the basis of arbitrarily selected average salinity levels. Intergrades between the categories and exceptions to the generalizations are necessarily common, but they do not seriously alter the over-all description. Permanent communities establish themselves and flourish within a salinity range of 10 to 30 parts per thousand. In years of drought or of excessive precipitation populations may appear sporadically in areas normally having salinity levels too low or high to support a population.

Oyster reefs located near the head of a typical estuary comprise the first category. In such regions the salinity ranges annually from 15 parts per thousand to 0 and averages near 10 parts per thousand or below. The sparse population reflects the marginal nature of this environment. Oysters are mostly small and rounded, with smooth, whitish shells. The rate of spatfall is low, and although young oysters grow well their first season, growth of older oysters is relatively slow. Average annual mortality rates are high, and the population is periodically decimated by excessive fresh water in years of flood. Primarily, such reefs are of commercial use as seed areas. In the occasional years of drought these populations may show, however, an excellent growth and yield a good harvest. Typically, these oysters are free from most fouling organisms, and there are few predators or parasites present. These oysters have many characteristics in common with populations growing at or above mean low water regardless of salinity level.

The next definite community type is found where salinity levels fluctuate between 10 and 20 parts per thousand with a yearly average near 15 parts per thousand. The population density of oysters on these reefs reaches a maximum because of high reproductive ability, availability of cultch, and a relatively low concentration of predators. The growth of individual oysters is moderately good and quite uniform so that the population forms rather definite year classes. Oyster valves are usually smooth and dense, although in some areas they may have moderate infections of the boring sponge and clam. The oysters form large or small interlocking clusters, depending on the nature of the bottom. Their narrow shape makes them difficult to handle commercially except as canning stock. When cultivated they yield clusters of two or three better shaped oysters that are suitable for the raw trade. The meats are of high nutritional quality but are frequently insipid to the taste. The increased number of associated animals on these reefs leads to intense competition for both food and space. Barnacles and mussels are frequently present in such numbers as to interfere with oyster culture. While these communities prosper biologically in most years, in times of drought they may experience severe losses due to predation by the drill. In flood years the growth of the population may be retarded for several months.

The third category of oyster reefs is found nearer the mouth of a typical estuary, in areas having an average salinity level of 25 parts per thousand. Annual fluctuations in salt content of water range from a low of 10 to 12 parts per thousand in the spring to about 30 parts per thousand in the dry season. The community here is characterized by unusually good growth, although this factor may be masked by the large amount of shell erosion and predation. The variety of animals living within the oyster community reaches a maximum at this salinity level. The reproductive potential of the oysters probably reaches a maximum here too, but the high population density found in communities at lower salinity levels does not occur here because of the large numbers of parasites and predators. Mortality rates of the very young oysters are relatively high. Having survived its first season the oyster's chances for survival are good. The shells have a massive appearance and may be greatly eroded. The valves show heavy concentric ridges, indicating periods of fast growth rates. These communities are consistent producers of large market oysters of excellent quality. But the environment has its greatest value when used as a bedding ground. Medium-sized seed planted here quickly matures and may be harvested before the usual predators and parasites are established. The decreased spat survival prevents the transplanted oyster from becoming "wrapped up" in young growth. The periodic complete harvesting of these areas when used as bedding grounds prevents or greatly retards the accumulation of undesirable commensals.

The fourth type of oyster community is found at the junction of the typical estuary with the waters of the Gulf where salinity levels are consistently high. Although oysters exist here the environment is just as marginal as in the first category considered. The population is again characterized by its sparseness, slow growth rates, and excessive mortality. The dearth of suitable cultch and the high concentration of predators are important factors in the low survival rate of the spatfall. In most years the commercial importance and the reproductive capacity of reefs in this location are of negligible importance. Following disastrous floods this community, by providing larvae, may be the all-important factor in repopulating the flooded areas where the oysters have been destroyed.

Factors other than salinity levels may exert a profound influence in determining the character of the oyster community. The most important among these are the nature of the bottom, the type of cultch, the amount of water current carrying a supply of food, and the degree of artificial cultivation. It is significant that when young oysters are moved to a new environment they quickly acquire the attributes of the population already present there. It is also of interest to note those instances in which a characteristic type of oyster has acquired a geographical name and becomes well-known in the trade. The practical oysterman may discover that there are other geographic locations which produce essentially the same type of oyster; perhaps we find that 100 boatloads of "name" oysters are annually marketed from a geographic area which can produce only 25 boatloads. This should not be regarded as a case of deception on the part of the producer, for a "name" oyster actually implies a certain quality of product, and similar environments can produce oysters of essentially indistinguishable quality regardless of how far apart they may be geographically.

Very specialized communities exist on wharf pilings, especially in channels having a high current velocity. Isolated marsh ponds may produce characteristic populations. Noteworthy among these is the occasional colony of "Marennes" oysters whose flesh is colored a deep green by the abundance of a particular diatom in its food supply.

Natural oyster reefs are still found occasionally and were quite common at the turn of the century. The only essential difference in their appearance from that of cultivated reefs lies in the fact that, being unharvested, the population builds up until it breaks the water surface. At low tide many oysters are exposed to the atmosphere. Growth along the ridges of these reefs is usually less than that of the population average. The shells are polished and have a reduced number of external and internal commensal organisms. The oysters are scattered in small clusters. There is a coarse substratum consisting primarily of shell fragments. Buried inches deep in the substratum and usually growing quite well, considering the seemingly unorthodox position, there is often a fair number of older oysters. Where depth of water over the reef is greater, the clusters of oysters become larger, and the individual oysters attain a larger average size. Although the oysters are very long, they are correspondingly narrow with deeply concave attached valves and flat or even concave upper valves. Attached to the older oysters may be three or four, perhaps more, younger generations. As a rule, the quality of meat of such oysters is inferior, although the amount of spawn produced by them may be tremendous. The periphery of these reefs is often sharply defined, the outermost fringe of oysters showing luxuriant growth, while a foot beyond lies a muddy ooze too soft to support a single shell.

The interdependence of the myriad of animals associated in this oyster community forms a complex system. In a stable environment their numbers and variety are strictly controlled by the availability of habitat niches even though their food supply is primarily obtained from without. Relatively slight changes in the external environment may drastically alter, however, the entire make-up of the community.

This description of the natural oyster community is probably equally applicable to the oyster community of past ages. The evidence for the antiquity of the oyster in the Gulf is impressive, and the early discovery of their value as food is shown by the Indian shell middens which dot the coast line. Vast deposits of buried shell exist in all of the Gulf States. These banks are usually in 8 to 10 feet of water under a layer of mud of varying thickness. The deposits range from a few inches to 25 feet and more in depth, and no one knows their extent. For the most part the oysters on these old reefs did not grow to any larger size, i. e., live any longer, than oysters do today. The average shell size in many deposits is considerably less than that found on a modern reef of planted oysters, and we may assume that they did not compare in quality with the cultivated oyster of today.

The enormous quantity of shells in these buried banks does not indicate an unusually high rate of productivity but rather speaks for the untold eons that passed in the formation of such deposits. These old reefs constitute an extremely valuable resource in modern times, since they are composed of relatively pure calcium carbonate (Shearon 1951). The chemical industries of Texas alone, in the decade beginning 1940, consumed more than 45 million tons of these shells. Similar deposits are extensively exploited in Louisiana and to a lesser extent in the other Gulf States. Examination of these reefs reveals striking similarities to the natural communities we find today. Many of the buried shells show light to heavy infestations with boring sponge; some shells are pitted with excavations like those made by the modern boring clam; encrusting bryozoans are present; and of frequent occurrence are the shells of conchs, quite similar if not identical, with the modern *Thais.*

The diversity of habitats existing along the coast of the Gulf causes a parallel diversity in the pattern of growth and reproduction in the oyster so that we may draw a generalized picture of the course of events and indicate the significant exceptions.

In midwinter the gonad tissue of mature oysters is inconspicuous, but by February or March, depending on water temperatures, active gametogenesis takes place. The gonad may form a layer a quarter of an inch or more in thickness by the time spawning commences in early spring, but frequently its thickness is far less. The gonad layer retains much of its original volume throughout the summer; spawning continues regularly until October. Mass spawnings of the population are clearly defined and typically occur several times throughout the summer in a given location (Ingle 1951). This is in contrast to the condition in northern waters where a single mass spawning of major importance usually occurs in early summer.

Oyster larvae are found in the plankton in the period from April through October. It is probable that their free-swimming period is significantly shorter in these waters than along the Atlantic coast because of the sustained higher temperature levels during the summer months. The production of larvae and the resulting spatfall may show peaks of intensity in any one or all of the summer months. At Pensacola the pattern is quite variable from year to year, but during the month of July larval production and spatfall are consistently lower than during the rest of the spawning season. These conditions contrast significantly with those on the Atlantic coast. In Long Island Sound, for example, although there is scattered spawning during the summer period, the majority of spawn is produced in a relatively short time about the end of June (Loosanoff and Engle, 1940). The relative abundance of larvae in the plankton at Pensacola in the period 1949–1951 shows a good correlation with the spatfall in the area, although the quantity present at any one time seems small in comparison with the amount of set produced. In this area there are no commercial reefs; the oyster population is confined to pilings and similar locations out of reach of the conch. In Mississippi Sound, where the oyster reefs are extensive, 50 percent of the volume of plankton samples collected during the height of the spawning season may consist of oyster larvae.

Spat production is heavy but erratic all along the coast; in certain localities spatfall and survival are particularly good. As is true on the Atlantic coast, the areas of best spatfall are frequently areas of relatively poor growth. From the earliest times Louisiana oystermen transplanted seed oysters from setting grounds east of the Mississippi and placed them in areas west of the delta where growth is especially rapid. It is quite possible that the poorer record of spat production in high salinity areas is due to predation rather than to a real decrease in setting rates. In the Pensacola area the cumulative spatfall during a season may be as high as 1,000 spat to the square inch. This intensity of spatfall poses a significant problem to the oyster industry. In areas where oysters set heavily they become so clustered in their growth that they are difficult to handle commercially and have meat of inferior quality.

Competent observers have reported spatfall during other months of the year at widely separated points along the coast, but these instances are exceptions to the general picture of larval production. The number of spat produced under these circumstances is always quite small. The most reasonable explanation for this situation is that oysters on the mud flats are induced to spawn sporadically in the wintertime because of the sharp elevations in temperature which may take place in small, poorly circulating bodies of water. Water temperatures of 10° to 20° C. in the main bays and estuaries during the winter are not high enough to permit spawning but may permit the growth and setting of the larvae produced in isolated bayous and marsh ponds.

Growth rates of oysters in the Gulf are reputed to be astounding when compared to the rates along the Atlantic coast. This reputation is based on impressions of oystermen, a few fortuitous natural experiments, and a very meager amount of scientific data based on exceptional conditions. It is certain that during its first year the oyster grows to a length of two or more inches on the average. Under special circumstances and under experimental conditions at Pensacola a growth of 3 and 4 inches has been obtained in 12 months. It should be noted that a growth of 2½ inches during the first season is not at all unknown in the Chesapeake area, and July spat have been reported growing to a length of 2¾ inches before their first hibernation period in Virginia (Mackin 1946). Since the growth of oysters in the Gulf is not interrupted by a hibernation period, it would be more surprising if they did not grow up to 3 inches during their first year. In those cases where oysters grow 5 to 6 inches in 24 to 36 months, and there are many such instances, the oysters are usually of the inferior "coon" type. Oysters growing in crowded positions can increase in size only in one direction, and so they soon become unusually long. Oysters growing as "singles" can increase in size in all directions, and single oysters in the Gulf do not exhibit unusual growth rates after their first season (Moore and Pope 1910). Cultivation procedures developed since 1900 by oystermen in Louisiana involve the transplantation of year-old seed to better growing areas and the marketing of the oysters from 18 to 24 or more months later. Good-sized market oysters produced along the Gulf coast probably average three or more years in age. In the Gulf area major increases in growth, measured by length and width, take place in the months of November through March when water temperatures range from 10° to 20° C. The major increases in size in New England oysters take place in the summer months at similar temperature levels (Loosanoff and Nomejko 1949).

The time required for a Gulf oyster to reach sexual maturity is significantly shorter than in northern waters (Menzel 1951). Approximately one-third of the oysters setting in the early part of the summer become sexually mature by the time they are a month old and still less than an inch in diameter. It is probable that a majority of the spat attain sexual maturity during their first season and make a significant contribution to the larval population of late summer. In other words, it is a normal event for two generations of oysters to be produced in this area each summer.

During the past century there have been many changes of a temporary or permanent nature in the continuity of oyster communities and in the physical location of the reefs. Man has caused or accelerated many of these changes. Other changes due to the natural succession of events in an estuarine environment are presumably of no greater importance today than they were in prehistoric times.

The many rivers draining into the Gulf annually deposit an enormous load of silt which produces multiple effects in the estuary. The major silt load deposited in the delta gradually pushes the head of fresh water seaward. In the past 50 years the Colorado River has filled in more than 6,000 acres of upper Matagorda Bay, and delta mud now lies on top of once productive oyster reefs (Baughman 1947, unpublished ms.). In its progress to the sea the water carries much silt with it, and this has additional effects on the oyster population. It decreases the penetration of sunlight into the water, thus limiting the production of plankton, the oyster's food supply. Fine silt, by coating the old shells on the bottom, makes them no longer available as cultch for the young oysters (Butler 1951).

An entirely different type of change has been brought about by man in the oyster areas west of the Mississippi River. In this region a number of bayous in the past contributed a regular supply of fresh water to the bays and inlets along the coast. Man has channeled these bayous and changed their exits to the sea so that they contribute

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fresh water to the area only in times of flood. As a result of these changes in the drainage system the inner bays and lakes lying some distance from the coast, formerly entirely fresh, have now become saline enough to support large populations of oysters. Connecting bays lying between them and the Gulf have, in turn, become more salty The increased salt content here encouraged the survival of the conch which has decimated or destroyed entirely many large reefs (Moore and Pope 1910). A secondary result from this channeling has been an increase in erosion along the shore. The annual load of silt brought down by the rivers or bayous no longer reaches the coastal areas, where in the past it counter-balanced shore erosion and created a fairly stable coast line. Shore erosion, now uncompensated, has destroyed some of the barrier reefs; formerly protected bays are now open to the Gulf and cannot support oyster populations. Conversely, some bays which formerly had connecting channels to the Gulf have become landlocked by sand spits, and their oyster communities have largely disappeared. There probably has been no great net change in the amount of bottom available for oyster culture, but the reefs have migrated inland away from the sea and have become more susceptible to the effects of seasonal floods in their new location. There are some places along the coast where man has opened up channels and deposited spoil banks in the construction of inland waterways. These operations have frequently changed salinity levels permitting an increased survival of oyster predators and, in some cases, have buried reefs in mud.

Extensive changes in oyster communities have also resulted from harvesting methods. Redfish Reef in Galveston Bay, which was more than 5 miles in length, produced a large annual harvest throughout the nineteenth century. In 1890, by the use of a tug and two power dredges, this reef was eradicated in a single year (Baughman 1947, unpublished ms.). Overharvesting without replacement of shell cultch inevitably causes the deterioration of a reef. In places where overharvesting has continued until the dead shells supporting the reef as well as the live oysters have been removed, it has been a matter of but a few years before the area deteriorated to such an extent that even nature could not rehabilitate it.

Oyster reefs are normally established in positions protected during average storm conditions. The occasional hurricanes experienced in the Gulf area may destroy large numbers of oysters in shallow water areas and on sandy bottoms. In 1947, for example, many miles of reef along the north edge of Mississippi Sound were covered with mud by wave action and destroyed (Engle 1948). This area has shown no significant natural rehabilitation in the past 5 years.

We have mentioned some of the factors which may permanently eradicate the oyster reef. There are other items which are of greater or lesser importance in affecting the continuity of the populations.

Crevasses.—Disastrous but relatively temporary changes result from exceptional floods from the river basins. In 1890 the flood of the Nita crevasse extended east from the Mississippi River and affected oyster reefs 180 miles away in Mississippi Sound. Forty miles of oyster reefs lying between Lake Borgne and Biloxi were seriously damaged at that time. The history of floods of the lower Mississippi River shows that, although they may wipe out huge oyster populations in a short time, these populations are quickly reestablished, often at a more luxuriant level than prior to the crevasse. The annual spring floods occurring in most river basins cause some mortality in the oyster population by lowering the salinity of the water, but in most years these losses are insignificant.

Temperature.—The oyster is extremely versatile in adapting itself to changes in temperature and is commonly found where the annual range is from $-2°$ to $+30°$ C. The Gulf oyster is less accustomed to severe cold weather than its Atlantic coast relatives, and occasionally large numbers of oysters growing at mean low-water level are destroyed during sudden winter freezes.

Pollution.—Pollution has constituted a serious factor in the continuity of oyster populations during the past 50 years, but due to more effective control measures, it is becoming of less importance. Oysters have been destroyed in several areas by the effluent from paper mills, for example, and other industrial wastes are reputed to have damaged large oyster-growing areas. The control of industrial wastes no longer constitutes an unsolvable problem. Pollution resulting from domestic sewage [2] is of great importance, not as it affects the survival of oysters, but as it affects their food value to man. On the west coast of Florida alone, more than a dozen shellfish-producing areas have been closed to harvesting as a health measure (Vathis 1950). To some extent all of the Gulf States are faced with this problem. Actually, the closing of polluted areas to harvesting constitutes a conservation measure as far as the continuity of the oyster population is concerned, but it results in a deplorable waste of a valuable food resource since satisfactory control measures are known.

Disease.—The oyster is undoubtedly afflicted with a large number of diseases, but their effects upon the animal are, for the most part, imperfectly known. The recent demonstration of the infection by the fungus *Dermocystidium marinum* is a significant contribution to our knowledge of the pathology of the oyster in the Gulf. The harmful effects of this parasite are greatest at high temperatures and high salinity levels (Mackin 1951).

Some specific parasite may be the causative agent of the disastrous mortalities which occur among transplanted oysters in some areas of Louisiana during the hot summer months. These mortalities, ranging from 35 to 95 percent of the population in different areas, were unreported 20 years ago. Their frequent occurrence since that time has necessitated entirely different cultural techniques. Now, oysters for rebedding purposes in these areas must be large enough so that a few months' growth will make them suitable for marketing. In the past it was the practice to bed much smaller seed oysters and let them grow for 18 months or longer before harvesting (McConnell 1950).

Oysters are widely subject to infestation with the sporozoan parasite *Nematopsis*. There is no evidence, however, that this micro-organism debilitates or is the cause of mortalities in the oyster (Landau and Galtsoff 1951). Of less common occurrence is the digenetic trematode, *Bucephalus*, whose larvae develop in and cause the deterioration of the oyster gonad. Several other unspecified diseases, as well as infections with bacteria, have been reported recently for oysters in Barataria Bay (Mackin 1951). It is probable that none of these diseases greatly affects the reproductive potential of the oyster community.

Predators.—Man has been the most serious threat to the continuity of oyster populations because of his wanton methods of overharvesting. Overharvesting in the past has taken the form not only of removing all the oysters from the reef but also of removing the underlying cultch which made the reef possible. Reefs so destroyed do not rehabilitate themselves naturally, and the cost of replacing the foundations is not feasible economically. Fortunately, our increased awareness of this problem during the past 50 years has reduced the threat of overharvesting except in isolated areas.

The most serious natural predator of oyster populations in the Gulf area is the conch or oyster drill, *Thais*. The two forms of this species have slightly different appearances; *Thais f. floridana* occurs mostly east of the Mississippi River and *Thais f. haysae*, primarily west of the river (St. Amant 1938). Depredations due to this conch are incalculable. In the Pensacola area and in the southern reaches of Barataria Bay, for example, it makes oyster culture impossible. The snail is distributed wherever oysters are found at salinity levels averaging above 15 parts per thousand. Its populations are periodically decimated in times of flood and show enormous increases in times of drought. The snail reproduces during the summer months simultaneously with the oyster. Large individuals may deposit a half million eggs which develop into free-swimming larvae. After a plankton stage of unknown duration the young snails settle to the bottom and commence feeding on oysters and other sedentary forms. Snails a millimeter in length and a week old can be found actively drilling oyster spat of the same size and age. Large snails have been observed by the author eating spat at the rate of four per hour under experimental conditions. The snails are known to live for at least 3 years and possibly many more under normal circumstances. Its voracious feeding habits, high reproductive capacity, and the fact that its larvae are distributed by water currents combine to make this snail the most destructive oyster predator in the Gulf environment. A few other gastropods present, such as the moon snail, *Polynices*,

[2] A detailed account of pollution in Gulf water is given in the last chapter of this book, pp. 555–575.

may feed on oysters to a limited extent, but their relative importance has not been studied.

The Gulf area is fortunate in not having to contend with the starfish which constitutes so serious a predation problem along the Atlantic seaboard. The black sea drum, *Pogonias*, is described frequently in the literature as a serious pest in the Gulf area (Moore 1907). This writer has no first-hand experience with its activities, but oystermen report it as a nocturnal visitor to areas containing newly bedded oysters. Large schools of fish may destroy thousands of bushels of oysters in a short time. Apparently this fish does not attack the natural oyster reefs.

Various species of crabs constitute a serious but imperfectly defined menace to the oyster population. The blue crab, *Callinectes*, is a common inhabitant of the oyster reef, and there are many observations of its activities in cracking open the soft new growth on oyster shells and eating the meats. In limited areas the stone crab, *Menippe*, is an occasional marauder. Its massive claws are able to crack open oyster shells with ease. Mud crabs of the family Xanthidae inhabit the oyster community in large numbers and undoubtedly consume many of the tiny spat. The list of predators includes the oyster "leech," *Stylochus inimicus*,[2] and other polyclad flatworms of several species which are common associates in the oyster community. These worms may cause serious damage, but evidence indicates that they are secondary rather than primary predators (Pearse and Wharton, 1938). They cause the greatest harm in areas where oysters are already in a weakened condition because of some other factor. In the healthy oyster community they are probably of little importance except in their role as scavengers.

Commensals.—Three commensal animals occur in numbers sufficient to affect the biology of the oyster seriously. However, their injurious effects are of greater importance to the oyster industry than to the continuity of the species. The boring sponge, *Cliona*, the boring clam, *Martesia*, and the blister worm, *Polydora*, dwell within the oyster shell, existing at various population densities depending upon the environment. The sponge and clam are more prevalent in areas of high salinity. The annelid is more commonly associated with soft, muddy bottoms extending into areas having lower salinity levels. All of these animals compete with the oyster for food. Their injury to the oyster is difficult to evaluate, but obviously they force it to secrete excess amounts of shell in order to keep the burrows of these organisms separated from the oyster meats. Both the sponge and clam form extensive excavations opening on the exterior surfaces of the shells, making the shells friable and hard to handle commercially. Such oysters usually have a massive eroded appearance, and typically, the meats are of inferior quality. The annelid lives on the internal surface of the valve where it is sealed off in a blister by the oyster. Its injurious effect is primarily a decrease in the esthetic appeal of oysters on the half shell, although in areas outside of the Gulf unusually large colonies of these worms have suffocated oyster communities.

The commensal crab, *Pinnotheres*, of frequent occurrence in oysters in high salinity areas along the Atlantic coast where it may be occasionally injurious, is uncommon in the Gulf. A related species, however, is often present in the bay scallop in Florida waters.

The animals and plants associated with the oyster community are legion. Some have importance in competing with the oyster for attachment surface, and some in competing for food. Their biological and economic importance to the oyster population are mostly a matter of conjecture. The relative abundance of the commensal forms varies greatly from one oyster reef to another. In low salinity areas these forms are relatively rare, but their numbers increase to species climax at different higher salinity levels. The following listing of the more common members of the community does not indicate their relative numbers or importance; any one of them at some time or place may completely envelop the oysters, decreasing the available food supply and preventing the attachment of oyster spawn:

- Algae, of various types.
- Sponges, both encrusting and boring.
- Hydroids and anemones.
- Polychaete worms.
- Other mollusks, including *Anomia*, *Crepidula*, *Ostrea*, and *Mytilus*.
- Barnacles.
- Bryozoa, both encrusting and upright.
- Tunicates.

[2] *Stylochus frontalis* Verrill according to L. H. Hyman. See page 301 of this book.

In discussing the competition among sedentary organisms for space on the oyster reef it is important to note that in some areas the oyster is its own worst enemy. Huge numbers of spat settle in areas large enough to support only one or perhaps two adult oysters. Obviously, in the struggle for existence, the faster growing spat soon overrun and smother their neighbors. Where available cultch is limited, spat mortality may be enormous.

At the turn of the century the United States Bureau of Fisheries made notable contributions to our knowledge of oyster biology in the Gulf by conducting extensive surveys at the request of the several States. As a direct result of these studies, conservation laws were enacted in Louisiana which greatly stimulated the oyster industry. Oyster cultivation practices were improved, and production increased significantly (Seferovich 1938). Oystermen of that State made a regular practice of obtaining seed oysters from reefs in low salinity areas east of the Mississippi River and replanting or bedding them west of the river in bays where salinity levels were higher and the environment fostered rapid growth. Such oysters became suitable for the market in 18 or more months.

In the past 15 years this culture method has changed radically because of high summer mortalities. As a result, the seed which are now bedded are actually market oysters, and they are relaid for only a few months before harvesting. Today, Louisiana is foremost among the Gulf States in conducting an active shelling and seed planting program, but other States are becoming increasingly active in this regard. It is significant that in Texas, where the least has been done in providing cultch for spat, the industry has seen its greatest decline.

Although the oyster has greatly decreased in many sections of our Atlantic coast line because of man's activities, it is improbable that the immense oyster population of the Gulf could be eradicated. However, there are many once productive areas in which the industry is now nonexistent because of over harvesting and lack of cultivation. The industry faces many problems in the Gulf area. A majority of them could be resolved by the application of well-known and tested cultivation techniques by the enactment of sound conservation measures based on established data and by the enactment of legislation which would stimulate production as well as protect the private planter.

One of the unsolved problems in the Gulf area is a method for economically controlling predation by the conch. When these methods are discovered, large and valuable areas that are now useless can be cultivated. Another and rather curious problem exists because of the unusually intense spatfall in many regions. On the North Atlantic coast the first problem of the industry is to procure sufficient seed oysters for cultural purposes, while along the Gulf coast the problem is to dispose of the superabundance of seed. The too heavy spatfall produces badly clustered, misshapen oysters; oysters that are almost impossible to separate for market purposes without killing more than are saved. Oysters growing in this manner rarely yield a select product. It will be necessary to devise new cultural techniques to utilize this tremendous spatfall. These methods must permit the attachment of only two or three oysters to a piece of cultch and still supply enough cultch so that the vast numbers of spat present are not lost to the industry.

An economic problem of perhaps greater importance is a need for the controlled use of mechanized equipment in cultivating and harvesting the crop. The short supply of labor is a significant factor in the lowered production of the industry. Hand methods are largely retained because their inefficiency constitutes, in a negative way, a conservation measure. But oystering with hand methods is hard work and good cultivation requires nearly year-round attention. As a result, the labor pool is largely claimed by the shrimp industry which offers high returns for a relatively short season. The question of using tongs or power dredges on the reefs is a recurrent argument.

It is not irrelevant to consider, on a theoretical basis, just what the Gulf oyster industry could produce in terms of food for man. Scientific plantings made in Louisiana 50 years ago, the experience of planters in that State since then, and recent work done in Florida, all provide parallel figures on which to base our estimate. An acre of good oyster bottom, properly handled, can produce 900 bushels per year under exceptionally good circumstances, and in commercial practice a yield of 500 bushels can be obtained. For this estimate I have arbitrarily selected a figure of 300 bushels per acre per annum. A bushel of Gulf oysters will yield 4 pounds of completely drained meat. When we assume that at least 1,400 square miles of Gulf oyster bottoms could be put into production, we find that on a sustained yield basis the industry could produce in excess of 500,000 tons of oyster-meat each year. The entire production of the United States now approximates less than 10 percent of this figure.

There are at least three other species of oysters in the Gulf, all members of the genus *Ostrea* (Gunter 1951b). *O. equestris* is a small species occurring discontinuously from Texas to Florida. *O. frons* has been reported most frequently from southern Florida, but it exists at Pensacola and has been found off the Texas coast. These two are quite similar; they exist at salinity levels usually above 25 parts per thousand and are most commonly found at the junction of Gulf and bay waters. Their setting periods coincide with the spatfall of *C. virginica*. In areas where one of these species occurs with *C. virginica* they may be confused because of their superficial similarity when about an inch in diameter. Large numbers of *O. equestris* were actually transplanted in Apalachicola Bay at one time on the mistaken assumption that they were seed of the commercial oyster. In the fall months *C. virginica* spat quickly surpass the spat of *Ostrea* in length. At the age of 1 year, *O. frons* and *equestris* still approximate one inch in both length and width, although rarely they attain a length of 2½ inches in an unusually favorable environment. Internally, both *O. frons* and *equestris* are distinguished from *C. virginica* by a variable number of denticles on the anterior edges of the valves and by the absence of pigment in the muscle attachment area. These oysters are larviparous, and during the summer months the mantle cavity frequently contains large numbers of offspring in a manner similar to the European oyster, *O. edulis*. Spat of the three oysters, *O. frons*, *O. equestris*, and *C. virginica* were found in abundance on the same cultch at Pensacola during the summers of 1949 and 1950. This mutual occurrence of the three species in time and space is probably infrequent. A third species, *O. permollis*, the sponge oyster, is rather common on the Florida coast in shallow water. It is a small, flat oyster, up to 2 inches in length, yellow brown in color and most frequently found living inside of masses of the bread sponge.

The ecology of the oyster in the Gulf of Mexico parallels, in many respects, conditions found along the Atlantic seaboard. Where significant biological differences exist between the two areas, they are due primarily to the higher temperature levels of the Gulf environment. The biological and economic problems facing the industry here have their counterpart in other oyster producing areas. The industry in the South can include among its distinctive advantages an unlimited area for the expansion of cultivated grounds and a seemingly inexhaustible supply of seed oysters.

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OYSTER REEFS OF THE GULF OF MEXICO[1]

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Caswell Grave (1901, 1905) showed that linear, ridge-shaped reefs of the common edible estuarine oyster now known as *Crassostrea virginica* develop from shell clusters at the more favorable shoreline or near-shore positions, growing out into a passing current and elongate at right angles to it, then branch or curve as the current is deflected by reef extension. This process seems to be valid for the reefs found in the bordering areas of many bays and estuaries. Another class of reefs, elongated parallel with median channels, does not follow Grave's process of terminal growth into a current from its flank but forms along a channel and elongates parallel with the dominant currents of the channel. Paired reefs of this type are found in many inner water bodies, as in central San Antonio Bay, Texas, and the lower James River, Virginia. The reefs of Atlantic estuarine rivers seem usually to be merely elevated ridges on large, oval to quadrate oyster beds. Those of the Gulf coast are not characteristically surrounded by thickly occupied oyster bottoms except along their immediate flanks.

Besides the linear ridge-shaped reefs, many short ridges, or rounded to oval forms are charted, locally called tow-heads.

Mudshell dredgers report that some reefs have a total depth of some 18 feet or more, in places with an interbedded layer or two of mud. Many reefs of Texas bays reach lengths of 1 or 2 miles, a few being 4 to 5 miles long. The longest reef complexes known are the two that curve broadly across the wide mouth of Atchafalaya Bay, Louisiana. The outer, more recently active reef complex is 25 miles long with many narrow channels through it. The older is dead and buried by several feet of sediment.

The known oyster reefs of most regions occur in the inner bays and estuaries in waters neither too exposed to heavy wave action nor too fresh from incoming alluvium-laden river waters. They seem to form chiefly on the more stable bottom areas. Along parts of the northwestern coast of peninsular Florida (28°15′–30°04′ N. Lat.), off the mouth of Atchafalaya Bay, Louisiana, and on the south and west shores of Marsh Island just west of the bay, reefs of *Crassostrea virginica* occur in the Gulf of Mexico within 5 or 6 miles from shore. Here, the Gulf waters are locally diluted to the necessary brackishness.

Several of the small reefs off Atchafalaya Bay have live oysters. Here a large flow of fresh water from the Mississippi enters the Gulf through its largest distributary, the Atchafalaya River. Off the northwestern coast of Florida compact limestones form the floor of the shallowly submerged continental shelf. The peninsula has a widespread artesian water body fed by surface waters entering through the extensively fissured limestones and the many sink holes of the karst topography. Numerous up-welling springs are reported in the stream mouths along this coast, and a few have been reported in the Gulf. The very broad, shallow, gently-sloping continental shelf protects the near-shore waters from breakers and surf, producing conditions in the Gulf similar to a lagoonal environment. The oyster reefs occur in these quiet waters of lowered salinity. They are distributed near shore where the artesian groundwater maps show the 10-foot contour on the piezometric surface to be at the shoreline. These Gulf reefs include forms that project out from a shoreline and also broadly curved and offset forms that are roughly parallel to the coast. Groups of the latter have jumbled patterns of occurrence.

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