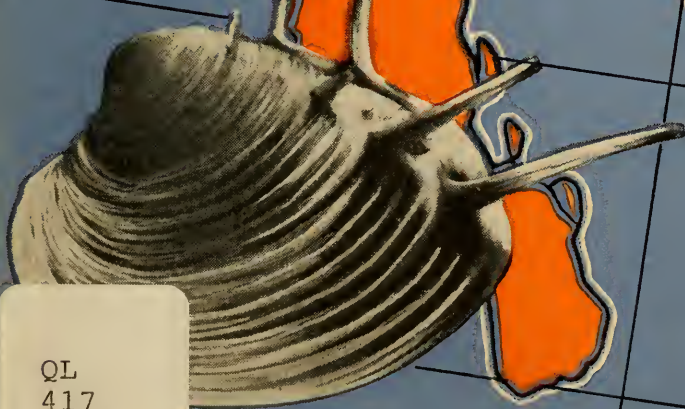


# ZOOGEOGRAPHY AND ECOLOGY MACRO-INVERTEBRATES

GULF OF CALIFORNIA  
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CONTINENTAL SLOPE  
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# ZOOGEOGRAPHY AND ECOLOGY OF SOME MACRO-INVERTEBRATES, PARTICULARLY MOLLUSKS, IN THE GULF OF CALIFORNIA AND THE CONTINENTAL SLOPE OFF MEXICO<sup>1</sup>

With Plates I-XV

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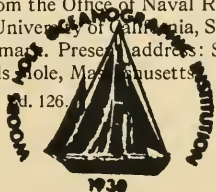
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### Abstract

A reconnaissance study of the zoogeography and ecology of benthic invertebrates in the Gulf of California and on the continental slope off west Mexico was carried out during the years 1958-1963. A series of characteristic assemblages were devised for various environments found in the Gulf of California, derived from both 272 biological samples and the distribution of approximately 1,150 identified species of invertebrates. Using a contingency matrix of common occurrences of 280 common species of invertebrates, compiled by a digital computer as a basis for preliminary analysis it was possible to designate 12 separate assemblages of invertebrates. These assemblages reflected distinct environmental regions of uniform depth, sediment, water temperatures and oxygen concentrations.



These environments and their assemblages are as follows: I. Intertidal and shallow rocky shores; II. Intertidal beaches and sand flats to 10 meters; III. Low salinity lagoons and mangrove mudflats; IV. Nearshore shelf, sand bottom, 11–26 meters; V. Intermediate shelf, clayey-sand to sandy-clay bottom, 27–65 meters; VI. Outer shelf, clay bottom, southern Gulf, 66–120 meters; VII. Outer shelf, sand bottom, northern Gulf, 66–120 meters; VIII. Northern Gulf basins and troughs, 230–1,500 meters; IX. Upper slope, central and southern Gulf, 121–730 meters; X. Middle slope, 731–1,799 meters; XI. Abyssal Southern Borderland basins and lower slope, 1,800–4,122 meters; and XII. California Borderland basins, 1,641–2,358 meters (limit of sampling).

The outstanding feature of the shallow water assemblages in the Gulf of California is the great diversity of species in any one environment. A survey of benthic communities throughout the world, revealed no parallel to this great diversity, whether in tropical or boreal regions. As many as 120 species of living mollusks were taken at numerous stations in the Gulf in less than 60 meters. A check of unsorted dredge samples from off Panama, revealed the same diversity there, indicating that great diversity must be a characteristic of the Panamic province as a whole. No more than a few individuals of any one species were taken by a grab or dredge at any one station. Diversities were verified by cumulative curves based on quantitative samples, compared with those made for European waters.

A preliminary survey was made concerning the relationship of general feeding types of invertebrates to the various environments. This survey indicated that suspension feeders outnumber other feeding types on the shallow sandy and intertidal rocky bottoms, while detritus feeders and scavengers outnumber other types on clayey bottoms and at greater depths. Although this is in accordance with other communities studied elsewhere, the Gulf of California assemblages differed in the presence of a tremendous number of predators, which remained rather constant from shore to abyss. The relationship between feeding types and sediment type did not hold true in the deeper portions of the shelf, where upwelling and associated high surface productivity are a common phenomenon. Regardless of sediment type in these regions, suspension feeders still predominated. Preliminary examinations of soft parts of some of these suspension feeders indicate that they may capture the abundant organic detritus as it rains down from the surface. There were also indications that there is a close relationship between environment and larval development of mollusks. Differing larval development of mollusks also offers an explanation for some of the disjunct distributions of many forms along the coast of Middle

America, and possibly contributes to the great diversity of species in some groups.

The distribution of shell remains in the sediments of the Gulf of California gave indications as to the past history of the Gulf. Presence of shallow-water species of shells in certain preferred depths indicated that formerly, the sea level stood much lower than at the present time. Dates for some of these shallow-water assemblages at the edge of the shelf, in about 110 to 115 meters, revealed that the ages ranged from 17,000 to 19,000 years B.P. Shells of typical California province (colder) shelf species were found in great abundance in the deeper sediments of the northern Gulf basins and troughs. Some of these were also found in deep waters at Cape San Lucas. This implies that during the colder Pleistocene and lowered sea level, many species of mollusks were able to migrate almost 700 miles to the south and up into the Gulf of California. A few of these species were taken alive, but only in the deep areas of the northern Gulf. Here the hydrographic conditions are similar to those now found off California in shallower depths, since intense tidal mixing brings about virtual isothermal and isohaline conditions from surface to bottom, with stable temperatures of between 12° and 15°C.

Qualitative comparisons were made between macro-invertebrate assemblages as found in the Gulf of California and Gulf of Mexico, as well as some counterparts in other parts of the world. The characteristic species of the Gulf of California environments appear to have exact counterparts, usually at the subgeneric level, in similar environments throughout the tropics and sub-tropics of the world.

### **Introduction**

The search for new means of recognizing ancient environments of deposition has utilized many methods and scientific disciplines. It has usually been assumed that the most successful way of attacking this problem is to thoroughly understand and recognize the various modern environments and the factors which characterize them. With this concept in mind, a long-term study of modern sediments was instigated by the American Petroleum Institute, under Scripps Institution of Oceanography in 1951. The results of this study are well-known to many, being a study of nearshore depositional environments in the Gulf of Mexico. The author spent some eight years in the study of the distribution of the larger or macro-invertebrates, living in or on the bottom, using them as primary indicators of Recent environments. These results have been published over

Fig. 1. Place-name map of Gulf of California region.



Fig. 2a. Station locations of biological samples, Gulf of California and west coast of Baja California.

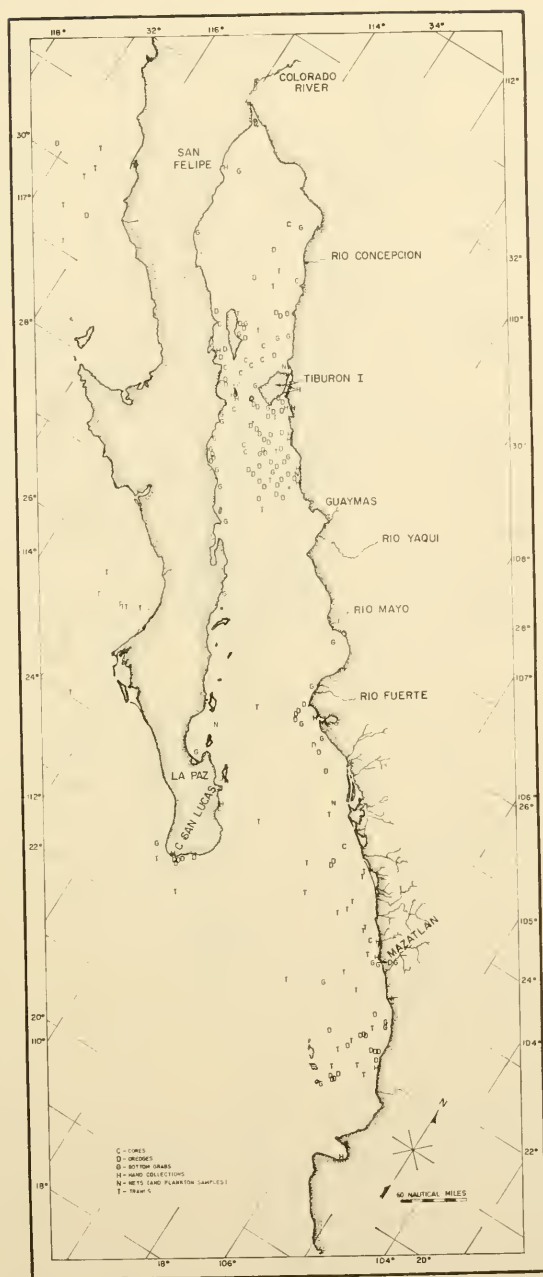


Fig. 2b. Distribution of types of sampling devices within the area of concentrated study. It can be seen from this figure that most of the stations in the sand flat and nearshore region in the southern Gulf and western side are grab samples. The majority of samples in the Tiburon region are shell dredge samples, the southern Gulf are trawl samples, the northern Gulf basin are core samples, and most of the slope samples were taken by trawls.



a period of years (PARKER, 1955, 1956, 1959, 1960, and PARKER and CURRAY, 1956), and were summarized in a volume by SHEPARD, *et al.* (1960).

The Gulf of Mexico provided one particular setting for depositional environments, but because of its climate, geography and geologic setting, did not include many of the modern counterparts of the ancient environments. For this, and other reasons, investigations were transferred to the Gulf of California (fig. 1) in 1958, which in its climate, geology and geography is a completely different type of region. Whereas the macro-invertebrate investigations were concentrated in the lagoons, bays and continental shelf of the Gulf of Mexico, the investigations of the Gulf of California took place mostly in depths of 10 to 35 fathoms (18 to 64 meters) on the continental shelf, and to depths of over 2,000 fathoms (4,000 m.) on the slope. Virtually no sampling was carried out in the lagoons, bays and river mouths. The investigation of the Gulf of California was also limited as to the number of stations occupied. Although nearly 2,000 biological samples were taken during the eight years of collecting in the Gulf of Mexico, only 200 stations were occupied in the Gulf of California. The present study cannot be considered more than a reconnaissance which gave an indication of the gross assemblages of deposition. It will, however, give some idea of where detailed studies could be carried out and provide a basis for a more comprehensive program.

The term assemblage is used throughout this study, since both the living organisms and the shells and tests of previously living animals found in the same samples were also included in the analyses. Biological communities are generally considered an interdependent assemblage of living animals (and plants) which are geographically bound by the various ecological factors within a biotope. Most animal communities are regarded as more discrete aggregations of abundant organisms, which are suspected to be more or less dependent upon each other. Because of the diversity of life found in most of the Gulf of California environments and the variety of gear (most of it non-quantitative) used, one had the feeling that each sample might be considered a separate community. It was, therefore, more convenient to designate assemblages, loosely bound together by a number of species, which although possibly not abundant or dominant in the quantitative sense, are found frequently enough throughout the biotope to be considered indicative of the biotope.

Not all of the stations occupied in this study were taken in the Gulf of California proper, since portions of the program were carried out as a study of the faunas of the continental slope. Those stations concerned



Fig. 3. Station locations of biological samples, continental slope from San Francisco, California to Guatemala. Bathymetry from Parker (1961).

primarily with the environments of the Gulf of California are located on figure 2a, while the stations taken primarily on the continental slope from California to Guatemala are shown on figure 3. As in the previous studies in the Gulf of Mexico, many kinds of sampling devices were used (fig. 2b). A series of Petersen and Van Veen grab samples were taken which could be compared with grab samples from other regions, although the total area covered by these samples ( $2.8 \text{ m}^2$ ) is so small that no direct comparison can be made between the Gulf of California region and other regions where more intensive bottom studies have been carried out using quantitative gear. The majority of shallow-water samples were taken with a small shell dredge, towed for five to ten minutes, or otter trawls. All sizes of trawls, the large beam trawl and the deep-diving dredge had inner net liners constructed of the same size mesh, about 1 cm. in diameter. The deeper stations were all taken with large beam and otter trawls or the high-speed, deep-diving dredge (ISAACS and KIDD, 1953).

Although physical and chemical measurements were not taken with every station, a large body of environmental data already existed from this and other investigations of the Gulf of California. Nearly every biological station had a sediment analysis made specifically for that station, or an excellent sediment map existed for the region where the stations were taken (see VAN ANDEL, et. al., 1964, in press). Depths, bottom-water temperatures, bottom-oxygen values, and, in some cases, salinities were also taken with the biological stations, or else the necessary data for the specific areas sampled were available from other sources. The principal physical factors considered in explaining the distribution of invertebrates in the Gulf of California are, therefore, depth, sediment, bottom-water temperature, salinity, turbulence or upwelling and oxygen.

There are also many biological factors which may be important in limiting the distribution of benthic faunas. For this reason, some of the research has been carried out at the Zoological Museum and Marine Biological Laboratory of the University of Copenhagen, Denmark, where a great accumulation of knowledge on the life processes of benthic marine invertebrates is to be found. The combination of associated physical factors, relation to marine geomorphological features, and dependence upon biological factors among the organisms themselves, should describe these sedimentary environments (on a faunal basis) in such a way that the interpretation of depositional environments of more ancient basins may be made a little easier.

### Acknowledgments

A large number of people both at the Scripps Institution of Oceanography and at the University of Copenhagen have contributed assistance and ideas to this study. First and foremost, the staff of the American Petroleum Institute, Project 51, especially J. R. CURRAY and T. J. VAN ANDEL, made it possible to carry out the sampling program. FRANCIS P. SHEPARD also contributed ship time from his own portion of the "Vermilion Sea Expedition" in 1959. R. W. ROWLAND, formerly of Scripps Institution, contributed valuable assistance in the field and in the laboratory, making it possible to assemble the data together into some semblance of order before the author left for Denmark. JERRY COOK, GAIL COOK and LINDA LIGHTBOWEN, summer students under a National Science Foundation program, also helped immeasurably in the compilation of data.

The Computation Facility, University of California, San Diego, and, in particular, EARL FERGUSON, ANNA DEVORE, ROBERT and EILEEN MITCHELL, were responsible for devising the computer programs used in this study. Without their assistance it would have been impossible to verify many of the assemblages on an objective basis.

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The author is also deeply grateful to the Zoological Museum of the University of Copenhagen for permission to use their facilities, collections and personnel during the period used to crystalize the thoughts and ideas in this paper. He is particularly indebted to HENNING LEMCHE, JØRGEN KNUDSEN, and especially to NIELS BJARNOV, for their criticisms and assistance. Valuable ideas and information were also gained from the University of Copenhagen, Marine Biology Laboratory, Helsingør, Denmark, particularly from GUNNAR THORSON, who has critically read the manuscript, Å. MØLLER CHRISTENSEN and W. K. OCKELMANN.

A large number of specialists agreed to identify the invertebrate groups which were unfamiliar to the author, and graciously donated their time to those identifications. Without their assistance, it would have been impossible to compile the immense list of organisms contained in this study. A list of these specialists and the groups sent to them is appended.

Dr. EDWARD C. ALLISON, San Diego State College	Hexacorallia
Dr. FREDERICK M. BAYER, University of Miami, Florida	Octocorallia
Dr. S. STILLMAN BERRY, Redlands, California	Micro-mollusks
Dr. LEO BERNER, National Science Foundation, Washington, D.C.	Salpa
Dr. CARL BOYD, Dalhousie Inst. of Oceanography, Halifax, Nova Scotia	Galatheaidea
Dr. EDWARD BRINTON, Scripps Institution	Euphausiacea
Dr. WILLIAM G. CLARK, formerly Scripps Institution	Mysidae
Dr. ARTHUR H. CLARKE, Jr., National Museum of Canada, Ottawa	Abyssal Buccinidae
Dr. ELISABETH DEICHMANN, Museum Comparative Zoology, Harvard	Holothuroidea
Dr. J. WYATT DURHAM, Museum Paleontology, U. of Calif. Berkeley	Echinoidea
Dr. WILLIAM K. EMERSON, Amer. Mus. of Nat. History, New York	Scaphopoda
Dr. JOHN S. GARTH, Allan Hancock Foundation, U. of S. Calif.	Brachyura
Mr. GILBERT GRAU, Hollywood, California	Pectinidae
Dr. JANET HAIG, Allan Hancock Foundation, U. of S. Calif.	Paguridae
Dr. CADET HAND, Dept. Zoology, U. of California, Berkeley	Anthozoa
Dr. G. DALLAS HANNA, California Academy of Sciences	Conidae
Dr. OLGA HARTMAN, Allan Hancock Foundation, U. of S. Calif.	Polychaeta
Dr. WILLARD D. HARTMAN, Peabody Museum, Yale University	Porifera
Dr. JOEL W. HEDGPETH, Pacific Marine Station, Dillon Beach, Calif.	Pycnogonida
Dr. JORGEN KNUDSEN, Zoological Muzeum, Copenhagen, Denmark	Abyssal Pelecypoda
Dr. HENNING LEMCHE, Zoological Muzeum, Copenhagen, Denmark	Opisthobranchiata
Dr. HEINZ LOWENSTAM, Calif. Inst. of Technology, Pasadena, Calif.	Brachiopoda
Dr. ERNST MARCUS, Universidad de Sao Paulo, Brasil	Abyssal Nudibranchiata
Dr. JOHN A. MCGOWAN, Scripps Institution	Cephalopoda
Dr. ALLYN G. SMITH, California Academy of Sciences	Amphineura
Dr. RUDOLPH STOHLER, Zoology Dept. U. of California, Berkeley	Amphineura
Dr. JOHN D. SOULE, Allan Hancock Foundation, U. of S. Calif.	Bryozoa
Dr. MATHILDE SCHWABL, Zool. Institute, Univ. of Vienna, Austria	Solenogasters
Mr. J. R. THOMPSON, U.S. Bur. Fish., Pascagoula, Mississippi	Peneaeidae
Dr. TORBEN WOLFF, Zoological Museum, Copenhagen, Denmark	Isopoda



Dr. JOHN YALDWYN, Australian Museum, Sydney, Australia	Decapoda (shrimp)
Prof. C. M. YONGE, University of Glasgow, Scotland	Mollusca
Mr. FRED C. ZIESENHENNE, Allan Hancock Found., U. of S. Calif.	Ophiuroidea and Asteroidea
Dr. VICTOR ZULLO, Marine Biological Laboratory, Woods Hole, Mass.	Cirripedia

Most of the illustrations in this paper were done by NIELS BJARNOV, JAMES R. MORIARTY, and SP6 JOSEPH FREITAS (United States Military Assistance Advisory Group in Denmark). The illustrations on faunal plate X were drawn by artist POUL WINTHER of Copenhagen. The photographs on plates XI–XV were supplied by DALE KRAUSE, University of Rhode Island.

### **History of Biological Exploration in the Gulf of California**

Considering the size of the region, comparatively little biological collecting has been carried out in the Gulf of California. Few areas along the coast are readily accessible to the average biologist, and until a few years ago, no marine stations had been established along the coast. There is now a small station, The Vermilion Sea Field Station, at Los Angeles Bay, Baja California, established by the San Diego Natural History Society. Considerable biological research is now being conducted there in a number of fields (McLEAN, 1961). There is also a small marine station operated by the Mexican Government at Mazatlan, Sinaloa, although little research has been carried out there, apart from assembling a small study collection of local marine animals.

Early collections from the Gulf of California and the Pacific coast of Middle America consisted mostly of mollusks. In the early 1800's, collections of mollusks were made by a business man, Hugh Cummings, who sent a vast collection back to Europe. This collection was eventually acquired by the British Museum of Natural History. Many of the mollusk species collected and identified in this present study were originally described from the Cumming's collection by such early taxonomists as Broderip, the Sowerbys, Hanley, Reeve and Deshayes. An historical account of this collections can be found in OLSSON (1961). Collections were also made by Colonel EZEKIEL JEWETT, and later described by PHILIP CARPENTER (1855–57, 1863, 1864). Other early mollusk collections were carried out by C. B. ADAMS (mostly in Panama) and FREDERICK REIGEN, a Belgian who lived in Mazatlan. These collections were also described by CARPENTER (1864). The mollusks described by C. B. ADAMS have been figured and his descriptions duplicated in TURNER (1956).

The first major expedition for the purpose of general biological collecting into the Gulf of California was carried out by the U.S. Fish Commission steamer *Albatross* under ALEXANDER AGASSIZ in 1891 and again in 1904-05. Many of the stations occupied by the *Albatross* were taken in deep water, and most of the deep-water invertebrate species (especially the mollusks) collected during this present study were originally collected and described through the efforts of the "Albatross Expedition". A complete list of stations and the early papers resulting from this expedition can be found in TOWNSEND (1901). A final expedition into the Gulf of California by the *Albatross* was undertaken in 1911, these results being again reported by TOWNSEND (1916). The papers resulting from this series of expeditions by the *Albatross* provide by far the greatest existing accumulation of data on the animals living in the deeper portions of the Gulf.

Between 1929 and 1931, HERBERT N. LOWE carried out a number of mollusk collections in the Gulf of California, which were later described by him and also by H. A. PILSBRY. A list of these papers may be found under the respective authors in KEEN (1958). Most of the mollusks described by LOWE are in the San Diego Museum of Natural History, and served as a basis for comparison in the identification of the present collection.

The 1921 expedition to the Gulf of California by the California Academy of Sciences provided additional information on the biology of the flora and fauna of the Gulf. These results were published by a number of investigators including BAKER (1926), BAKER and HANNA (1927), OLDROYD (1918) and SLEVIN (1923). The "Templeton Crocker Expedition" of the New York Academy of Sciences in 1936, under WILLIAM BEEBE (1937), provided new information on mollusks and decapods, as well as many other invertebrate groups from intensive dredging and shallow-water collecting. The mollusks were described in great detail, along with abundant ecological information by HERTLEIN and STRONG (1940-1951). Papers dealing with the other invertebrate groups may be found in *Zoologica*, the publication of the New York Zoological Society, in the years from about 1940 to date. A rather large collection of intertidal invertebrates was obtained by the "STEINBECK-RICKETTS Expedition" of 1939. Some of the data resulting from this trip was included in the narrative of the expedition by STEINBECK and RICKETTS (1941).

The next major expedition into the Gulf of California, and the first one to study the oceanography and geology of the Gulf was the 1939-1940 "E. W. Scripps Cruise to the Gulf of California", under the sponsorship

of the Geological Society of America and Scripps Institution of Oceanography. The results of this cruise, including the paleontology and some biology, are summarized in ANDERSON, *et al.* (1950). A later list of the mollusks collected by this expedition can be found in EMERSON and PUFFER (1957), and a further reworking of some of the geological data can be found in BYRNE and EMERY (1960). Several expeditions were also made into the Gulf of California by the Allan Hancock Foundation with the Velero III and IV (FRASER, 1943). The biological data from these cruises has been published at various times by GARTH, HAIG, ZIESENHENNE, GRAU, SOULE and others in the *Allan Hancock Pacific Expeditions Reports*, Volumes 1 to 23. Information on stations collected by the Allan Hancock Foundation subsequent to 1942 can be obtained from the Foundation.

Finally, the last major collecting cruise into the Gulf of California prior to the present "Vermilion Sea Expedition" was the "Puritan-American Museum of Natural History Expedition" in 1957. A general account of the expedition can be found in EMERSON (1958), who has also written several short papers on the Pleistocene mollusks of the region, resulting from the efforts of this expedition. SQUIRES (1959) gives an excellent account of the corals collected on the Puritan cruise and SOULE (1961) has discussed the bryozoans.

Small collections of mollusks have been made from time to time by mollusk collectors at Puerto Peñasco, San Felipe, Guaymas, La Paz and Mazatlan, Mexico, although references are too numerous to be given here. Dr. S. Stillman Berry has described many new species of mollusks from the Gulf and has discussed their biology in his *Leaflets in Malacology* (privately printed and available from BERRY). Notes on Gulf of California mollusks can also be found in the *Annual Reports of the American Malacological Union, Pacific Division*. The collections of Mrs. Faye Howard of Pacific Palisades, California have provided the basis for lists by a number of people, including McLEAN (1961), and her notes on the reproduction of marine gastropods from the Gulf of California were made available to the author through Professor GUNNAR THORSON. One other expedition to the Gulf of California in recent years should also be mentioned, "The Ariel Expedition", undertaken by members of the Conchological Club of Southern California. Using a shrimp boat, a number of excellent collections were taken on the middle and outer shelf portions of the Gulf. An account of some of the mollusks taken can be found in SHASKY (1961).

Although scattered, there seems to be considerable literature available on the biology of the Gulf of California. Not mentioned above are also a

few papers on the biology of commercial shrimp written under the Mexican fisheries investigations, and a large number of papers on fisheries biology and primary production by biologists working under the California Cooperative Oceanic Fisheries Investigations and the Bureau of Commercial Fisheries of the U.S. Fish and Wildlife Service. None of the above studies has attempted an overall ecological analysis of the Gulf of California, although many do discuss the zoogeographic divisions of the Gulf as related to various floral and faunal groups. Two issues of *Systematic Zoology*, published in 1960 (GARTH, *et al.*, 1960) were devoted to a symposium on the zoogeography of the Gulf of California.

### **Methods of Collecting and Analyzing the Data**

Collections of biological material for this study were made during the period from November, 1958 through November, 1961 by a number of expeditions. These expeditions were: "Tuna Oceanographic Cruise II", November, 1958; "Vermilion Sea Expedition I", April-May, 1959; "Vermilion Sea Expedition II", May-June, 1959; "Vermilion Sea Expedition-Shepard", April, 1959; "Southern Borderland Cruise II", February, 1960; "Curaray-Orca Cruise", March-April, 1960; "Holt Expedition", December, 1960; "Baja Slope Expedition", May, 1961; and "Curaray-Gulf of California, Winter Cruise", November, 1961, all made under the sponsorship of Scripps Institution of Oceanography. Cruises "AEC-1", March, 1960, "AEC-2", March-April, 1960, and "AEC-3", November, 1960, were carried out by the Advanced Systems Development Division of Pneumodynamics Corporation, El Segundo, California.

Since none of these cruises was undertaken for the specific purpose of benthic biological sampling, with the exception of the "Baja Slope" and "Holt" expeditions (both in the Pacific on the west side of Baja California), sampling was somewhat haphazard, depending entirely upon when time was available for sampling the benthos. Most of these cruises were primarily geological or geophysical in nature. No systematic program for the collecting of quantitative grab or bio-mass samples could be carried out, although a number of orange peel and small Van Veen samples were taken on "Vermilion Sea Expedition I", and a few Petersen Grab samples were taken by the author during "Vermilion Sea Expedition-Shepard". All other samples were taken either with various dredges and trawls or by diving and hand-collecting. Some conception of the principle mode of sampling for each environment sampled can be gained from



figure 2b, and Table III. All grab samples were washed through a series of sieves, the smallest diameter of the screens being 1 mm, while a uniform inner mesh size was used in all trawls, regardless of trawl dimensions. The type of gear used at each station taken is given under the station data in the appendix. All material living and dead was retained, and after thorough sorting, all animals groups which could not be identified at Scripps Institution were sent out to various specialists mentioned in the acknowledgments. The author sorted all samples into the various systematic groups before sending to specialists, and personally identified 95% of the mollusks. Some small groups of mullusca were sent to specialists for verification.

It was obvious after a short time, that the volume of data collected during this program was too large to handle in a conventional manner. First of all, over 1,150 species of invertebrates were identified, and at least another third are yet to receive names. Altogether over 270 stations were taken, although only 200 were taken in the Gulf of California. Each station was characterized by date, time collected, depth, latitude, longitude, bottom temperature, bottom oxygen, sediment type, collecting device and the organisms found there. When attempting to put this information together, it could be seen that there were too many variables to integrate by inspection alone. At about the time when it became necessary to process this information, an electronic digital computer (a Control Data Systems 1604) was installed at the School of Science and Engineering, University of California, San Diego. Since the data from the geological studies of the Gulf of California were already being entered on to IBM cards and programs written to process their data, it was suggested that the biological data could also be processed in a similar manner.

It was first necessary to construct a system for putting the information on to IBM cards, so that the maximum use of the data could be made with a minimum number of cards. Three sets of cards were found to be sufficient for recording all of the data. The first set of cards was for the storing of station data (an example of the print-out is shown in figure 4a). Originally, many of the stations had different sets of numbers, corresponding to the various expeditions. Later in this study, all early stations were numbered consecutively, and additional stations added in the same numbering system. Each station card contains station number, date of collection, time of collection, depths, latitudes and longitudes to tenths of minutes, bottom water temperatures to tenths of degrees Centigrade, oxygen values to tenths of a ml/L., sediment types (using code numbers devised by the geologists), collecting devices, also coded, total number of species taken at the station, and total numbers of living and dead individuals per station.





[illegible]

Fig. 4b. Sample print-out of IBM species-data cards.

The cards were later re-sorted systematically for printing. The total number of station occurrences of each species is listed next and, finally, all station numbers at which each species occurred, plus the number of living and dead individuals for each species at each station (fig. 4b). The third card was devised to be paired with the species data card and contains the identical species number, a letter designating the class or phyla, and the complete scientific name to subgenus and species (fig. 4c). This last



Two programs for handling these data were then written by programmers in the Computation Facility of the University of California, San Diego, using FORTRAN as the machine language. The first program was written as a test of whether this system of data storage could be used satisfactorily for grouping together species into natural classifications as related to the distribution of physical factors. EARL FERGUSON of the Computation Facility wrote most of the program, with some assistance from ANNA DEVORE. The computer was programmed to list all species found at various depths, temperatures, oxygen limits, sediment types and geographic localities. Unfortunately, the limits of these variables were chosen arbitrarily, based on previous inspection of the data. The computer first listed all stations falling within the various ranges of each variable, using station cards only. The next step entailed a search through all of the species-data cards, in which the machine stored the numbers of all species occurring at all stations previously listed for each category. Finally, all species numbers were matched with the species-name cards, and complete print-outs were made of all the species names occurring under each increment of depth, temperature, oxygen, sediment type and geographical region (example on fig. 5a). The entire operation, taking 28 minutes, would have taken several months by hand. The next step in determining the influence of various physical factors on the distribution of invertebrates would be to have the machine choose the limits of the variables by a multi-correlation analysis. This has not been done as yet, since a somewhat simpler method was devised for a preliminary analysis of the assemblages.

The second program was modified from one originally written for EDWARD FAGER of Department of Oceanography at Scripps Institution, and was written by ROBERT and EILEEN MITCHELL. FAGER's program was devised for data catalogued in a somewhat different form, and so had to be rewritten to utilize the present data. FAGER (1957, 1963) demonstrated that through a contingency matrix of joint occurrences of common species, using the geometric mean of the proportion of co-occurrences, that certain natural groupings of animals would result from a sampling of a region, which would correspond to environmental boundaries. Using only the presence or absence of species at every sample location, minus a term that corrects for sample size, the computer was asked to produce statistically valid groupings from 350 species taken more than five times in this sampling program. The other 800 species taken in this study were considered too infrequently taken to be considered in this analysis. The computer program, which did not take into account type of sampling device, first compared the distribution within the 270 stations of every species with every other species. Pairs of species, with pre-established lower







currences per species. Another 22 species formed combinations of not less than three species with those species having between five and seven occurrences. Since almost every index species listed for one group may also be part of several other groups, in actuality, only 10 or 12 valid distinct groupings of species resulted. Most of these groups occurred on the continental shelf in from 11 to 126 meters.

The next step in producing stations and faunas which characterize particular environments, was to perform a separate analysis by personal inspection of the index groups with the largest number of associated species. This was done by listing all species in each group, and then listing all station occurrences at which each species was taken, *living only*, although the computer program was based on both living and dead occurrences. It was then possible to determine only those living species which were important components of the station groups. Those stations which proved to have a large number of commonly associated living species were then examined as to location and common physical factors. Fortunately for this study, most of the resultant station groupings were very distinct, both as to geographical location and the same range of physical factors. Therefore, instead of attempting to determine what species occurred in any one set of physical factors, the matrix actually provided sets of stations with common physical attributes, bound together by index or important living species. Finally, all living species taken at these characteristic stations were listed, and those with the most station occurrences within the group of stations were listed for various environments as given in Table II. In some cases, particularly environments I, II, IV and V, lists of index species as given directly by the computer program are given in the text, in order to show that there were certain species occurrences which tied these stations together. More often than not, however, these lists did not represent either the most characteristic species nor the common living ones, and the somewhat more subjective analysis which produced the lists in Table II, are more reliable indicators of environment. The computer method itself appears to be an excellent tool for defining environmental and faunal boundaries as pointed out by FAGER (1963). Unfortunately, the sampling as produced by this project was inadequate to do justice to the problem. As can be seen in Table III (the lists of sampling devices for each environment), a strong bias will be produced as to the kinds of animals which will predominate in each environment. Certain areas were sampled primarily by shell dredges, others by large trawls, and one by grab samplers (fig. 2b). Although most of the environments were sampled by a variety of instruments, there were

not enough stations taken by each type in each environment to permit strictly valid comparisons between either environments within the Gulf of California region or other environments in other parts of the world. The results as given here, do give one an idea of some of the animals living in the various parts of the region, which from a strictly zoogeographical viewpoint is valuable, since few studies have been made in one region from shore to over 4,000 meters. The text of this program and sample results can be obtained from the author or Scripps Institution of Oceanography.

The stations and consequent species groupings for the various environments in the Gulf of California, correspond very closely to environments which were thought to exist from the subjective appraisal of these data. These computer groupings were devised by almost a purely mathematical process, which will give nearly the same result regardless of operator. Once the program had been written, new data could be added quickly and the matrix repeated in a few minutes of machine time. It would have taken many months to carry out this analysis by hand or by personal inspection, which would also provide almost unlimited opportunity for error. The program would have been infinitely more useful, if the stations had been more numerous and of equal size, since the results could have been further substantiated by abundance of individuals, as well as by mere presence or absence.

Of importance to the paleontologist is the fact that a similar paleoecological program could be carried out in older sediments from nearby localities if the fossil sampling is detailed enough. For instance, in areas such as the Pliocene or Miocene of Panama, Costa Rica, Columbia and Ecuador, where many of the same species or ancestors of the same Gulf species occur in large numbers and in varying environments, a similar matrix of common occurrences could be constructed, giving certain units of each formation uniform characteristics based on a common set of species. These sets of species could then be compared to those assemblages given here, with the hope of identifying similar environments of deposition. It is also possible to submit data from the previously mentioned Gulf of Mexico studies to a similar analysis, in order to substantiate the more or less subjective analyses performed before. A wealth of paleontological information exists from borings and outcrops of Miocene to Pleistocene age along the Gulf of Mexico coast, which could be compared by computer techniques to those results obtained from the sampling of the Recent.

Besides the computer analysis of these data, several other methods were used to establish the various assemblages in the Gulf of California. About 350 areal distribution maps of common species were drafted and com-

pared with the distribution of the various ecological factors. A graph of the depth ranges, both living and dead (Table I – Appendix) for all 1,150 species identified so far was devised in order to obtain an indication as to where the majority of species were concentrated. The complete scientific names of all species taken in this study can also be found in Table I. For this reason, describer and date of description has been omitted from species names in the main body of the text. The geographic and depth ranges of most of the important species found in this study were also checked against the known ranges in the literature (KEEN, 1958; OLSSON, 1961; and various papers resulting from the Albatross expeditions). The preliminary discussion of the purely biological factors which may influence the composition of the various assemblages resulted from examination of some of the original material, a survey of existing literature on closely related species of invertebrates from tropical regions, and from discussions with the staff of the Copenhagen University Zoological Museum and Marine Biological Laboratory in Denmark.

### **Description of the Region Sampled**

The majority of the biological samples collected under this Scripps Institution survey were taken in the Gulf of California proper, or a region which is tectonically related to the Gulf of California. This consists of the Gulf of California itself, bounded by the peninsula of Baja California on the west, the Colorado River delta on the north and the mainland coast of Mexico to approximately Mazatlan, Sinaloa (fig. 1). It should also include the Tres Marias Islands, the large irregular basins to the north and south of these islands, and coast of Mexico to Bandaras Bay, since this region is tectonically part of the whole complex.

### **Geology and Topography.**

A description of the bordering geology and geomorphology of the Gulf of California region received considerable treatment by ANDERSON (1950) and by BYRNE and EMERY (1960). It is sufficient to say that, in contrast to the region studied previously by the author in the Gulf of Mexico, very few broad alluvial plains with abundant rainfall and river discharge are present along the coast of the Gulf of California. Much of the Gulf is surrounded by high mountains, with precipitous peaks descending almost to the shoreline. Rocky shores are particularly abundant along the Baja California coast, whereas broad, sandy beaches and mudflats are restricted to the Colorado Delta area, the Costa de Hermosillo and Costa de Nayarit

(CURRAY, in VAN ANDEL, *et al.*, in press). There are many small pocket beaches on both sides of the Gulf, which do provide a niche for sandy-beach fauna, but sandy beaches are not as extensive as they are along the coast of the Gulf of Mexico.

Estuarine coastal lagoons are rare in the Gulf of California proper, which receives virtually no rainfall, but very large lagoons are to be found south of Mazatlan, where the climate becomes humid. Information concerning these lagoons was obtained from FRED B PHLEGER and JOSEPH R. CURRAY (oral communication), and from the literature, particularly KEEN (1958). There are a number of semi-enclosed bays on the west side of the Gulf, where normal Gulf conditions occur, and a few strictly tidal to hypersaline lagoons on the east side from Guaymas to the north. There are also some very large lagoons near the vicinity of Los Mochis (fig. 1). Little is known concerning their fauna. The configuration of the shoreline of the Gulf of California is so variable that a tremendous number of ecological niches are present for marine and intertidal invertebrates.

The continental shelf region was sampled in considerable detail, although in only two main regions, namely, off the Costa de Hermosillo and Costa de Nayarit. Here the shelves are relatively broad and gently sloping, providing niches for many assemblages which parallel those found on the broad shelves of the Gulf of Mexico. On the other hand, the rocky and sandy continental shelf on the west side of the Gulf of California from Angel de la Guarda Island to Cabo San Lucas (fig. 6) is very narrow, and in some places virtually non-existent. The west side of the Gulf is therefore inhabited primarily by epifaunal species of invertebrates, since little soft level-bottom area is available for infaunal species. Alternatively, the upper Gulf, north of Tiburón and Angel de la Guarda Islands, is very similar to the Gulf of Mexico shelf. One fairly deep, broad basin (Tiburón Basin) exists between the islands, but in general there is a broad, gentle shelf descending from the Colorado delta to depths of about 200 meters (fig. 6).

In contrast to the strictly northern portion of the Gulf, the southern and central portions are characterized by deep channels and basins, with steep rocky sides descending to over 2,000 meters. The bottom of the basins themselves are flat, but the total area suitable for level-bottom communities is rather small compared to the total area of the Gulf. The bathymetry of the Gulf of California was first drawn up in detail by SHEPARD (1950), based principally upon soundings obtained on the "E. W. Scripps Cruise" in 1940. BYRNE and EMERY (1960) gave a simplified version of this chart, but added no new information. A new chart of the bathymetry



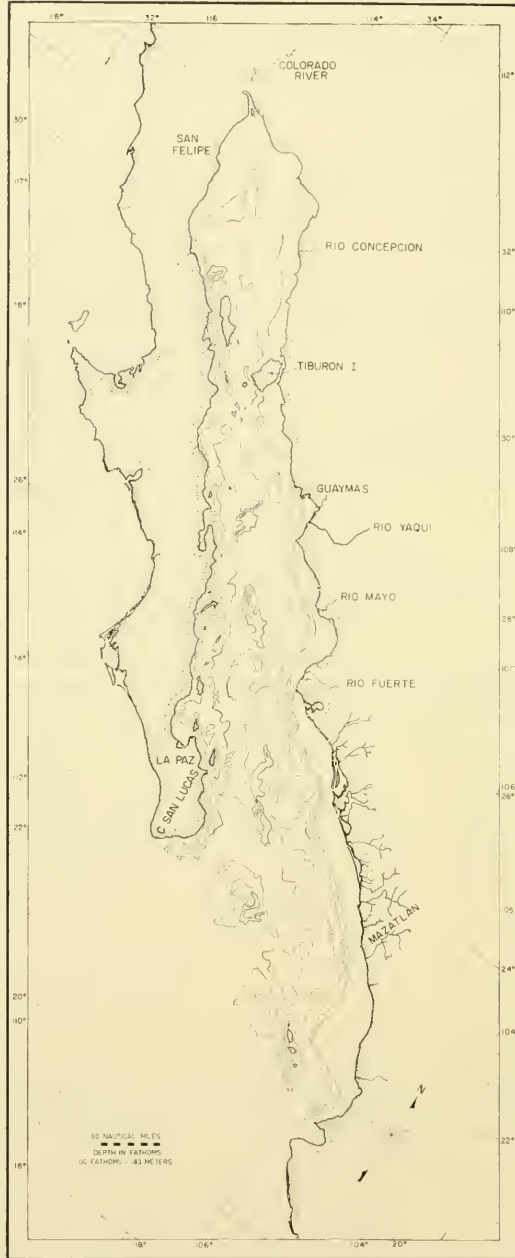


Fig. 6. Bathymetry in fathoms of the Gulf of California. Contours from FISHER, RUSNAK and SHEPARD (VAN ANDEL, *et al.*, 1964, in press).



of the Gulf of California has been compiled by ROBERT L. FISHER, GENE A. RUSNAK and FRANCIS P. SHEPARD (VAN ANDEL, *et al.*, in press), based on new soundings obtained on the various "Vermilion Sea" expeditions. A simplified version of FISHER's chart is shown in fig. 6. The bathymetry of the continental slope and abyssal regions from California to Panama is shown on figure 3.

### Sediments of the Gulf of California.

A general description of the sediments of the Gulf of California, based on 310 samples taken by Scripps Institution on the "E. W. Scripps Cruise" and by various cruises of the Allan Hancock Foundation, is given in BYRNE and EMERY (1960). A more detailed map of the sediments has been compiled by VAN ANDEL *et al.* (in press). Both are in relatively close agreement as far as the gross sedimentary characteristics of the Gulf are concerned, although many more sample analyses are involved in VAN ANDEL's version and the one prepared by him for this paper (fig. 7). CURRAY in VAN ANDEL *et al.* (in press) has drawn up detailed charts of the sediments for the two areas most important to the biological studies (Costa de Hermosillo and Costa de Nayarit). These charts are based on grain-size analyses and other sedimentary properties (fig. 8 reproduces one of these). Using these charts, it is possible to trace the close correlation between certain macrofaunal communities or assemblages and sediment type.

According to BYRNE and EMERY (1960, pp. 996), the sediments of the subtidal portions of the Gulf can be described in the following manner. The extreme northern end in the vicinity of the old Colorado River mouth is characterized primarily by silty sand (based on a nomenclature devised by SHEPARD, 1954). Proceeding south to a point midway between the two large islands in the Gulf, the sediments change to silty clay, the typical sediments for shrimp fishing grounds both in the Gulf of Mexico and Gulf of California. The area which marks the transition between the northern and southern Gulf in the vicinity of the Tiburón Basin is predominately sand. More detailed sampling as a result of the Vermilion Sea expeditions (in part, fig. 8) in the area shows a great range of sediment types, ranging from rock and gravel to silty clay, although there is a preponderance of sandy sediments. The rest of the central and southern portion of the Gulf below 200 meters is characterized by both BYRNE and EMERY and VAN ANDEL as silty clay. There are a few patches of clayey silt on some of the topographic highs, and portions of the Guaymas Basin are covered with diatomaceous sediments.

Detailed sediment maps of the shelf portions of the Gulf south of Tiburón Island and Angel de la Guarda Island are almost impossible to

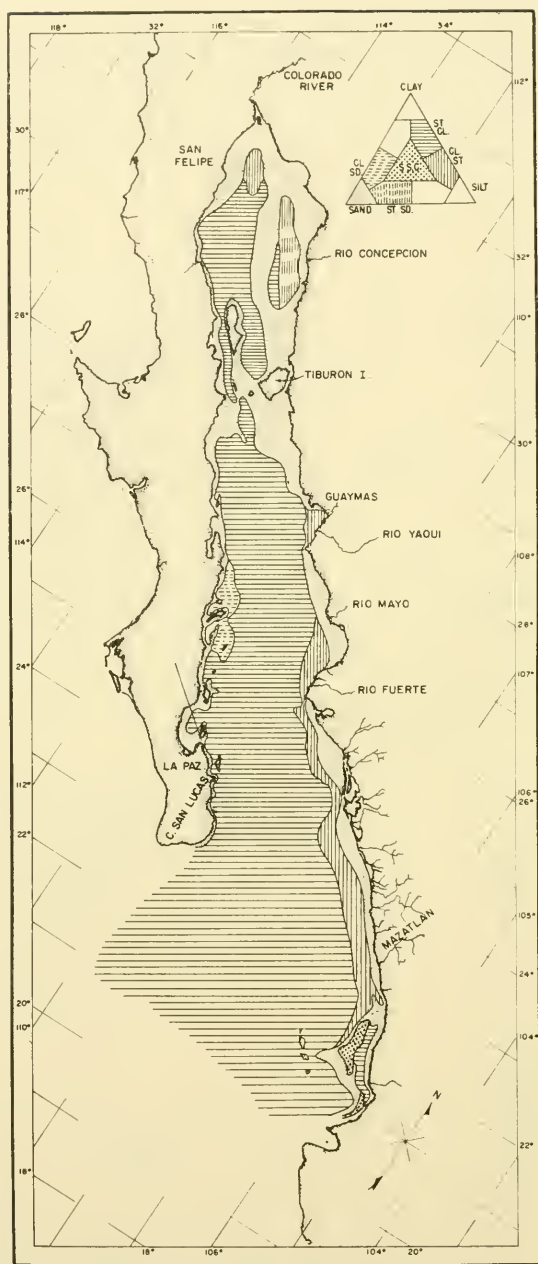


Fig. 7. Sediments of the Gulf of California, based only on size analysis of samples taken on Vermillion Sea Expeditions I and II. Sediments classified according to SHEPARD (1954). (After VAN ANDEL, in press).

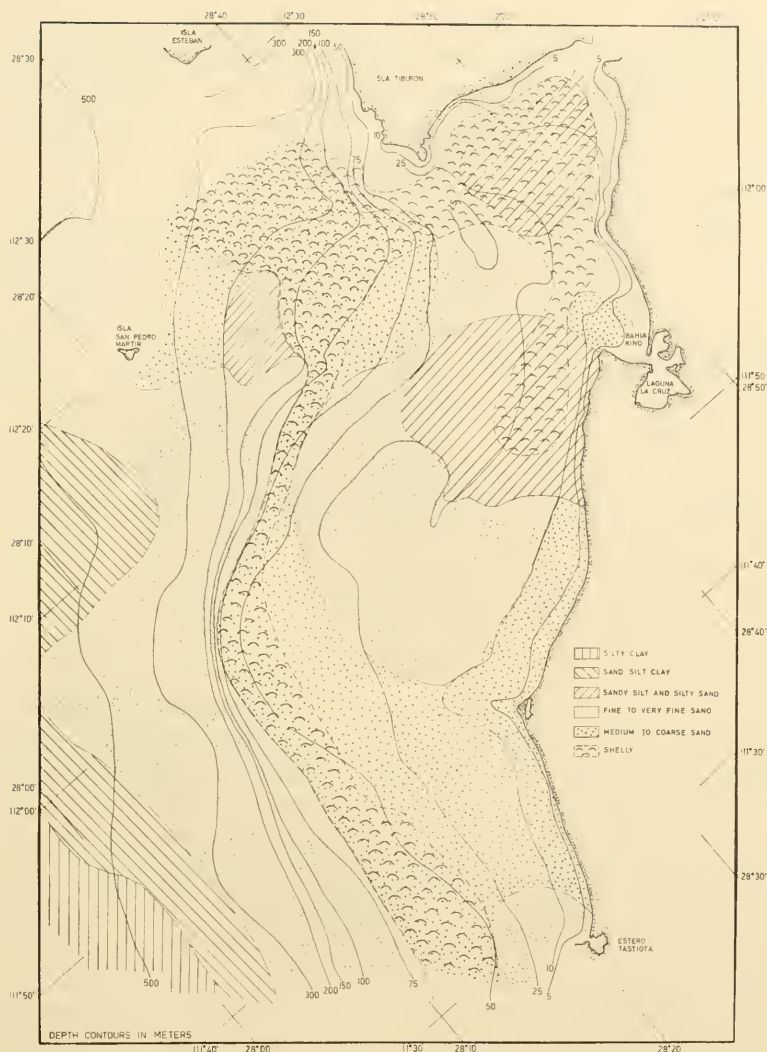


Fig. 8. Sediment distribution for the Costa de Hermasillo region, south of Tiburon Island. Depth and sediment countours based on a chart drawn up by JOSEPH R. CURRAY, Scripps Institution. Shelly zone added by this author.

construct from the available data, except for the two broad portions studied by CURRAY in VAN ANDEL, *et. al.* (1964, in press). On the west side, the bottom is primarily rock, gravel and sand. There is no source of fine sediment, and with the steep sides of the shoreline and violent weathering, one can expect to find only coarse to very coarse sediments. As mentioned before, the northern portion of the Gulf continental shelf is characterized

by finer sediments, deposited by previous fluvial cycles of the Colorado River. Where there are steep sides and rocky headlands on the east or mainland side of the Gulf, the sediments are again coarse and sandy. If the shelf broadens, the sandy sediments soon disappear, being replaced by clayey silts and silty clays on the outer edges of the shelf (fig. 7). However, two areas where this is not the case are those studied by CURRAY off Hermosillo and San Blas (figs. 7 and 8). Both of these broad shelves are at least partially a result of the growth of large river deltas during Holocene lowered sea level, plus subsequent inundation, re-working and high rates of deposition during the last rise of sea level during the past 19,000 years (CURRAY, 1962). The conditions which produced these submerged deltas have therefore complicated the sediment distribution so that both areas are characterized by small patches of varying sediments irregularly distributed. This patchiness of coarse and fine sediments has also produced considerable patchiness in the distribution of the invertebrates. The faunal communities are not located strictly parallel to each other in descending depth as in the Gulf of Mexico, but often run in confused patterns, mostly related to sediment size.

#### Bottom Dissolved Oxygen Concentrations.

Fortunately for this study, there existed a considerable body of information on the hydrography and physical oceanography of the Gulf of California. Beginning with the "E.W. Scripps Cruise", a number of cruises have been undertaken to the head of the Gulf solely for the purpose of measuring various hydrographic factors. Most of these cruises were carried out by Scripps Institution in collaboration with the South Pacific Fisheries Investigations of the U.S. Fish and Wildlife Service and the California Cooperative Oceanic Fisheries Investigations. The results of the first seven cruises were discussed in detail by RODEN (1958) and RODEN and GROVES (1959). Since that time, several more cruises have been carried out under the same program, in addition to which hydrographic data was collected by the "Vermilion Sea Expeditions" and various "Tuna Oceanography Cruises" sponsored by the Saltonstall Fund studies at Scripps. Although a number of cross-sections were given in the published studies of oxygen distribution in the Gulf, there was no discussion of the areal distribution of bottom oxygen. The present author compiled the raw data for all known deep casts, averaged the bottom values for all of the stations where data existed (fortunately, the same stations were occupied at almost every season and on several occasions), and plotted them on a bathymetric chart of the Gulf of California (fig. 9). No attempt was made to obtain

an accurate picture of oxygen variation in the very shallow waters, but it was possible to get some idea of average oxygen concentration at all depths from over 3,000 meters in the entrance of the Gulf to about 40 meters along the coast (fig. 9).

These data were first isoplethted at .5 ml/L. intervals, and then smoothed out to give the picture of oxygen distribution as shown in fig. 9. As can be seen in the northern Gulf, there is normally an orderly progression from high oxygen to low oxygen from shallow to deep water, but the presence of the "oxygen-minimum zone" from Tiburon Island to the south complicates the picture considerably. Values drop suddenly at about 100 to 200 meters to below .5 ml/L., continuing with low values to depths of about 1200 meters, where they rise to 1 ml/L. in the southern basins and even higher at the entrance to the Gulf. One exception to this pattern can be found in the Guaymas Basin, where there is less than .5 ml/L. at the bottom. This basin also contains the largest concentration of diatomites. These diatomites are finely layered, and show no signs of disturbance by burrowing organisms. The lack of animals necessary to disturb layered sediments can probably be attributed to the absence of enough oxygen to sustain macro-invertebrate life. Similar adverse conditions have been described by EMERY and HÜLSEMANN (1962) in the Santa Barbara Basin in the continental borderland off Southern California. This basin is somewhat shallower (550 meters), but oxygen values are quite similar and even lower than the Guaymas Basin, ranging from .5 ml/L. at sill depth of 475 meters to .1 ml/L. at the bottom. As in the Guaymas Basin, sediments are neatly layered, showing graded deposits resulting from turbidity current deposition, interspersed with alternating diatomite and terrigenous deposits. Upwelling and related high plankton productivity although not on a seasonal basis brings about a depletion of oxygen at the bottom, as in the Guaymas Basin. Thus, during times of very low oxygen, fine layers are preserved owing to lack of benthic organisms. During non-upwelling portions of the cycle, there is an increase in oxygen permitting the existence of burrowing animals which destroy some of the laminae. The primary difference between the Santa Barbara Basin and Guaymas Basin is that oxygen depletion seems to be more or less permanent in the Guaymas Basin, since no disturbance laminae occurred anywhere in the Guaymas cores, and no signs of life have been found in dredge samples.

The areas with lowest oxygen values on the upper portions of the slope of the Gulf of California can be correlated quite closely with the areas of intense upwelling and associated plankton or diatom blooms, as shown in fig. 10 (taken from RODEN and GROVES, 1959, and BYRNE and EMERY,



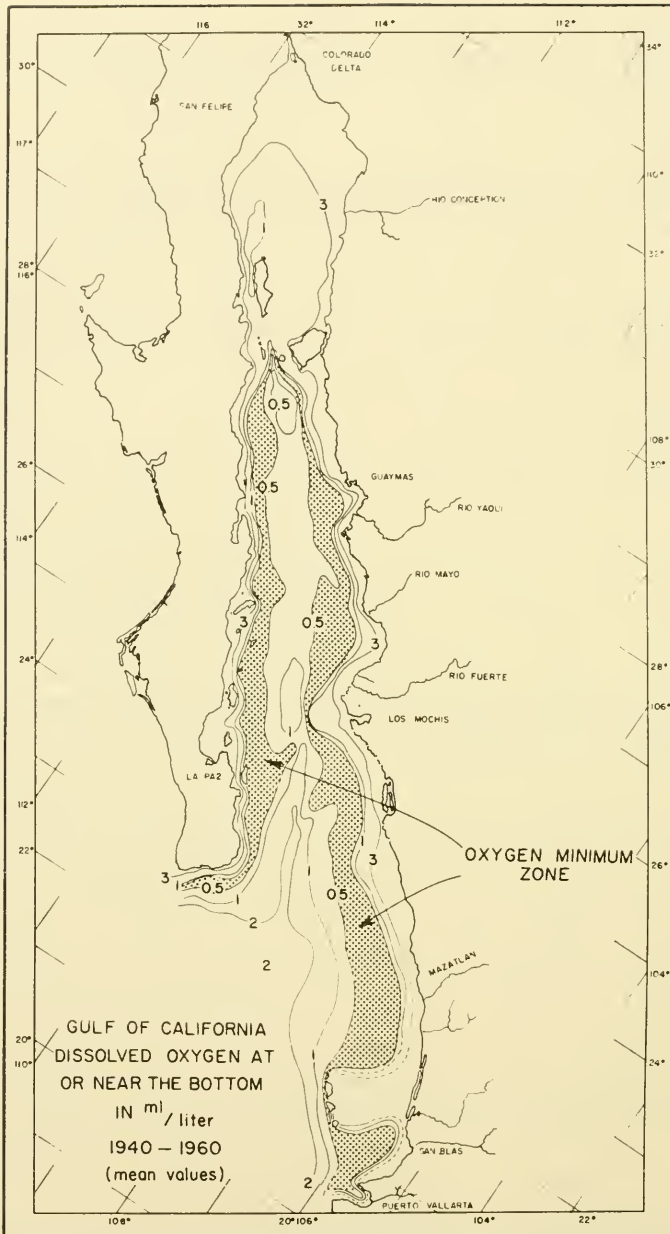


Fig. 9. Dissolved oxygen concentrations, Gulf of California, based on several hundred observations, taken at various seasons over a 20-year period.

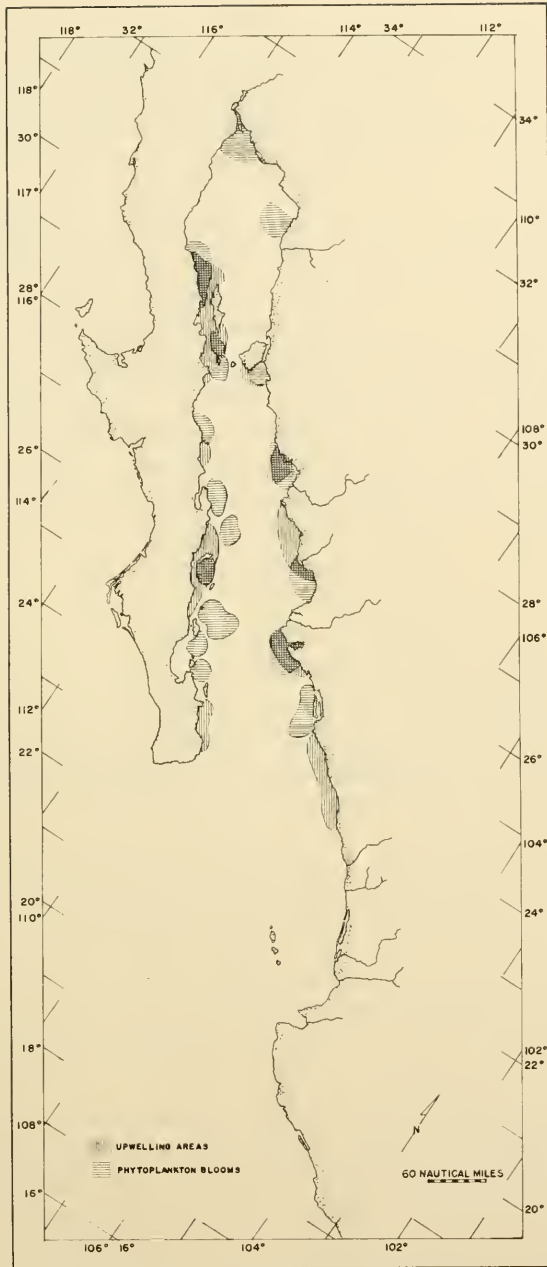


Fig. 10. Areas of upwelling and accompanying phytoplankton blooms in the Gulf of California, compiled from BYRNE and EMERY (1960) and RODEN and GROVES (1959).

1960). The tremendous plankton blooms (BYRNE and EMERY, 1960), which have been observed since the Spanish originated the name "Vermilion Sea" for the red tides in the Gulf, account for the extremely high production of all forms of surface life in the Gulf from whales down to small invertebrates (STEINBECK and RICKETTS, 1941). These same conditions are also found in the Gulf of Tehuantepec, investigated by the present author as part of this study. Because of the almost hurricane strength winds which sweep across the Isthmus of Tehuantepec, throughout most of the year, a semi-permanent upwelling dome occurs in the Gulf, much of it overlying the continental slope. Dredges taken in depths of from 200 to 1,000 meters in this region produced no typical benthic life, but large amounts of semi-fossilized wood, completely unaltered leaves, pine cones and fish bones were obtained. GOLDBERG and PARKER (1960) investigated the chemical composition of the bottom waters and the age and composition of the phosphatized wood. It was quite evident that at these slope depths where no life and well-preserved floral and faunal remains were found, oxygen was almost non-existent, but phosphate was very high. Those portions of wood buried in the sediment and still in a fresh condition, proved to be older than 28,000 years B.P., as determined by C-14 age-dating by Hans Suess of Scripps Institution. The antiquity of the wood would lead one to believe that the bottom oxygen-minimum conditions along the coast where upwelling is now present have existed for a long time. Wood in similar state of preservation was also found in roughly the same depths along the east side of the Gulf of California from Mazatlan to Guaymas.

A complete reversal of the depleted oxygen situation exists in the San Lorenzo and Ballenas Channel region between Angel de la Guarda Island and the islands to the south and the coast of Baja California (fig. 9). The depths of this channel range from 1,000 to over 1,500 meters (500 to 800 fathoms). Throughout most of the rest of the Gulf these depths are characterized by very little to almost no oxygen at the bottom. However, because of the tremendous tidal transport through this narrow strait, turbulence is effective throughout the whole water column and oxygen values are between 1 and 3 ml/L., which is sufficient to sustain almost any form of marine life. This phenomenon has been discussed by RODEN and GROVES (1959, pp. 17-19). It might be mentioned here that the high oxygen concentrations in this channel support a fairly rich fauna including a number of species of solitary corals.

The faunas at the southern, deep part of the Gulf also reflect the high oxygen conditions, which appear to be related to the underlying deep

Equatorial Pacific bottom water. Trawls taken in the region marked by the 1 and 2 ml/L. isopleths in fig. 9 in the southern Gulf were exceedingly rich, and roughly of the same composition as those taken in slope depths elsewhere along the coast of Middle America. However, fewer numbers and kinds of animals were taken in the central Gulf basins which have lower oxygen values.

The oxygen concentrations on the continental shelf portions of the Gulf of California are not quite so important in influencing the faunal assemblages, as they are at least over 1 to 2 ml/L. As shown in fig. 10, there are areas along the shelf where upwelling does occur, and oxygen may occasionally be depleted fairly close to shore. This is especially true north of Mazatlan, where the oxygen-minimum zone on the bottom comes quite close to shore despite the width of the shelf. This condition seems to influence the faunal assemblages which change considerably north of Mazatlan in depths of from about 65 to 120 meters (36 to 65 fms.). Since the general character of the sediments also changes, it cannot definitely be stated that oxygen alone is the controlling factor.

#### Bottom Water Temperature Characteristics.

Surface water temperatures to a depth of 400 meters have been discussed by RODEN (1958) and RODEN and GROVES (1959). Using Roden and Groves' data, plus unpublished values obtained from various recent Scripps hydrographic cruises in the Gulf region, it was possible to construct a bottom isotherm chart of water temperatures for the Gulf, exclusive of shallow inshore areas (fig. 11). As can be seen from this figure, there is an orderly progression from shore to the deepest portions of the Gulf of from more than 14°C. to 2°C. in the deep southern sections. From between San Lorenzo and Tiburón Islands, south to Puerto Vallarta, the edge of the continental shelf is fairly well marked by bottom temperatures of between 14° and 10°C. From shelf-edge to the bottom of the central basins, temperatures gradually change to about 4°C. However, the southernmost basin from Los Mochis south, and the upper end of the Middle American Trench area have bottom water temperatures of 2°C. or less, which are characteristic of the bottom water of the equatorial Pacific.

One exception to the rule of decreasing temperature with descending depth is the deep channel between Angel de la Guarda and San Lorenzo Islands and Baja California, and the moderately deep Tiburón Basin. Here, as was demonstrated in the case of bottom oxygen values, temperatures are nearly uniform from surface to over 1500 meters, resulting from the intense tidal mixing in this channel and basin. For instance, in RODEN

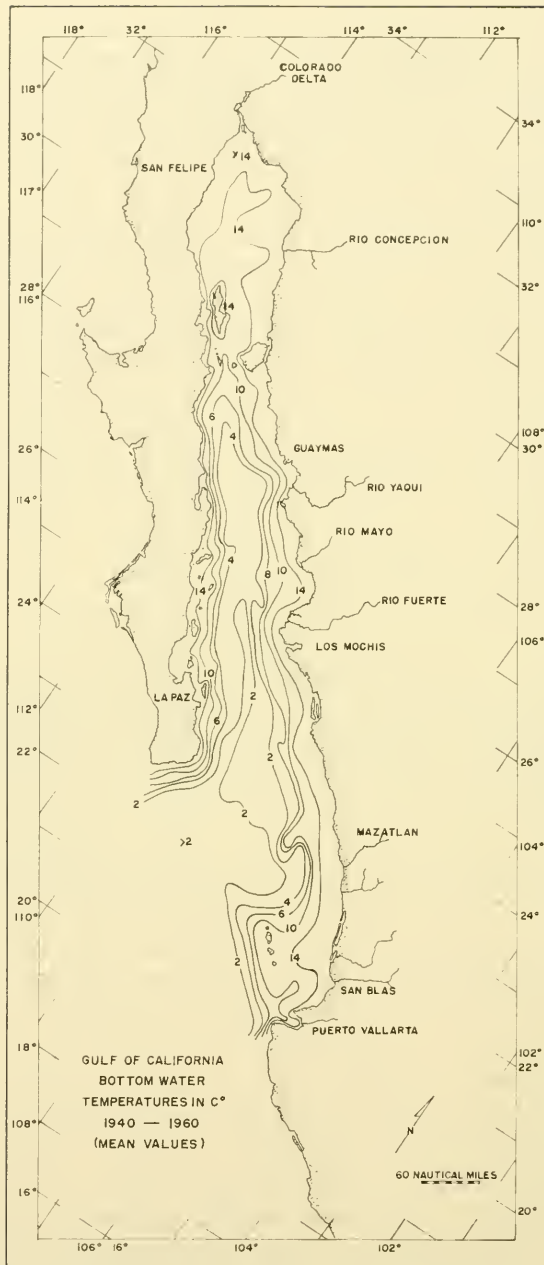


Fig. 11. Bottom water-temperature isotherms, Gulf of California, based on several hundred observations, taken at various seasons during a 20-year period.



and GROVES (1959, p. 18) it can be seen that in the month of April, surface water temperatures are at about  $15^{\circ}$ , while bottom temperatures at below 1,000 meters are still as high as  $12^{\circ}\text{C}$ . During the warmest month of August, surface waters may be as high as  $28^{\circ}$ , but at 200 meters, temperatures are down to  $15^{\circ}$ , and at 1,000 meters no lower than  $12^{\circ}\text{C}$ . These warm temperatures, found at such great depths, have a marked effect on the composition of the fauna in the bottom and on the sides of these channels and in Tiburón basin. Vertical stratification of assemblages, as it occurs in the central and southern Gulf corresponding to changing depths, disappears, and many species usually found in 150 to 200 meters may also occur at the bottom in depths of 1500 meters. This offers some proof that temperature is at least one of the more important controlling factors in determining faunal distribution on the bottom, and that pressure alone is apparently not too limiting a factor.

The inshore or shelf water temperatures have been discussed in detail by Roden and Groves, but a brief description can be given here. A pronounced seasonal variation has been observed in all portions of the Gulf, but the variation in the northern region above the large islands is the most extreme. In the vicinity of San Felipe and Puerto Peñasco, the annual range of water temperature in shallow water is about  $16^{\circ}\text{C}$ ., from about  $14^{\circ}$  in the winter to over  $31^{\circ}\text{C}$ . in August. This extreme temperature range possibly excludes many benthic animals, and in fact the south side of Tiburón Island is the extreme northern end of the range for a large number of invertebrate species (fig. 12). The summer temperatures are warm enough to permit the existence of many Panamic or tropical forms, but the cold temperatures are limiting to many species with a presumed low tolerance to extreme change.

At Guaymas and in the shallow waters south of Tiburón Island, the annual range is from nearly  $18^{\circ}$  to  $31.5^{\circ}\text{C}$ ., or a range of  $13.8^{\circ}$ , still limiting to many tropical forms. However, at Mazatlan water temperatures range from only about  $20^{\circ}$  to  $30^{\circ}\text{C}$ ., a difference of about  $9^{\circ}$  to  $10^{\circ}$ . The Mazatlan area also seems to be the northern limit for a number of strictly tropical species, as well as the extreme southern limit for many of the endemic Gulf of California species. Fig. 12 illustrates the various geographical limits of a number of the common, shallow-water Gulf of California species as compared to annual range of surface water temperatures. Of the 253 species of invertebrates chosen to illustrate this point (those with at least 5 living station occurrences), 8 species are found no further south than the vicinity of Tiburón Island on the east side of the Gulf. Also, 34 more species are not found north of the Hermosillo-Tiburón region.

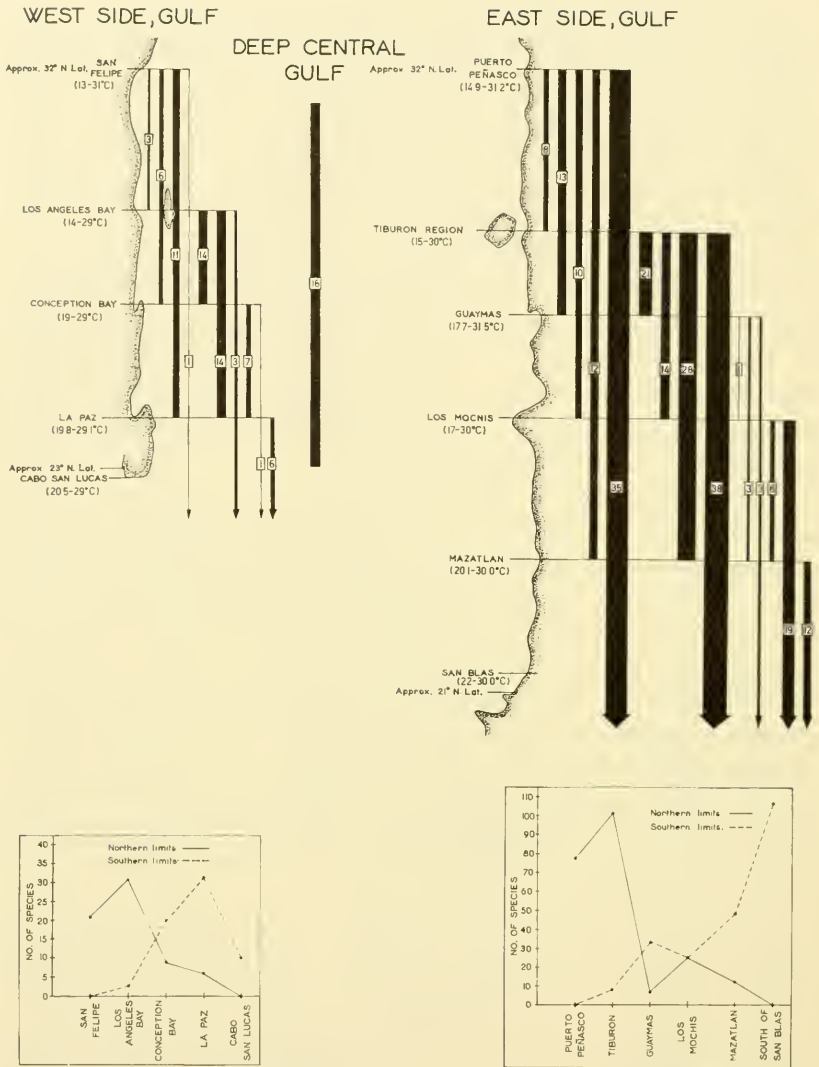


Fig. 12. Zoogeographic breaks in faunal distribution in the Gulf of California, based on living ranges of common invertebrate species, as revealed from distributional data from this study only. Thickness of the bars is related to the number of species within each zoogeographic break. The two small sets of graphs demonstrate the total number of species with northern and southern limits at each temperature break on both sides of the Gulf.

There is a partial break in distributions at Los Mochis, where a major headland exists, although the presence of a temperature barrier at this point is not known. It is known, however, that the Los Mochis region represents a transition from arid to sub-humid climate, as well as a change

in regional geology. About 100 species range no further north than Tiburón, and 15 species are found only between Los Mochis and Tiburón. Twentyfive species have northern limits at Los Mochis, which is also the southern limit for 25 other species. The next major break in distribution is Mazatlan, with 12 species having a northern limit and 49 species having southern limits there. There is also an indication that San Blas may be an area with slightly different temperature characteristics, since a number of species have their northern limits at this point (KEEN, 1958). It must be realized that fig. 12 is based only on ranges of the species as found in this study under variable sampling conditions. The ranges for many of these species, as reported in KEEN (1958), are quite different, but as it was not stated whether they were taken alive throughout the reported range, these data were not used. Since the sediments are radically different on this portion of the shelf, no one factor can be considered decisive. At least south of Mazatlan, shallow water bottom temperatures will seldom, if ever, drop below  $20^{\circ}\text{C.}$ , a temperature which is often considered the lower limit for true tropical animals.

The temperature distribution on the shelf and along the coast of the west side of the Gulf of California is not so well known, as there is a conspicuous lack of stations where data of this nature has been recorded. One can assume that inshore water temperatures at San Felipe, ranging between  $16^{\circ}$  and  $17^{\circ}\text{C.}$  between maximum and minimum, will roughly correspond to those at Punta Peñasco, and are perhaps a little lower in the winter. At Los Angeles Bay and along the Ballenas Channel region, the annual range of temperature is much less, and maximum temperatures are far lower than on the opposite side of the Gulf. They vary from about  $14^{\circ}$  or  $15^{\circ}$  to around  $28^{\circ}$  or  $29^{\circ}\text{C.}$ , and have an annual range of  $15^{\circ}\text{C.}$  These temperatures are also limiting to a number of species. Both a smaller number of Panamic or tropical and a larger number of California or warm-temperate species of invertebrates have been reported there.

Water temperatures along the shores of the central portion of the Gulf of California peninsula from San Lorenzo Island to La Paz range from about  $19^{\circ}$  to  $29^{\circ}\text{C.}$ , according to a cross-section shown in RODEN and GROVES (1959, p. 21). The range between maximum and minimum water temperature is less than at Los Angeles Bay ( $10^{\circ}\text{C.}$ ), but considerably higher, thus permitting the existence of a much larger number of Panamic species.

Temperature records exist for the La Paz region, which is situated in protected waters, and therefore are probably not representative of true conditions on the outer coast of the southern portion of Baja California.

Roden and Groves state that temperatures at La Paz average from  $19.8^{\circ}$  to  $21.1^{\circ}\text{C}$ ., with a range of  $9.3^{\circ}$ , which is quite similar to the temperature distribution at Mazatlan, and typical of a true tropical environment. Figures are also given for Cabo San Lucas, which is slightly warmer, having only  $8.5^{\circ}\text{C}$ . difference between winter and summer. Cape San Lucas seems to have the narrowest range of temperature in the Gulf, being comparable to oceanic equatorial Pacific surface temperatures. This may explain why a number of Indo-Pacific invertebrates and fish can be found only in this region (WALKER, 1960, and ROSENBLATT, 1959). These animals or their larvae must be transported by oceanic currents from the central Pacific islands to this small cape where suitable ecological conditions, consisting of a small coral reef and warm clear waters, can be found. In many respects, Cape San Lucas has an environment similar to a tropical Pacific island, and thus may be the closest habitat of this kind to be met with along the coast of Middle America. The faunal breaks along the west side of the Gulf (fig. 12) can also be closely correlated with various shallow water temperature regimes and other physical barriers.

#### Salinity Distribution in the Gulf of California.

No independent study of the salinities in the Gulf was carried out by this investigator. It was observed from earlier studies that salinity differences from one end of the Gulf to the other, and from surface to bottom, were of such small magnitude that they were assumed to be relatively unimportant in influencing the distribution of most benthic animals. RODEN and GROVES (1959, p. 15) show a difference of only one part per thousand salinity from winter to summer, and from Punta Peñasco to Mazatlan. The isohalines at 10 meters depth for April and August are reproduced on figs. 13a and b. Likewise, from surface to 1800 meters depth, salinity deviates from only  $36.0/_{\infty}$  to  $34.6/_{\infty}$ , a difference too small to be of significance to most marine animals.

There are certain inshore regions of the Gulf of California, however, which are characterized by salinity changes large enough to be significant to animal distribution. These areas are the lagoons and bays along the east coast of the Gulf from the Costa do Hermosillo to San Blas, Nayarit. The salinities in these lagoons and estuaries are influenced both by prevailing climate and by seasonal climatic changes. Those lagoons situated north of Los Mochis in the arid to semi-arid Sonoran coastal climate, seldom receive enough runoff or river discharge to make them brackish, but often the extreme high summer temperatures and high evaporation rate may bring about long-period hypersaline conditions (NICHOLS, 1962 and 1963).

Because of these adverse conditions, few benthic animals can live in these lagoons permanently, and they are frequently barren of macro-invertebrate life. NICHOLS (1962, 1963 and personal communication) has studied one of these Sonoran lagoons (Laguna La Cruz) and states there was evidence that oysters and mussels may have at one time been very abundant, but are not living there now. Personal observations of Indian middens in the vicinity of the same lagoon north of Guaymas revealed the existence of a number of lagoonal or brackish-water mollusk species. These species may have been living in the Sonoran lagoons during the supposed pluvial period occurring about 900 to 1,000 years ago in the northern Gulf region (HUBBS and MILLER, 1948 and personal communication).

The lagoons from Rio Fuerte south to Mazatlan are still situated in a semi-arid climate but receive considerably more fresh water from the rivers, which are more or less permanent. These lagoons permit the existence of seasonal populations of shrimp and permanent beds of oysters, but little is known of the other inhabitants. It is known, for instance, (FRED B PHLEGER, personal communication) that the salinities in this group of lagoons may fluctuate widely, being almost fresh during the brief rainy seasons, and hypersaline during the peak of the dry season. The exact range of salinities is at present unknown to this author.

A series of large lagoons south of Mazatlan to San Blas are very distinct geologically (CURRAY, in VAN ANDEL in press) and hydrographically. They are for the most part in the low salinity range, although the northern ones may have high salinities in the summer. A permanent population of shrimp, *Corbula*, oysters and *Anadara* clams live there, which are utilized for food. These lagoons from the San Blas region to Manzanillo are true estuarine or low-salinity lagoons, whose counterparts were studied along the humid portion of the Texas-Louisiana coast (PARKER, 1959). Rainfall and river discharge are sufficient to maintain a permanent low salinity regime in at least some portions of every lagoon. Unfortunately, no exact figures are available to this author as to the range of physical factors, although they have been studied in some detail by FRED B PHLEGER and GIFFORD EWING (in preparation). Personal collections of faunas from these lagoons were not made, but a few forms were collected for the author by JOSEPH R. CURRAY and FRED B PHLEGER.

#### General Circulation within the Gulf of California.

The circulation in the Gulf of California has been discussed by RODEN (1958, pp. 32-37), but a short discussion of the general characteristics must be given here to supplement the survey of the general physical description



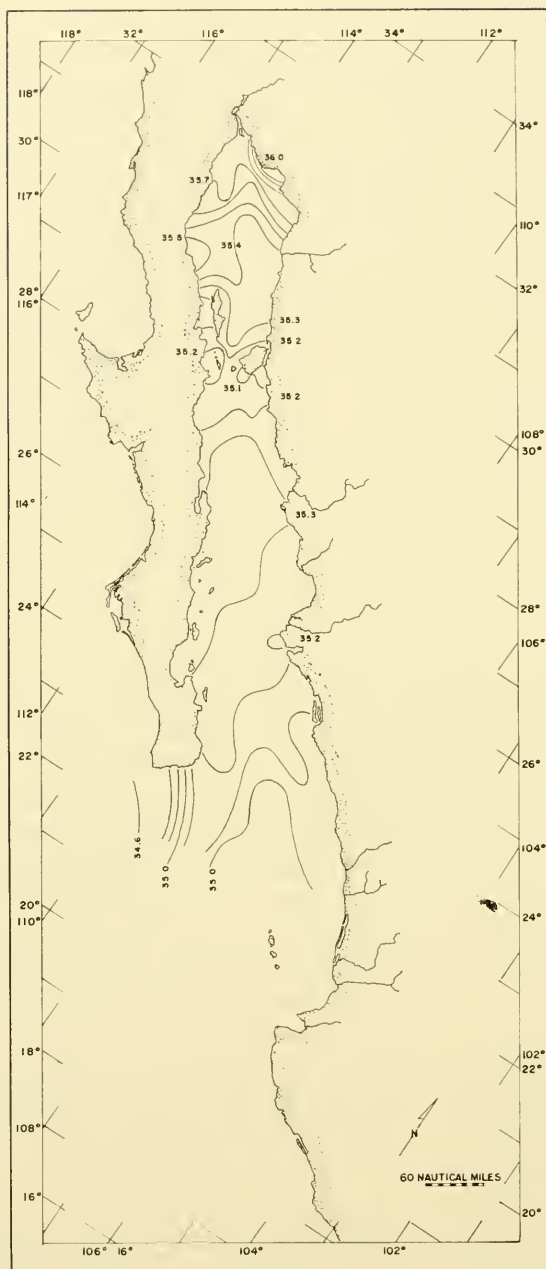


Fig. 13a. Areal distribution of salinity ( $‰$ ) at depths of 10 meters for April, 1957 (from RODEN and GROVES, 1959).

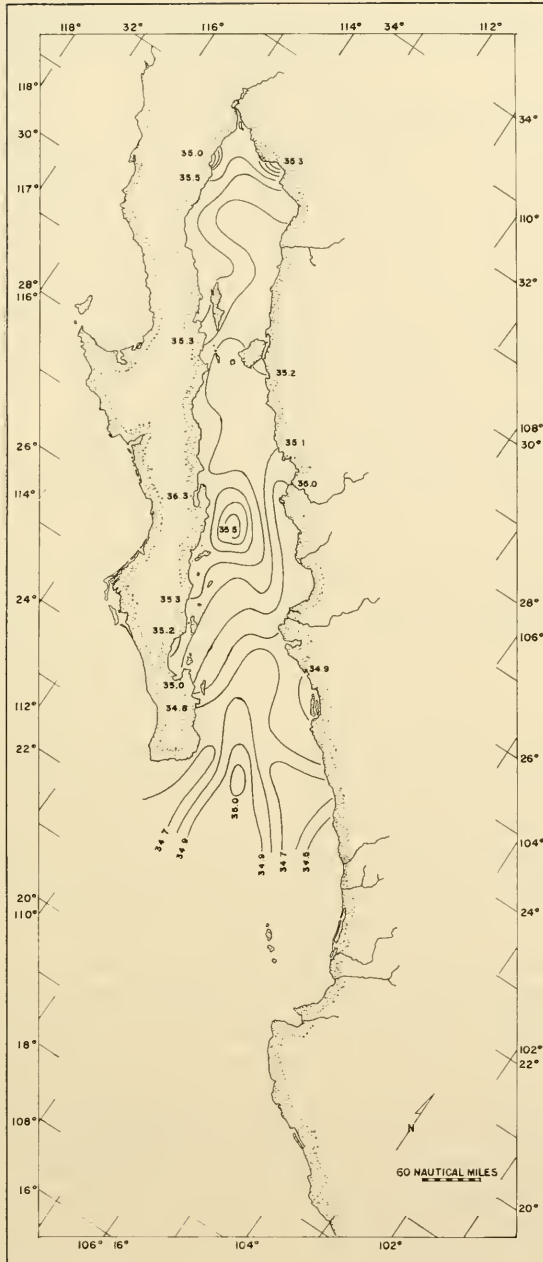


Fig. 13b. Areal distribution of salinity ( $^{\circ}/_{00}$ ) at depths of 10 meters for August, 1957 (from RODEN and GROVES, 1959).

of the Gulf of California. According to RODEN, the circulation in the Gulf is somewhat complicated and not completely known. In the winter months, the outflow of water is thought to occur at the surface, and inflow at greater depths. In the summer, this situation is reversed.

During the winter months (December—March), the high salinity waters in the northern Gulf are cooled, filling the northern basins and moving southward along the coast of Baja California. This movement of water, plus strong tidal currents through the narrows between the large central islands attains speeds of several knots. This situation causes the turbulence which, in turn, is responsible for the abnormally high bottom oxygen and temperature values described previously for this region. According to U.S. Hydrographic Office charts (1947), coastal surface currents move south along the Baja California side of the Gulf in the winter months. In July, water moves into the Gulf at the surface along the east side and center of the Gulf, with some water moving in a southward direction close to the southern portion of the Baja California peninsula. According to RODEN (1958), the monthly average speed of these currents in the southern and central portions of the Gulf is between 5 cm. and 20 cm/sec.

Except for the anomalous situation in the tidal channels between the large islands in the Gulf, these surface currents probably have little effect upon the adult sub-littoral benthic animals. They are important, however, in influencing the planktonic larval transport of many benthic animals. The fact that the currents moving into the Gulf from the south seem to terminate in the vicinity of Tiburón Island, may account for the fact that few truly Panamic species with planktonic larvae are found in the northern Gulf above Tiburón Island. Although water does flow north through Ballenas Channel, the colder surface water temperatures, due to turbulent upwelling, may restrict the movement of Panamic species into the northern Gulf on the west side. The fact that many mollusk and crustacean species taken on the east side of the Gulf do not appear on the west side, and vice versa, might also be explained by the fact that the currents on opposite sides of the Gulf flow in opposite directions. The longshore currents on the east side, with a prevailing movement to the north, also influence the distribution of the fine sediments, so that clayey bottoms are generally found to the north of the few permanent river mouths. Indirectly, then, the currents influence the distribution of clay bottom dwellers in providing their special niche in specific areas.

## **Description of the Macro-Invertebrate Assemblages and Environments**

The present sample coverage and available data is inadequate for a thorough discussion of all of the possible assemblages that might exist in the Gulf of California, but it is at least possible to describe the more important ones and especially those that are likely to occur in the fossil record. The number of ecological niches, both large and small, is very great for such a relatively small region, particularly along the rocky, dissected coast of the west side of the Gulf. The fine-grain carbonate mud environments are the only ones completely missing from this region. There are small patches of coral reefs (SQUIRES, 1959), but they do not compare in size with those of the Caribbean and Indo-Pacific regions. On the other hand, with the exception of the fine-grain carbonate environments, almost all other possible environments of deposition which have occurred during the Tertiary history of the Americas can be found in the Gulf of California. The polychaetes some of the Ophiuroids and Asteroids, Anthozoans, Sponges and Bryozoans have not yet been identified; therefore, these assemblage lists are incomplete, especially with regard to the smaller and sometimes most abundant animals, which have served to characterize communities in other regions.

### **1. The intertidal and shallow rocky shores assemblage.**

The fauna of the intertidal rocky shore environment inhabits the major portion of the shoreline of the Gulf of California and along the coast of Middle America. It is also possibly the most easy to recognize, either in situ or in older sediments. Many papers have been written on the composition of the rocky intertidal fauna and flora of the world, particularly the series of papers by the Stephensons, too numerous to cite here, and a review by DORY (1957). The majority of these papers have been concerned with the intertidal zonation in temperate or boreal regions, where attached algae play an important role in influencing the composition of the fauna. Very few papers give a comprehensive idea of the composition of the intertidal rocky shore fauna of the fantastically rich Gulf of California region. Some idea of the diversity of mollusks to be found in this habitat can be obtained in STEINBECK and RICKETTS (1941), KEEN (1958), MCLEAN (1961) and DUSHANE (1962). It would be impossible to list here all of the animals known to occur in this environment, but at least the most common ones found in this study and a few others known to be abundant from other papers are given in Table II of the appendix.

The computer list of species common to stations occupied in this habitat was very incomplete, and of little value in assessing the true nature of the fauna living on rocky shores. Collecting in this environment was not at all systematic, since this study was originally to be confined only to level bottom areas. The species assigned to this environment with the greatest significance by the computer were: the gastropods *Nerita scabricosta*, *Purpura patula pansa*, *Turbo fluctuosus*, and *Pyrene fuscata*; and the pelecypods, *Barbatia reeveana*, *Isognomon chemnitziana*, *Ostrea conchophila*, *Anomia adamas*, and *Cardita affinis californica*. *Anomia* and *Ostrea* were only found as dead shell within the samples, although this author observed large numbers of them attached to the rocks. Actually, the above gastropod species were observed to be very abundant in all rocky localities examined, along with numerous chitons, patellas, neritids, littorines, and turbinids. The four stations considered most indicative of this environment, and the portions of the shoreline inhabited by the rocky shores animals are shown on fig. 14. So far, 53 living species of invertebrates have been identified from the intertidal rocky shores environment, and another 18 species known to live on rocky shores from the literature were also taken in the vicinity of the rocks, but only as dead shell. A few of the typical mollusks are figured on Plate I. Only mollusks are figured on these plates, since the other invertebrates are still in the hands of the various specialists and could not be photographed at the time this paper was being written.

McLEAN (1961), in his list of invertebrates from Los Angeles Bay, gives 105 species of mollusks which occur either on the rocks or in the sand among the rocks (really two separate habitats). DUSHANE (1962) also lists 145 species of mollusks living around the rocks in a small cove at Puertocitos, somewhat south of San Felipe on the west side of the Gulf. Many more species were reported by these authors than were found in the present study. A much larger list of intertidal mollusks can also be gleaned from KEEN (1958). Since this study was originally proposed as a study of level-bottom faunas, this environment is discussed only briefly in order that paleontologists working on fossil deposits surrounding the Gulf of California and along the Pacific coast of Central and South America may have some frame of reference for separating out this assemblage from those assemblages which are normally found on level bottom.

## II. Intertidal sand beaches and sand flats to 10 meters.

The waters edge of the sand beaches and adjacent sand flats to depths of about 10 meters are characterized by a fauna which closely resembles that found on the sand beaches and in the nearshore Gulf of Mexico as



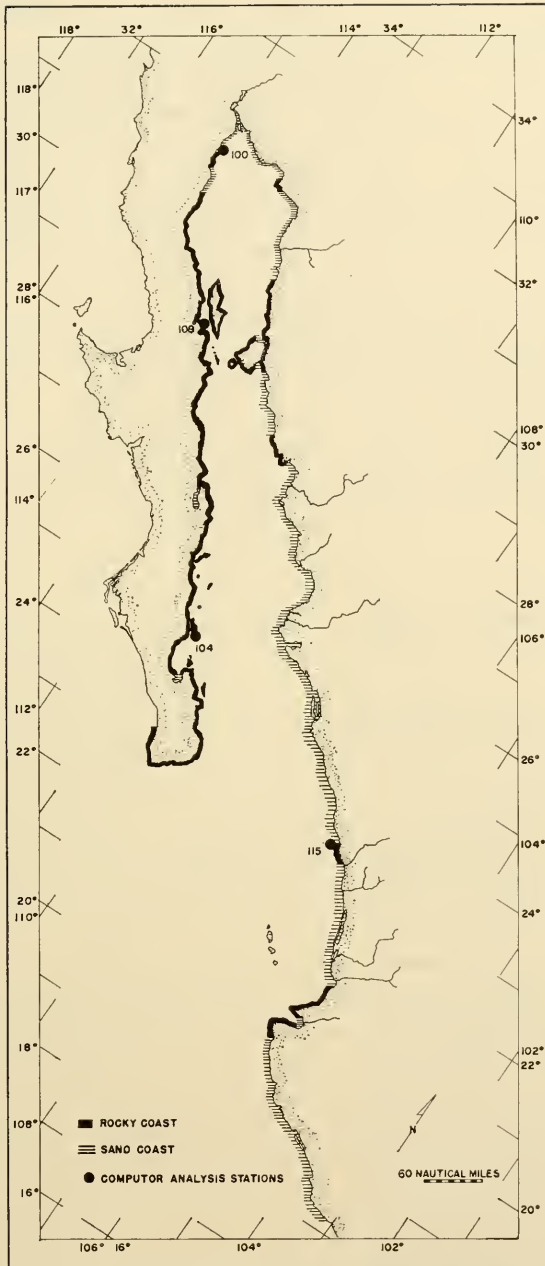


Fig. 14. Distribution of sandy and rocky areas along the coast of the Gulf of California. Station locations for rocky shore localities bound together by matrix-associated species.

described by PARKER (1956 and 1960). In extent, this environment and its assemblage covers almost as much shoreline as the rocky shores, as shown in fig. 14. One third to one half of all known mollusk species from the Gulf of California have been reported from this environment, since the majority of records are a result of collecting along sand beaches which are most accessible from human habitation. It is difficult to ascertain from the literature which species were found in the living state in this environment alone. Thus the characteristic species, which are listed in Table II are those from the present collection, with the exception of a special list extracted from McLEAN (1961) given below.

As on the rocky shores, collecting along the sandy shores was also somewhat haphazard, and most of the samples along the shore were taken by hand. The subtidal portion of the environment, however, was sampled mostly by grab samples (Table III, fig. 2a), i.e.: 3 orange peels, 5 Van Veens, 1 dredge, 2 minidredges and 2 by diving. Because most of the hard-shelled animals which may live to depths of 10 meters may also wash onto the shore and become incorporated into sand beach deposits, no distinction was drawn between the tidal and subtidal portions of this environment. There is certainly a different group of animals living in the deeper portions of this environment than right at the shoreline.

Only three species were assigned to a group of stations in this environment by the computer program, *Cardita megalostropha*, *Tivela byronensis* and *Heterodonax bimaculatus*, of which only *Heterodonax* can be considered a characteristic species, the other two not even having been taken alive. In a number of localities it was observed by the author that *Heterodonax* could be scooped up by the handfuls by digging just below the sand surface at the water's edge. The other two species, although not taken alive during this study, are listed as typical nearshore sand bottom species by other authors. The typical animals found at the water's edge, as observed by this author are: *Cerithium albonodosum*, *Bulla gouldiana*, *Heterodonax*, numerous species of *Donax*, *Uca crenulata* and *Ocypode occidentalis*. The other species given in Table II are typical of the sub-tidal portions of this environment. In the sub-tidal portions the most abundant living species and also the most characteristic are: the gastropods, *Strombus gracilior*, *Oliva spicata*, *Olivella anazora*; the pelecypods, *Transanella puella*, *Megapitaria squalida*, and the most important *Tellina felix*; and the echinoid *Euclidaris thouarsi*. The list of abundant, although not taken alive, species on Table II for this environment is also given, since it is known that most of these species have been recorded as living in this environment by others, and can be considered useful index species for the paleontologist. Although all species given in Table II occur in this environment, not all occur

together in the same geographic region. Most of them range along the coast from the head of the Gulf to Panama, but a few are restricted to the southern Gulf, or are not found north of Mazatlan.

There are many other species of invertebrates known from other collections, which are more abundant on the sand beaches and on sand bottom to depths of 10 meters, and are perhaps more typical of this environment than those given in Table II. McLEAN (1961) lists two sand dollars, *Encope grandis* L. Agassiz and *Encope californica* Verrill, as living on the sand flats at Los Angeles Bay, and although *Encope* tests were frequently noticed on the beaches, no living specimens were collected along the beach during this present study. DUSHANE (1962) also gave a large list of mullusks found on sand or sand-mud bottom at the same depths near Puertocitos. She included at least 112 mollusk species which definitely live in this environment. The mollusks found alive on the sand flats to depths of four or five meters in Los Angeles Bay by McLEAN are given in a list below in order to illustrate the diversity of species from one locality in one environment.

Prosobranchs  
*Calliostoma eximum*  
*Neritina luteofasciata*<sup>1</sup>  
*Balcis* cf. *rutila*  
*Cerithium sculptum*  
*Cerithium albonodosa*<sup>1</sup>  
*Cerithidea mazatlanica*  
*Natica chemnitzii*  
*Polinices bifasciatus*  
*Polinices uber*  
*Polinices reclusianus*  
*Strombus gracilior*<sup>1</sup>  
*Strombus granulatus*<sup>1</sup>  
*Hexaplex erythrostomus*  
*Nassarius iodes*  
*Nassarius moestus*  
*Nassarius tiarula*<sup>1</sup>  
*Oliva spicata*<sup>1</sup>  
*Olivella dama*  
*Cancellaria cassidiformis*  
*Conus ximines*  
*Terebra variegata*

Tectibranchs  
*Bulla gouldiana*<sup>1</sup>

*Haminoea angelensis*  
*Haminoea strongi*

Pulmonates  
*Melampus olivaceus*

Lamellibranchs  
*Anadara multicostata*  
*Anadara cepoides*  
*Glycymeris gigantea*  
*Glycymeris maculata*  
*Glycymeris multicostata*  
*Pinna rugosa*  
*Atrina tuberculosa*  
*Trachycardium consors*  
*Trachycardium panamense*  
*Trigoniocardia granulifera*  
*Laevicardium elenense*  
*Laevicardium elenense apicinum*  
*Pitar newcombianus*  
*Megapitaria squalida*<sup>1</sup>  
*Dosinia ponderosa*  
*Protothaca grata*  
*Heterodonax bimaculatus*<sup>1</sup>  
*Lyonsia gouldii*

<sup>1</sup>) Species also taken alive in the sand beach and sand flat environment in the present study.

The majority of the above species were also collected by the present author on sand beaches, although not found in the living state. Many of the species, however, were taken alive at greater depths, and may be more abundant in the deeper assemblages. A much larger list can be obtained from KEEN (1958), although it is nearly impossible to tell which mollusks of KEEN's list are confined to these depths alive. A few of the typical mollusks are given on Plate II.

### III. Low-salinity lagoon and mangrove assemblage.

This environment was not studied in detail along the Pacific coast of Mexico, although a few small hand collections were taken by this author (Table III) and specimens were collected by other members of Scripps expeditions from various brackish lagoons along the Mexican coast. This discussion is confined to mollusks, but it is well known that several species of commercially important shrimp and crabs occur in large numbers within the lagoons between Mazatlan and Panama. Little information is available as to the other kinds of invertebrates inhabiting the lagoons and mangrove swamps. Inlets into the lagoons south of Mazatlan are small, restricted, and are apparently closed rather frequently. For this reason, few strictly marine animals will be able to survive in the lagoons, and salinities are seldom high enough to support a wholly marine fauna. A list of the typical mollusks found in this environment, as selected from KEEN (1958) is given below. Certain species in this list are quite important as food, especially *Anadara tuberculosa*, *Ostrea columbiensis* and *Ostrea corteziensis*. A few of these low-salinity mollusks are figured on Plate III and all are illustrated in KEEN (1958).

#### Prosobranchs

*Neritina luteofasciata*  
*Neritina latissima*  
*Cerithidea mazatlanica*<sup>1</sup>  
*Cerithidea montagnei*<sup>1</sup>  
*Littoridina*, sp.

#### Tectibranchs

*Bulla gouldiana*<sup>1</sup>

#### Pulmonates

*Melampus olivaceous*<sup>1</sup>  
*Ellobium stagnalis*

#### Lamellibranchs

*Anadara tuberculosa*<sup>1</sup>  
*Mytella falcata*  
*Ostrea columbiensis*  
*Ostrea corteziensis*<sup>1</sup>  
*Polymesoda mexicana*<sup>1</sup>  
*Polymesoda* (7 more species known)  
*Cyrenoida panamensis*  
*Mytilopsis adamsi*  
*Rangia mendica*<sup>1</sup>  
*Corbula inflata*

<sup>1</sup>) Collected as a part of this study.

#### IV. Nearshore, sand and sand-mud, 11-26 meter assemblage.

This is by far the most prolific assemblage in species and numbers of individuals of invertebrates in the Gulf of California, so far as the present sampling is concerned. In accordance with Liebig's "Law of the Minimum", as restated in PARKER (1959), there is good reason for the great diversity and size of the population, since the ecological conditions are optimum for most marine species. Salinities are constant and at normal oceanic values, and water temperatures have a much smaller annual range than in the inshore environments. The water is also relatively quiet at these depths which are below wave base for the rather small-sized waves of the Gulf of California. Sediments therefore range from sand to sand-mud and mud-sand, or in SHEPARD'S (1954) terminology, sand, silty sands, clayey sands, sandy silts and sand-silt-clay. These sediments are less well-sorted than those in the previous environments, permitting greater amounts of organic detritus to accumulate, thus making it possible to support a larger population of deposit-feeding animals. These, then, are optimum conditions for the existence of most marine invertebrates. A total of 258 species (living and dead) from all stations, and 172 living species from the 27 characteristic stations were identified from this environment. A comparison of the number of species taken at all depth ranges is given in fig. 15.

The separation between the northern and southern Gulf is relatively distinct in this environment. The contingency matrix provided the basis for two separate assemblages, both on sand bottom and in from 11 to 26 meters depth, one in the Tiburon region and the other south of Mazatlan. There is a possibility that separate groupings of animals resulted because of different kinds of sampling gear. The majority of samples in the northern region were taken by shell dredge (10 shell dredges, 2 Van Veens, 1/15 m<sup>2</sup> and 2 3-meter otter trawls), while in the southern region grab samples outnumber dredges and trawls (4 Petersen grabs, 1/10 m<sup>2</sup>, 3 Van Veen, 1/20 m<sup>2</sup>, 2 orange peels, 1/15 m<sup>2</sup> grabs, 3 3-meter otter trawls, and 1 mini-dredge) as shown on Table III. Regardless of the difference in balance of collecting devices between the two areas, at least some dredging and grab sampling was carried out in both places. Examination of the list of living animals only from the northern and southern nearshore shelf region (Table II) shows roughly the same size and kinds of animals from the two regions, even though the species were often different within the same subgenus. For instance, 25 species were taken in common between the two areas, or slightly less than one quarter of the total of northern species and slightly less than half of the total of southern species. There were two more species of corals, almost twice as many species of prosobranchs and



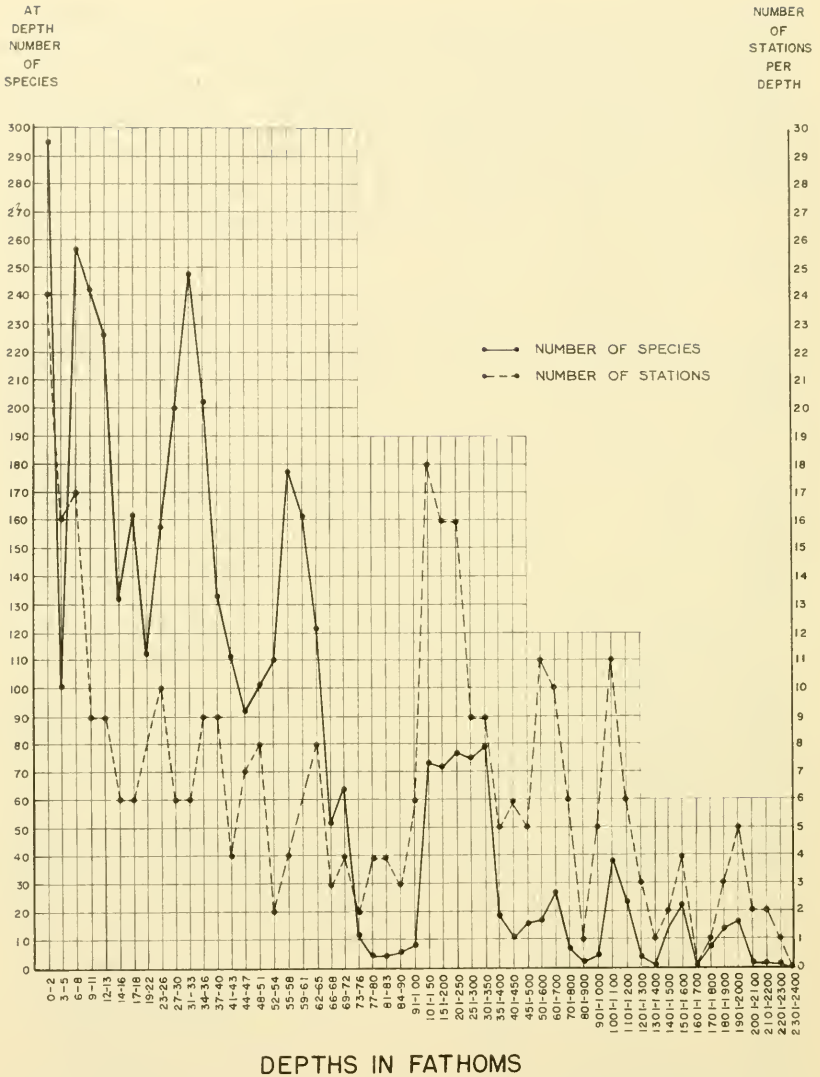


Fig. 15. Graphs of the number of species occurring at various increments of depths from shore to abyss, as compared to the number of stations occupied in the same depths. Species totals include both living and dead occurrences.

crustaceans, but six times as many echinoid species in the northern than the southern region. However, there were the same number of lamelli-branch species, indicating that the catch effort for infauna was about the same, but that the excess shell dredging in the northern region produced more epifaunal or motile forms than the grab sampling in the south. With

the slight information available from the present physical data, it would seem that extremes of water temperature play an important part in producing a somewhat different infauna in the southern than in the northern part of this environment. As shown in fig. 12, inshore water temperatures range from 15° to 30°C. in the Tiburón region, while south of Mazatlan, the range is much less and higher (22° to 30°C.). This is somewhat substantiated in that if one compares the two lists in Table II, it can be seen that there is usually a replacement of species within the same genus between the two areas, and that if one looks at the published ranges of these species, the southern species are those which have not been previously cited in the northern Gulf. Sediments were also somewhat finer and less well-sorted in the southern region. One of the reasons so few grab samples were taken in the Tiburón region, was that none of these sampling devices would work in the hard sand and shell-sand bottom. The shell dredge was the only device that would dig down into the bottom, and in fact was frequently the only source of sediment samples for the geologists, as their coring devices would not operate either in the hard bottom. The Tiburón region is also affected by upwelling (fig. 10), while no upwelling takes place in the San Blas region. This factor alone creates not only differing water temperatures, but also varying food supply.

Actually, the Tiburón region in depths of four to thirty meters is very complex in patterns of invertebrate distribution and no different from any other marine bottom in this respect. Five different groupings of animals resulted from the contingency matrix, each with a slightly different set of stations in common (fig. 16). Since both living and dead occurrences were used to establish the stations groupings as shown in fig. 16, these patterns may not be very significant. They are given, primarily to show the complexity of distributions which may result from such a program. Table IV gives the list of the species which comprised the index groups from the computer program, listed as to their importance and number of stations common to each within its group. The tabulation of the known physical factors for each group is also shown.

Since the above computer analysis produced a somewhat confused and probably false impression of the true assemblage (since both living and dead records were used), a more reliable assemblage was devised from a combination of all of the index groups, using the somewhat more subjective method of analysis mentioned in the discussion of methods. All species which were involved in the matrix analysis were listed and compared as to common station occurrence and abundance only as living records. It was then possible to select the stations where the greatest number of these

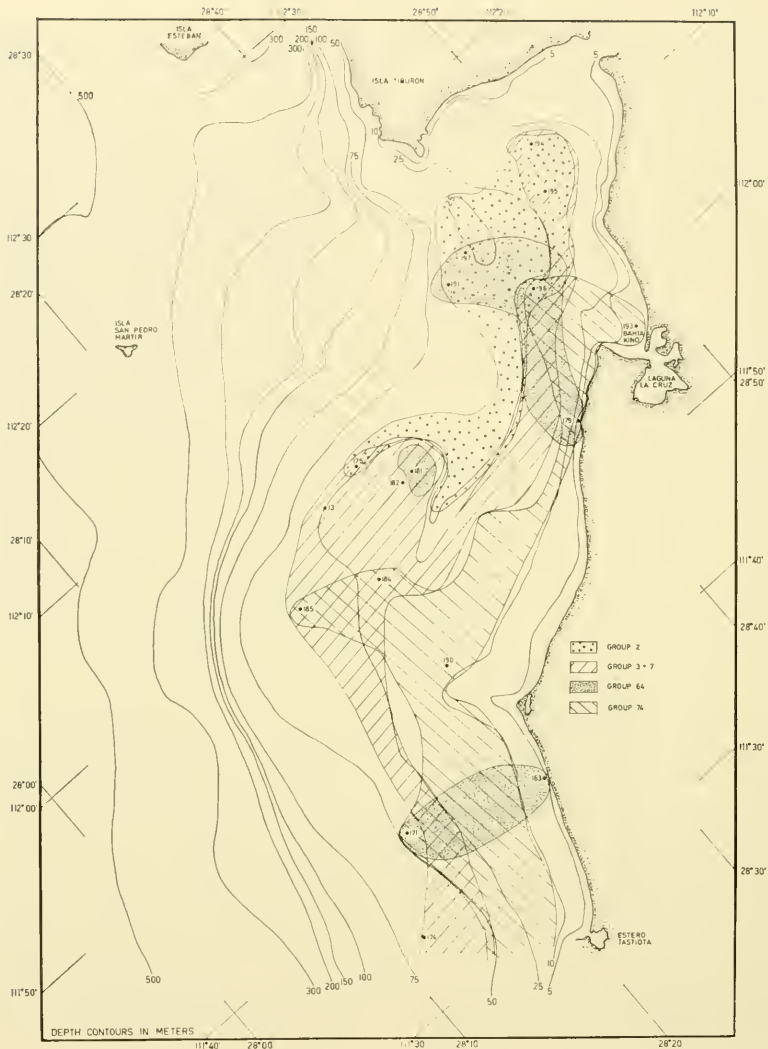


Fig. 16. Areal distribution of "index groups" of assemblages in the northern nearshore shelf environment. Station composition and range of ecological factors for each group can be found in Table III. The boundaries of the groups are somewhat subjective, agreeing in general with the bathymetry and sedimentary patterns. Station numbers shown are those with highest affinity, although others were involved in determining the boundaries, but were much less important.

common species were found, and also those species which were either unique to or had the greatest percentage of occurrence within these stations. A map of the station locations resulting from this analysis is shown on fig. 17.

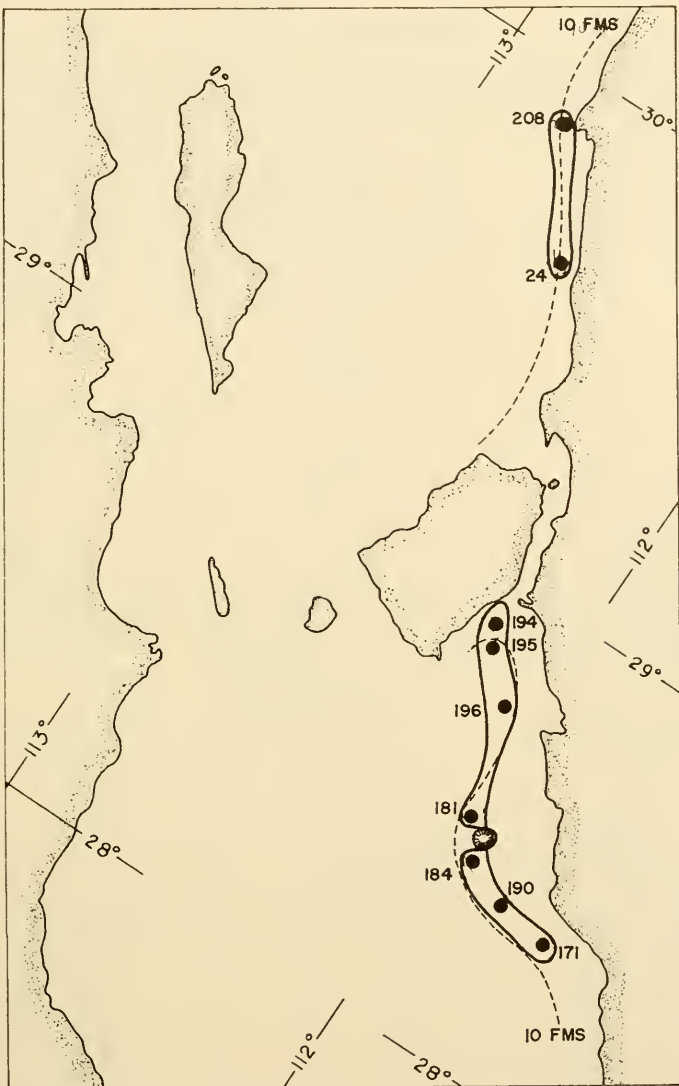


Fig. 17. Areal distribution of composite group of stations characterizing the nearshore shelf environment in the northeastern Gulf region. These stations had the greatest number of common occurrences of species from all index groups.

In terms of strict abundance (as a *qualitative* term [see THORSON, 1957, p. 474]) within the nine stations considered characteristic of the 11 to 26 meter nearshore shelf environment in the northern Gulf, the following species can be considered the most important, and may actually form the basis for a community, when more systematic sampling is carried out.

Many of the really abundant forms are epifaunal in nature (actually attached to objects on the bottom), which can be attributed to the nature of the bottom, being in many places a shell-sand, with large quantities of dead shell furnishing a place for attachment. These animals, *Heterocyathus*, and two species of *Astrangia* (corals), the immense numbers of Calyptraeidae (*Calyptraea*, *Crucibulum* and *Crepidula*), the equally numerous barnacles and pagurids living in dead gastropod shells, are dominant in a sense, but cannot be considered part of the infaunal level-bottom community. The most abundant infaunal animals were the prosobranchs,

Table IV.

Species	Index Group Numbers				
	2	3	7	64	74
<b>Gastropods</b>					
<i>Crepidula arenata</i> .....			×		
<i>Crepidula excavata</i> .....				×	
<i>Polinices intemerata</i> .....				×	
<i>Polinices reclusianus</i> .....			×		
<i>Strombus gracilior</i> (Index species grp. 64).....				×	
<i>Hexaplex erythrostomus</i> .....				×	
<i>Distorsio decussatus</i> .....	×				
<i>Nassarius versicolor</i> .....			×		
<i>Strombina gibberula</i> .....		×			
<i>Olivella fletcheriae</i> .....			×		
<i>Terebra specillata</i> .....		×			
<i>Acteocina angustior</i> .....			×		
<b>Lamellibranchs</b>					
<i>Nuculana elenensis</i> .....					×
<i>Barbatia alternata</i> .....				×	
<i>Anadara obesa</i> .....	×				
<i>Lioberus salvadoricus</i> .....		×			
<i>Chlamys circularis</i> (Index species grp. 2).....	×				
<i>Lucina prolongata</i> .....		×			
<i>Ctena mexicana</i> .....	×				
<i>Laevicardium elatum</i> .....				×	
<i>Laevicardium elenense</i> (Index species grp. 7).....			×		
<i>Trachycardium panamense</i> .....			×		
<i>Trigoniocardia biangulata</i> .....			×		
<i>Megapitaria squalida</i> .....			×		
<i>Dosinia dunkeri</i> .....			×		
<i>Chione mariae</i> .....			×		
<i>Tellina amianta</i> .....			×		
<i>Tellina inaequistriata</i> .....		×			
<i>Macoma siliqua</i> .....	×				
<i>Semele guaymasensis</i> .....			×		
<i>Donax gracilis</i> (Index species grp. 74).....					×
<i>Ensis californica</i> (Index species grp. 3).....		×			
<b>Crustaceans</b>					
<i>Portunus pichelinqui</i> .....		×			

(continued)



Table IV (continued).

Physical Factors					Index Group Numbers				
					2	3	7	64	74
Station Numbers	Depth in fathoms	Temp. in °C.	Oxygen in ml/l.	Sediment type					
24	13	16	2.5	Sand			×		
114	4	30	4	Sand	×				
163	1	20	4	Sand				×	
172	7	20	3	Shell sand	×				
175	14	13	1.2	Mud sand	×				
179	1	14	3	Sand			×		×
181	9	18	3	Sand		×		×	
184	9	14	3	Sand		×	×		×
185	31	13	2.4	Sand			×		×
190	7	20	3	Sand					×
191	14	15	3	Mud sand				×	
194	7	20	3	Mud sand	×	×	×		
195	12	18	3	Mud sand	×		×		
196	13	16	3	Sand	×	×	×	×	×
208	7	19	2.6	Sand	×			×	
212	31	13	2.4	Sand		×	×		
Average Environmental Conditions		Depth in fathoms:			10.6	19	16.6	7.4	9.4
		Temp. in °C.:			17	14.3	14	19.2	18
		Oxygen in ml/l.:			2.6	2.8	2.7	3.2	3.2
Sediment type:									
Mud 3/5   Sand 6/7   Sand 3/4   Sand 6/7   Sand 8/8									

Table V.

Species	% of Occurrences in Computer Stations, alive	% of Total live Occurrences in Whole Gulf	Index
<i>Laevicardium elatum</i> .....	88	71	80
<i>Hexaplex erythrostomus</i> .....	44	100	72
<i>Donax gracilis</i> .....	44	100	72
<i>Ensis californicus</i> .....	44	100	72
<i>Strombus gracilior</i> .....	33	100	66
<i>Tellina tabogensis</i> .....	33	100	66
<i>Polinices reclusianus</i> .....	66	60	63
<i>Trachycardium panamense</i> .....	66	50	58
<i>Olivella fletcheri</i> .....	55	60	58
<i>Crepidula excavata</i> .....	55	57	56
<i>Terebra specillata</i> .....	44	66	55
<i>Lioberus salvidoricus</i> .....	33	75	54
<i>Anadara obesa</i> .....	33	75	54
<i>Laevicardium elenense</i> .....	60	40	50
Lesser Importance, Living			
<i>Trigoniocardia granifera</i> .....	44	50	47
<i>Crepidula arenata</i> .....	20	60	43
<i>Nassarius versicolor</i> .....	44	40	42

*Polinices reclusianus*, *Strombus gracilior*, *Cantharus pallidus*, *Nassarius versicolor*, *Oliva incrassata*, *Olivella fletcheriae*, *Hexaplex erythrostomus*, *Mitra hindsi*, *Pleuroliria picta*, *Terebra specillata* and *Terebra variegata*; the lamellibranchs, *Nuculana elenensis*, *Nuculana fastigata*, *Anadara obesa*, *Chlamys circularis*, *Trachycardium panamense*, *Laevicardium elatum*, *Laevicardium elenense*, *Megapitaria squalida*, *Chione mariae*, *Tellina tabogensis*, *Macoma siliqua*, *Donax gracilis*, *Ensis californicus* and *Lyonsia gouldii*; the echinoids, *Lovenia cordiformis* and *Moira clotho*; and the ophiuroid, *Amphiodia occidentalis* (LYMAN). The family of mollusks with the most number of individuals was certainly the Cardiidae, followed by Veneridae and Turridae. Few polychaetes were noted and so far the only ophiuroids and asteroids identified are: *Amphiodia occidentalis* and *Astropecton californicus*.

As mentioned previously, the 11 to 26 meter sand bottom assemblage extends the length of the Gulf and probably to Ecuador, but the individual species composition changes somewhat to the south. Some of the differences between the north and south portions of this environment can certainly be attributed to differing sampling devices. This is especially true with respect to the decapod crustaceans, which were quite abundant in the northern region, collected mostly by dredge, and relatively uncommon in the southern region collected by grab samplers. On the other hand, the most common infaunal species were either of the same species or of the same genus in both regions, illustrating the uniformity of the assemblage along the entire coast. The contingency matrix did provide a basis for selecting stations representative for the southern nearshore shelf by finding several groups of closely associated species belonging to the stations shown on fig. 18. Sampling devices used for those stations are on Table III. A list of the living invertebrates from the 13 stations on fig. 18 is given in Table II, which when compared with the list of species for the Tiburón region also in Table II, gives an idea of both the similarity and uniqueness of the two faunas. A number of typical mollusks from this environment (both north and south) are illustrated on Plate IV, while others can be seen in KEEN (1958) or OLSSON (1961).

#### V. Intermediate shelf, 27 to 65 meters.

The contingency matrix provided a very distinct set of stations, which served as a basis for examination of the faunal associations in these depths. Unfortunately, the northern portion of the intermediate shelf was sampled primarily by shell dredges with a one meter opening (Table III), while the southern part was sampled mostly by 12 and 3-meter wide otter trawls

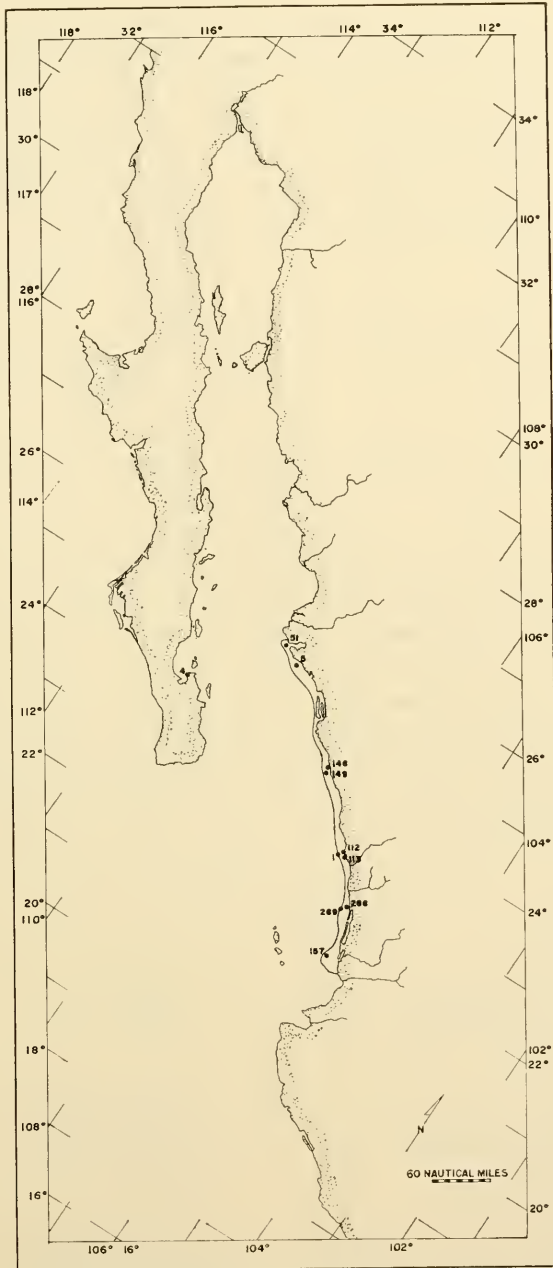


Fig. 18. Distribution of stations from which the distinct matrix group of animals characteristic of the nearshore shelf in the southern Gulf were taken.

(Table III). No grab samples were taken in any part of this environment, which must account for the relative scarcity of infaunal species as compared to regions sampled elsewhere in the Gulf where grab samplers were occasionally used. As can be seen in the lists of living animals from both the northern and southern portions (Table II), crustacean and prosobranch species far outnumber any other kind of organisms, and these kinds of animals are most likely to be taken by dredges and trawls.

Even though no grab samples were taken, which might serve to show a true difference between nearshore and intermediate shelf faunas, there is no doubt that the intermediate shelf assemblage is a distinct one, with depth boundaries at about 27 to 65 meters. The fact that decapod crustaceans proved to be important index species in providing a characteristic set of stations for this environment, both in the north and the south, lends more support to this idea, since these animals are motile, and would be expected to range over several communities or environments, unless the physical boundaries might be fairly sharp. The contingency matrix indicated a close association between 18 invertebrate species in the Tiburón region in depths from 25 to 76 meters. The distribution of these stations and three other closely associated stations is shown in fig. 19. As shown in Table III, these stations were taken by 7 shell dredges, 4, 3-meter otter trawls and 2 rock dredges. Although the list of associated species, as given by the matrix is primarily an epifaunal one, and the mollusks are both living and dead species, it is given here for reference. The complete list of invertebrates identified so far from the Tiburón intermediate shelf region is given in Table II.

Species	Degree of Association		Degree of Association
Gastropods		<i>Solecurtus guaymasensis</i>	
<i>Polinices uber</i> (dead)	11	(dead)	16
<i>Fusinus dupettithouarsi</i>	12	<i>Plicatula inezana</i>	18
<i>Natica grayi</i>	15		
Lamellibranchs		Crustaceans	
<i>Nemocardium pazianum</i>	6	<i>Euprognatha bifida</i>	
<i>Chione mariae</i>	8	(Index Species)	1
<i>Diplodonta subquadrata</i>		<i>Mesorhea belli</i>	2
(dead)	9	<i>Randallia americana</i>	3
<i>Macoma siliqua</i>	13	<i>Collodes tenuirostris</i>	4
<i>Cyclopecten pernomus</i>		<i>Pagurus gladius</i>	5
(dead)	14	<i>Cancer amphioetus</i>	7
		<i>Paradasygius depressus</i>	10
		<i>Cymopolia zonata</i>	14

Most of the characteristic living species are listed in Table II, but the following species can be considered the most abundant infaunal invertebrates:

Prosobranchiata	<i>Crassatella gibbosa</i>
<i>Solariella triplostephanus</i>	<i>Nemocardium pazianum</i>
<i>Natica grayi</i>	<i>Chione mariae</i>
<i>Murex recurvirostris</i>	<i>Macoma siliqua</i>
<i>Fusinus dupettithouarsi</i>	<i>Trigoniocardia granifera</i>
<i>Pleuroliria albicarinata</i>	
Echinoidea	Asteroidea
<i>Clypeaster europacificus</i>	<i>Luidia columbia</i> Lütken
Lamellibranchiata	Ophiuroidea
<i>Anadara nux</i>	<i>Amphiglyptis perplexa</i>

A number of the species from these 13 stations as given on Table II were also taken in shallower water and a few were found in deeper waters. All stations were taken on sand bottom in an area where bottom temperatures range between 30° and 14°C. and the waters are well-oxygenated. As an assemblage, there is a considerable difference between this one and the one inshore of it, in that there was an enormous number of mollusk species found only as dead shell, and not usually found living in these depths elsewhere along the coast. Most of these species normally live in depths of from 1 to 30 meters. A list of them can be compiled from Table I by noting all species in the complete list which were taken from the 13 stations shown on fig. 19. These dead, but shallower shells, are important to the paleontologist, however, in that they are part of an assemblage which will eventually become buried and form a distinct fossil deposit indicative of a transgressive sea. It is presumed (and somewhat substantiated by carbon-14 dates) that the sand deposits in which these shells are found have resulted from lowered sea level during the early part of the Holocene. The shells of animals which once lived close to shore became mixed with deeper species as the sea level rose, and the shoreline moved inwards. It is known that strand line deposits resulting from lowered sea level at around 7,000 to 11,000 years ago occur at depths of from about 40 to 80 meters throughout the world (CURRAY, 1960, 1962). Figs. 20a and b show the distribution of two of the typical decapods found in this environment, *Cancer amphioetus* and *Randallia americana*. The distribution of two mollusks, the gastropod, *Solariella triplostephanus*, and the pelecypod, *Trigoniocardia biangulata* are shown in figs. 21a and b. The distri-



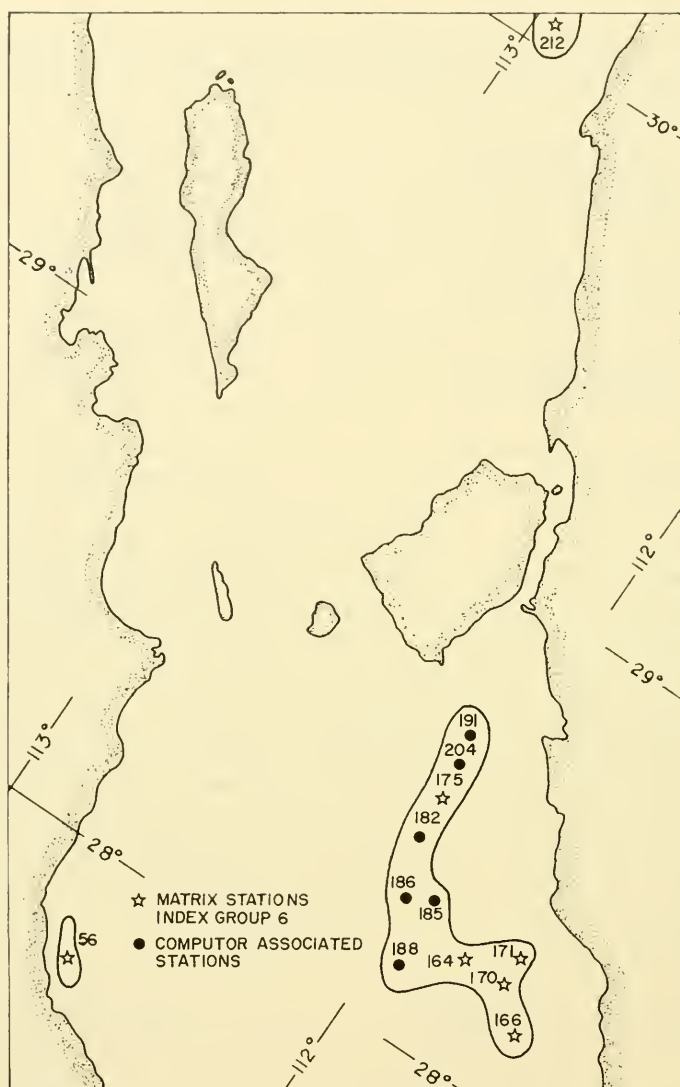


Fig. 19. Areal distribution of the northern Gulf, intermediate shelf environment, based on stations brought into close association by matrix-associated species, especially index group number 6 (*Euprognatha bifida*).

butional boundaries of these species, it can be seen, correspond closely to the boundaries of the environment, fig. 19. Many other species of invertebrates have a similar distributional pattern in this region, even though sample coverage was relatively dense from shore to 200 meters (fig. 2b), which is an additional proof that a distinct assemblage and

probably community exists in the area circumscribed by the 13 stations in fig. 19.

This same environment probably continues uninterrupted along the coast to at least Panama, but samples were taken at these depths in sufficient numbers only south of Los Mochis to San Blas. A similar assemblage was also devised in which about one third of the species was taken in common to the two sections. There were, however, a number of invertebrate species taken in the southern intermediate shelf region which were not taken in the north, and these served to separate the areas by means of the contingency matrix. As with the nearshore shelf, temperature seems to play a part in creating different faunas in the north and south, since many genera have species only found in the north and others only in the south. The greatest difference between the two assemblages may, however, be a result of the difference in sampling. Certainly the large trawls were able to capture more of the large motile decapods and large prosobranchs. These two groups were twice as abundant in the southern region where trawls were used, than in the Tiburon region where they were only used four times. The species most frequently occurring at the seven stations which proved by preliminary computer analysis to be distinct are listed in Table VI. The seven typical stations were taken on silty clay and ranged in depths from 36 to 75 meters, as shown on fig. 22. In order to substantiate the importance of the animals in Table VI for this environment, the same system of computed indices of uniqueness was computed as was for Table V. It can be seen immediately that no infaunal species (unless you consider the prosobranchs as living in the bottom) figured in the computer analysis. What is significant, however, is that the species in Table VI are very restricted in their distribution, even though they are capable of much greater mobility than the other invertebrates.

A number of other stations were also occupied in the southern portion of the intermediate shelf. Most of these stations contained the animals listed in Table VI, but not in such a close association. The seven matrix-associated stations constitute a nucleus or center for the whole assemblage, while the others are on the periphery, and have a more heterogeneous group of animals. These 12 stations are shown on fig. 22. A list of the living species collected from all 12 of these southern stations is given in Table II. The most abundant infaunal species on sand bottom off San Blas were: the prosobranchs, *Calliostoma bonita*, *Astele rema*, *Architectonica placentalis*, *Natica broderipiana*, *Natica colima*, *Polinices uber*, *Distorsio decussatus*, *Bursa nana*, *Murex recurvirostris*, *Hexaplex brassica*, *Coralliophila hindsii*, *Cantharus capitaneus*, *Mitra erythrogramma*, *Knefastia walkeri*,

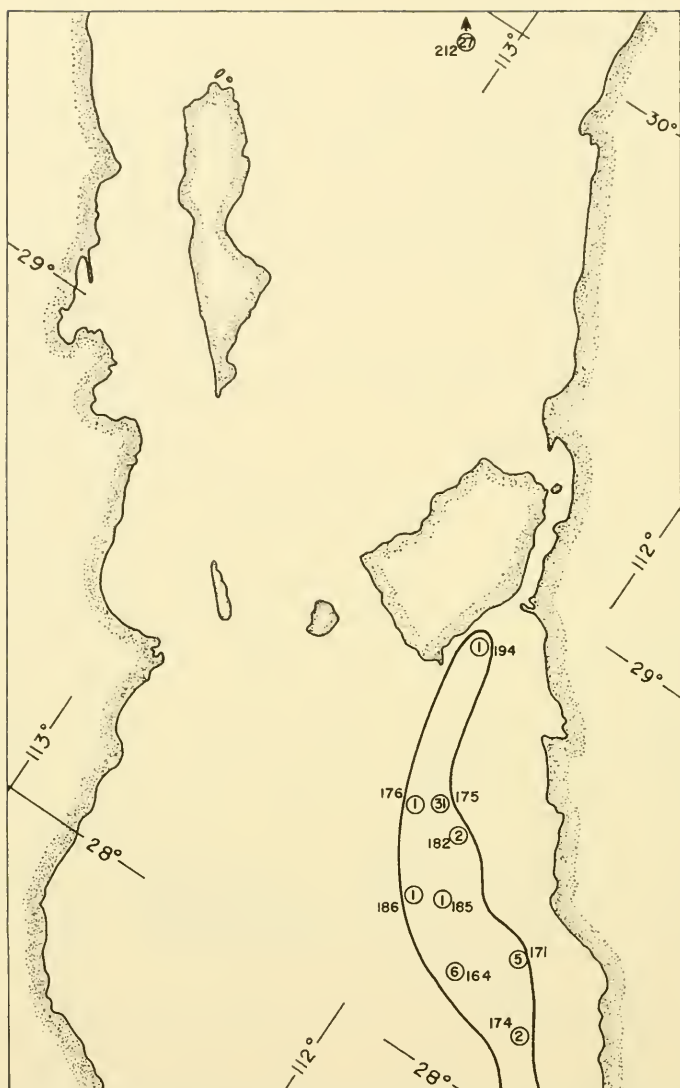


Fig. 20a. Distribution of the decapod crab, *Cancer amphioetus*, confined to the northern Gulf, intermediate shelf region. Number of specimens at each station circled.

*Clavus roseolus*, *Hindsiclava andromeda*, and *Pleuroliria picta*; the scaphopod, *Dentalium oerstedii*; and the lamellibranchs, *Nuculana morella*, *Glycymeris tessellata*, *Chlamys circularis*, *Cardita spurca beebei*, *Trachycardium belcheri*, *Lophocardium cummingii*, *Tellina pristophora*, and *Semele paziana*. The abundant and perhaps characteristic species of

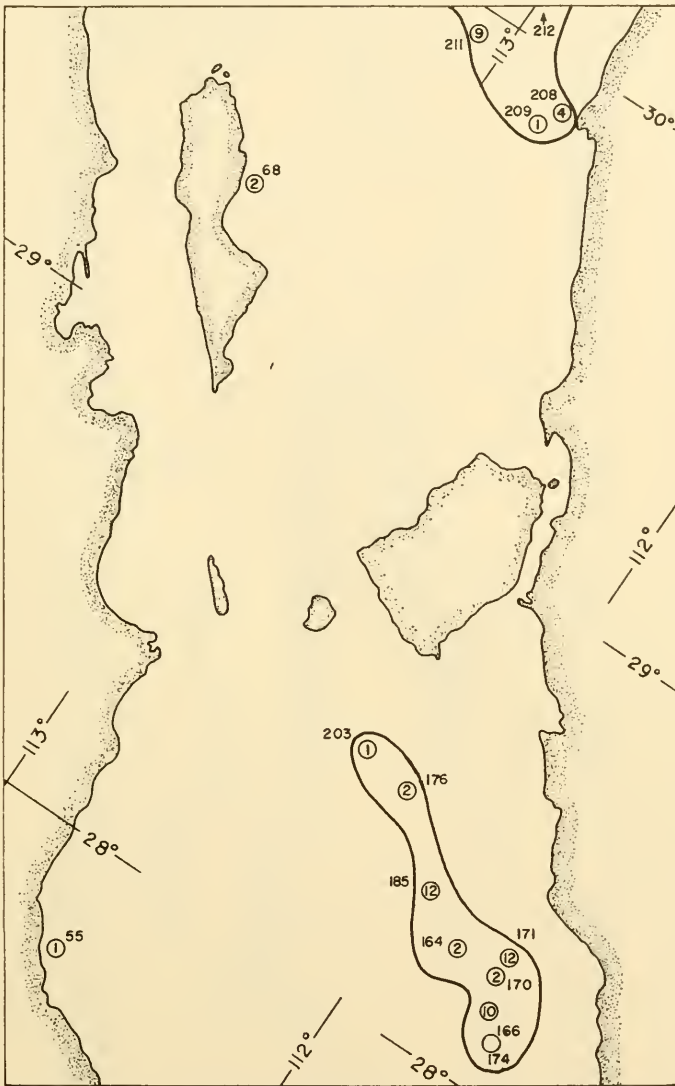


Fig. 20b. Distribution of the decapod crab, *Randallia americana*, indicative of the northern Gulf, intermediate shelf region. Number of specimens at each station circled.

infauna on the clayey bottoms of the southern intermediate shelf are: the gastropods, *Architectonica nobilis*, *Natica elenae*, *Distorsio constrictus*, *Bursa nana*, *Harpa crenata*, *Hormospira moclusa*, *Conus recurvus*, and *Conus scalaris*; the scaphopod, *Dentalium oerstedii*; and the lamellibranchs, *Noetia delgada*, *Glycymeris tessellata*, *Chlamys circularis*, *Plicatula inezana*,

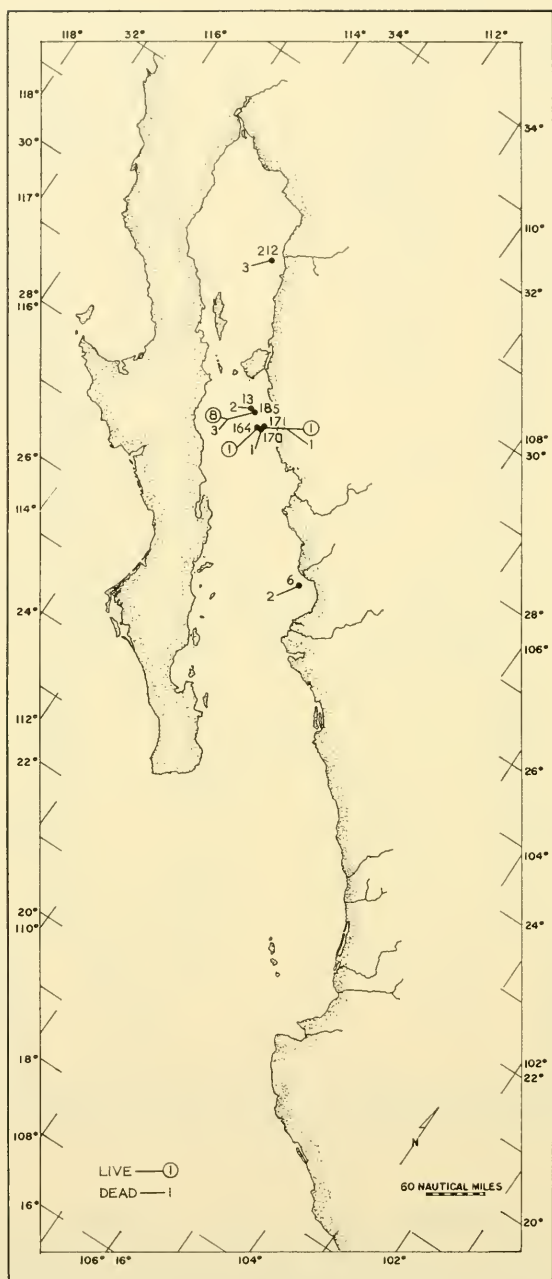


Fig. 21 a. Distribution of the gastropod, *Solariella triplostephanus*, indicative of the northern Gulf, intermediate shelf region. Number of specimens encircled.



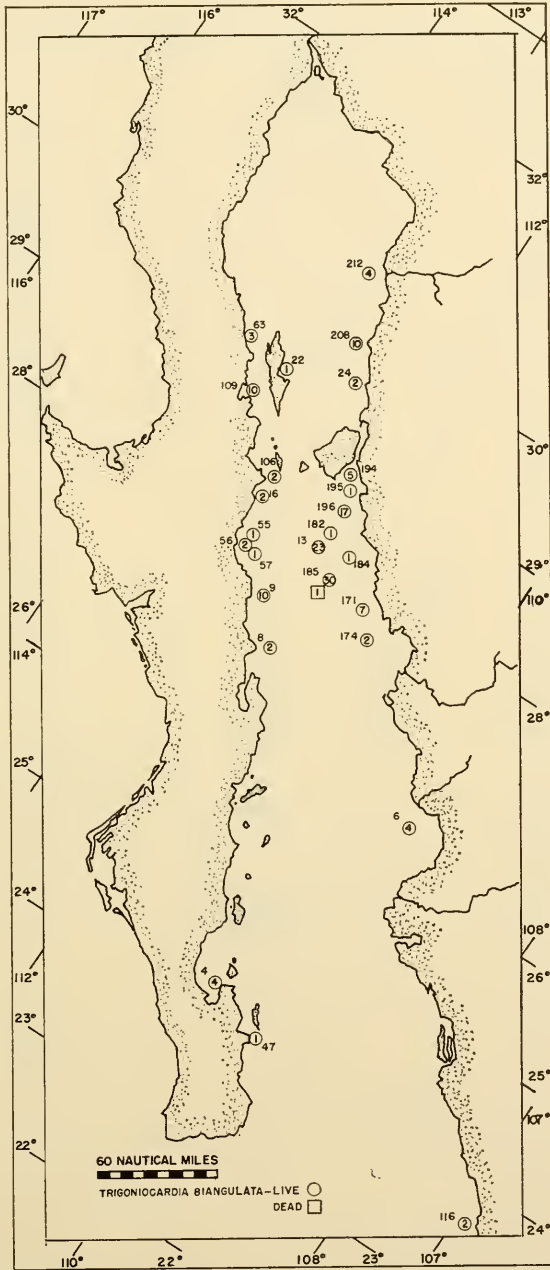


Fig. 21b. Distribution of the pelecypod, *Trigoniocardia biangulata*, characteristic of the intermediate shelf in the central portion of the Gulf, although occasionally found in the southern Gulf. Number of specimens also given.

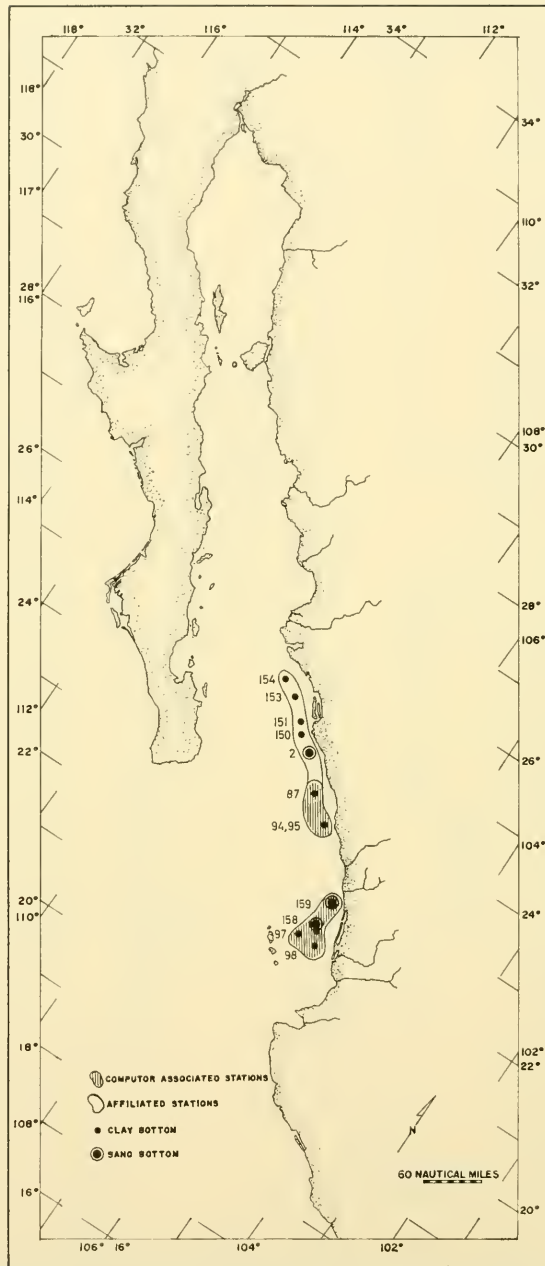


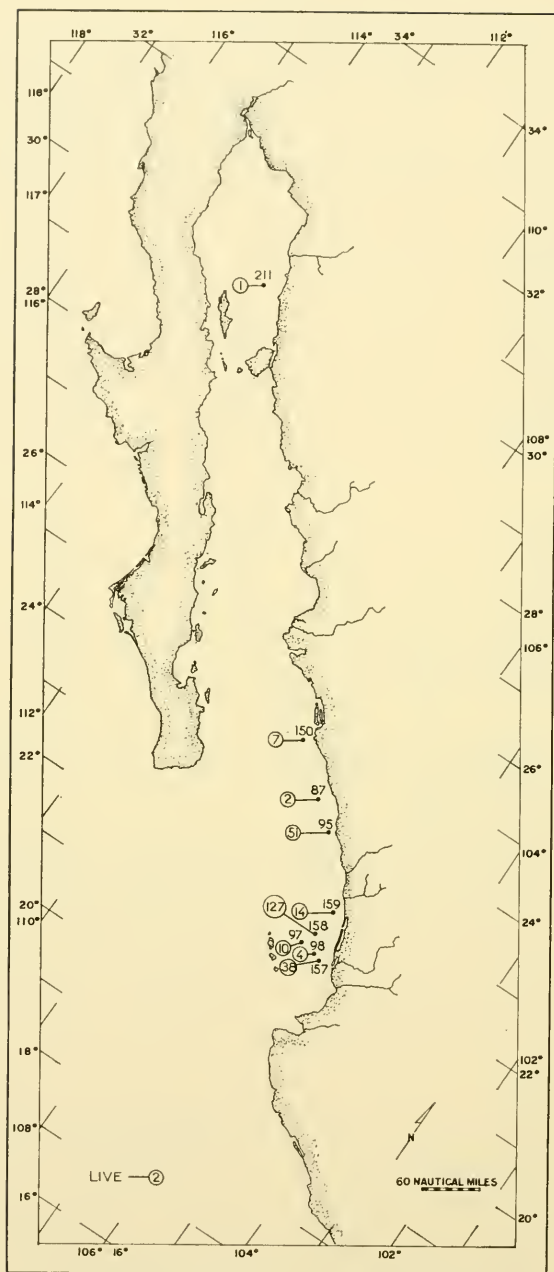
Fig. 22. Location of computer affiliated stations on sand and clay bottom upon which the southern Gulf, intermediate shelf assemblage is based.

Table VI.

Species	% of Occurrences at Computer Stations	% of Total Occurrences of Species within Gulf	Index
Crustaceans			
<i>Iliacantha hancocki</i> .....	86	66	76
<i>Portunus acuminatus</i> .....	71	71	71
<i>Persephone townsendi</i> .....	71	71	71
<i>Stenorhynchus debilis</i> .....	71	62	66
<i>Medaeus lobipes</i> .....	71	62	66
<i>Dardanus sinistripes</i> .....	86	38	62
<i>Pyromaia tuberculata</i> .....	86	27	57
<i>Paradysgius depressus</i> .....	57	44	51
<i>Randallia bulligera</i> .....	43	60	51
<i>Leilolambrus punctatissimus</i> .....	43	60	51
<i>Hepatus kossmani</i> .....	43	43	43
Gastropods			
<i>Distorsio decussatus</i> .....	100	86	93
<i>Cantharus capitaneus</i> .....	100	53	76
<i>Calliostoma bonita</i> .....	57	66	61
<i>Architectonica nobilis</i> .....	57	50	53
<i>Crucibulum spinosum</i> .....	86	17	51
<i>Hexaplex brassica</i> .....	43	60	51
<i>Strombina fusinoidea</i> (mostly dead) . . .	57	44	50
<i>Hormospira maculosa</i> .....	71	26	48

*Anodontia edentuloides*, *Trachycardium belcheri*, *Pitar catharius*, *Chione mariae* and *Semele paziana*.

A comparison was made between the occurrences of the species from the southern intermediate shelf on sand or mud and as to whether they were also found in the northern portion of this environment. Of the 128 species of invertebrates found alive at the 11 stations, 40 species were common to both sand and silty clay, and 16 of these also occurred in the north on both sediments. Only 28 species were restricted to clay bottom in the south, of which three were also found on sand in the north. On the other hand, 57 species were found only on sand in the south (two stations), eight of which were also found on sand in the north. All of the species (living and dead) from the southern intermediate shelf can be found in Table I. The distribution maps of the two southern crustaceans, *Iliacantha hancocki* and *Portunus acuminatus* are shown on figs. 23a and b, while the distribution of two gastropods, *Bursa nana* and *Cantharus capitaneus* is shown on figs. 24a and b. The more common mollusks are figured on Plate V.



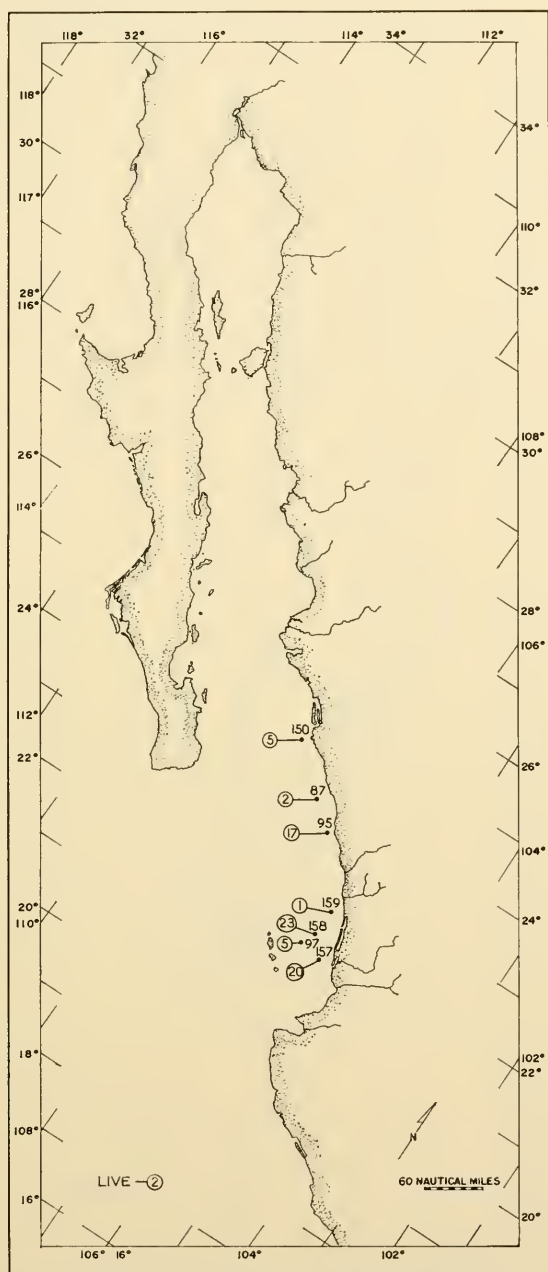


Fig. 23b. Distribution and abundance of the decapod crab, *Portunus acuminatus*, confined to the southern Gulf, intermediate shelf.



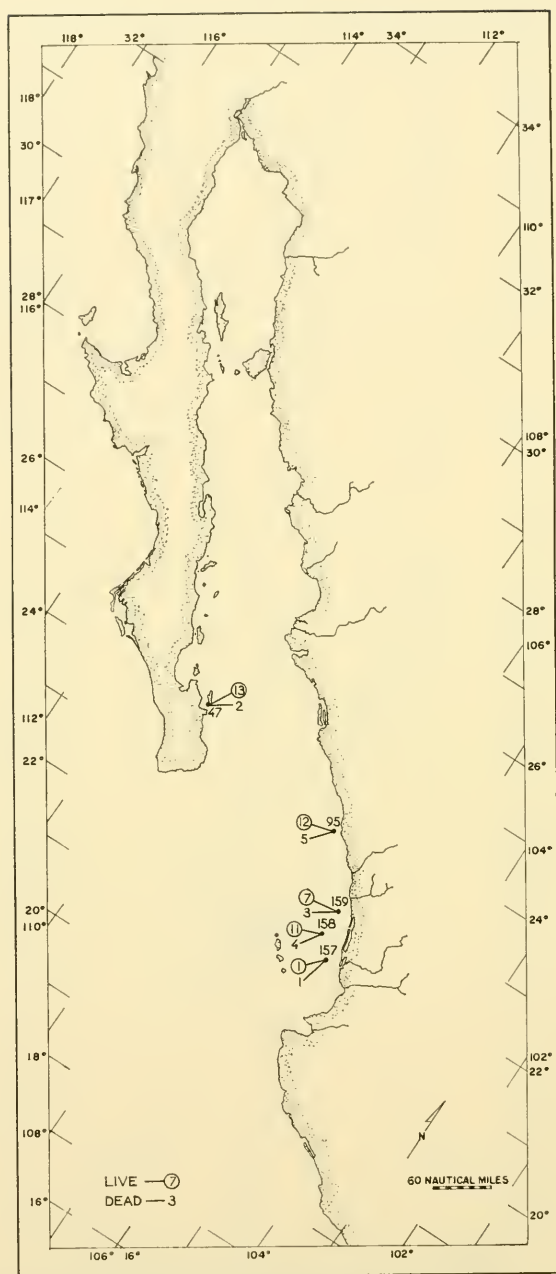


Fig. 24a. Distribution and abundance of the gastropod, *Bursa nana*, confined to the southern Gulf, intermediate shelf region.

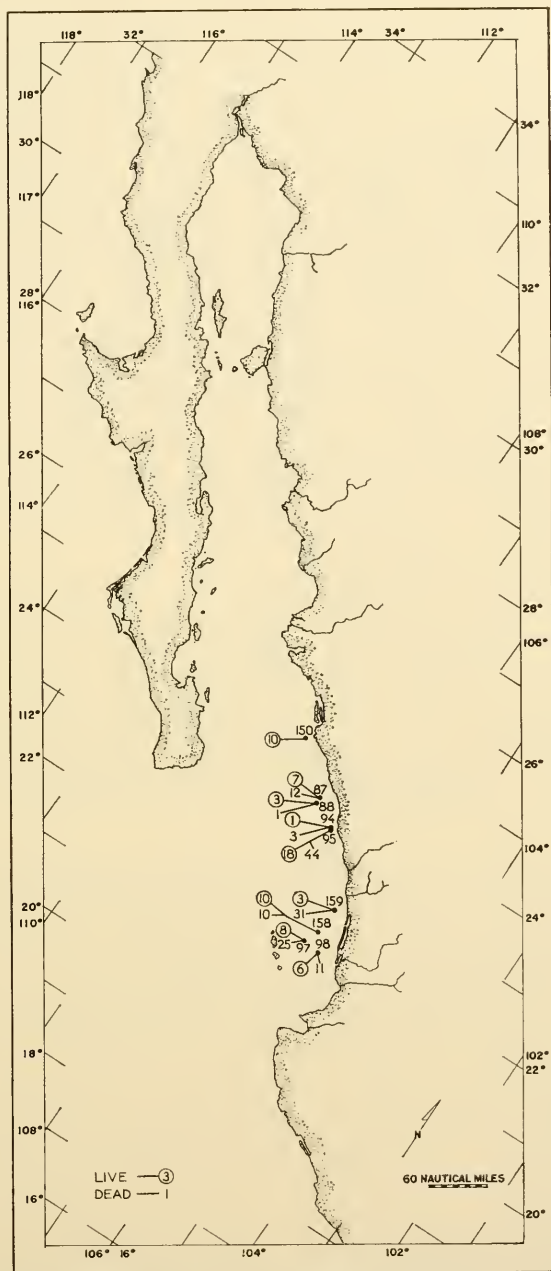


Fig. 24b. Distribution and abundance of the highly characteristic gastropod, *Cantharus capitaneus*, in the southern Gulf, intermediate shelf environment.

## VI. Outer shelf, 66 to 120 meters, clay bottom, southern Gulf.

A portion of the outer shelf environment in the Gulf of California from Los Mochis to just south of Mazatlan was verified by the contingency matrix as being a distinct region. Six stations proved to be closely associated by five commonly occurring species, which were abundant enough in numbers per station to identify the environment. The number of species seem to decrease at these greater depths and especially in the matrix-designated region which is based on eight stations taken in a silty clay bottom (fig. 25). The eight stations were sampled by six kinds of devices (Table III and fig. 2a), yet each device produced essentially the same species attesting to the uniformity of the assemblage. The devices used were: one orange peel grab, two shell dredges, two 12-meter and one 3-meter otter trawls, one rock dredge and one box dredge. The five associated species were: a polychaete, *Protula superba*, two gastropods, *Conus arcuatus* and *Crucibulum*, sp. (allied to *C. striatum* of the Atlantic), and two lamellibranchs, *Chione kellettii* and *Anadara mazatlanica*.

A complete list of the living species (with the most abundant in number starred) from the outer shelf clay bottom environment can be found in Table II of the appendix, while all species living and dead from these stations can be ascertained from a study of Table I. Two of the outer shelf stations in the southern Gulf were taken on sand bottom, but only two species (both epifaunal in nature) from these stations were also found on clay bottom. The more important mollusks are illustrated on Plate VI.

## VII. Outer shelf, 66 to 126 meters, sand bottom, northern Gulf.

All stations in depths of from 66 to 126 meters from just south of Tiburón to Punta Peñasco in the northern Gulf were taken on sand bottom. This assemblage was completely different from the one found on clay bottom in similar depths to the south. These stations (fig. 25) occurred on what appears to be a residual sand bottom resulting from eustatically lowered sea level, since nearly every station had a large number of dead mollusk shells of species usually found living close to shore. A total of 93 living species of invertebrates, mostly epifaunal, were collected from 18 stations, giving an average of only five species per station. Owing to the heterogeneous composition of the 18 stations on sand bottom in the north, no closely associated group of species resulted from the contingency matrix. Only two species of invertebrates occurred at enough stations in this environment to be considered abundant (in the sense used by REMANE, 1940): the echinoid, *Clypeaster europacificus* and the pelecypod,

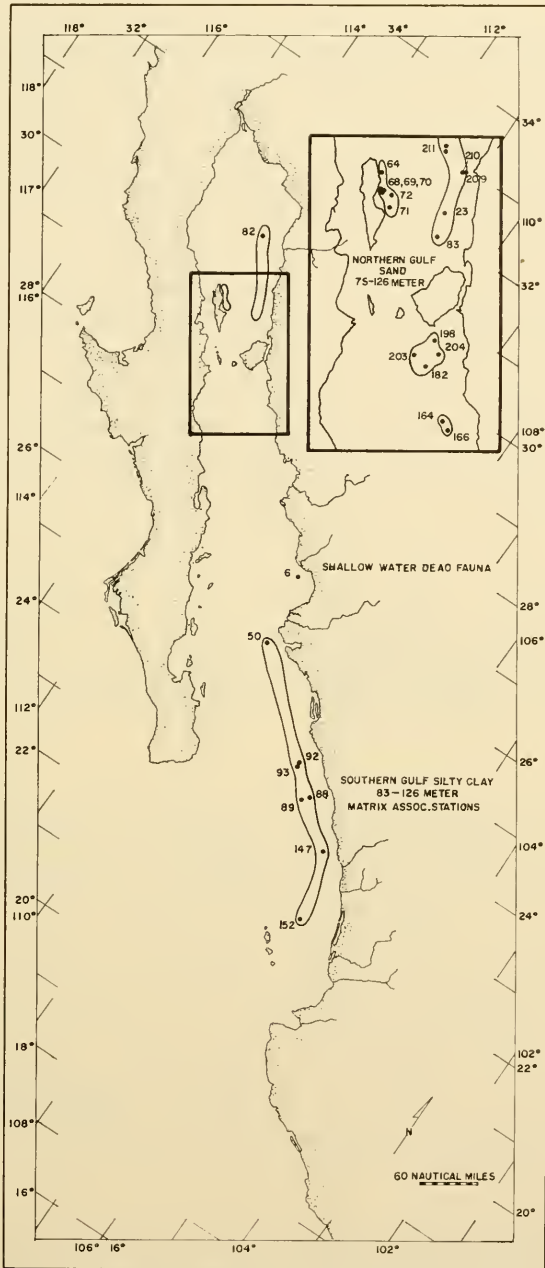


Fig. 25. Location of matrix-associated stations in both the northern Gulf, sand bottom and southern Gulf clay bottom environments on the outer shelf.

*Lucinoma annulata*, which are also found in deeper waters in the northern Gulf. A large number of pelecypods, found as dead shells, were consistently found in these and only these stations, but because of the presence of so many dead shallow-water species, one cannot be certain that they lived at these depths. The most interesting aspect of this assemblage was the large number of living gastropod and crustacean species. Many of these species also occurred on inshore sand bottom to depths of less than 20 meters. Apparently, the nature of the bottom is more important than depth in the northern Gulf, so far as limiting the distribution of the more mobile invertebrates is concerned. One likely reason for depth being non-restrictive is that due to intense tidal action, the waters are thoroughly mixed from top to bottom. Although almost half of the samples were collected by shell dredge, five other devices were used (Table III), which may have also contributed to the heterogeneity of the assemblage. These samples were: seven shell dredges, one 10-meter and three 3-meter otter trawls, five rock dredges, one orange peel grab, and one 1/10 m<sup>2</sup> Petersen grab.

All invertebrates taken in the northern Gulf outer shelf environment, living and dead, can be determined from Table I, while living species only, with the most abundant forms starred are given in Table II in the appendix. A few of the common mollusks are figured on Plate VI.

#### VIII. Northern Gulf basins and troughs, 230 to 1,500 meters.

Owing to the peculiar temperature and sediment conditions in this deep portion of the northern Gulf of California, this environment may well be unique in the world today. The great tidal exchange through these basins and channels create virtually uniform temperature, salinity and oxygen conditions from about 30 to 50 meters close to the surface down to the bottom at 1,500 meters. This turbulence plus the geological background of the areas created an almost uniform sand to gravel bottom in all depths (fig. 7). Since two very important ecological factors (water temperature and sediment size) which are apt to bring about vertical stratification of fauna are eliminated, it is interesting to see what effect, if any, the influence of pressure has had on the composition of the fauna in the deeper portions.

The species found in this environment must be separated into two parts, one composed of the living species and another which is composed mostly of shell remains. Normally, dead shells would not be considered too important, but in this instance it is interesting enough to be dealt with



separately. First of all, only 34 living species of invertebrate were taken, although 19 stations were occupied (fig. 26). The sampling of this environment was based on six rock dredges, five piston cores (10 cm. diameter), two gravity cores (4 cm. diameter), two box dredges, two shell dredges, one deep diving dredge and one orange peel grab. The living animals were taken by the various dredges, while the unusual shell remains were found in the cores and orange peel. Except for the deep diving dredge (really a trawl), no large-opening samples were taken, which accounts for the lack of large crustaceans which are so important in the other Gulf of California assemblages. Because neither large trawls or grab samples were taken in this environment, there can really be no valid comparison between the other assemblages and this one. What was taken by this gear should be mentioned, nevertheless, as these same devices were used in conjunction with other gear in other parts of the Gulf and did not produce this combination of faunas elsewhere. The living faunas are largely epifaunal, since most of the dredges were taken on a rock or gravel bottom. Those living species unique to the northern basins are listed below:

Hexacorals		Octocorals	
<i>Balanophyllia</i> , sp.	2 stat.	<i>Acanthogorgia</i> , sp. nov.	2 stat.
<i>Coenocyathus bowersi</i>	1 stat.	<i>Callogorgia flabellum</i>	1 stat.
<i>Desmophyllum crista-galli</i>	3 stat.	<i>Eumuricea horrida</i>	1 stat.
<i>Dendrophyllia cortezi</i>	1 stat.	<i>Eumuricea</i> , sp. nov.	1 stat.
Brachiopods		Echinoids	
<i>Laqueus californianus</i>	1 stat.	<i>Brissaster townsendi</i>	1 stat.
<i>Morrisia horneii</i>	2 stat.	<i>Hesperocidaris perplexa</i>	1 stat.
<i>Terabratulina kiiensis</i>	1 stat.		
Gastropods		Crustaceans	
<i>Fusinus traski</i>	1 stat.	<i>Salmoneus</i> , sp.	1 stat.
Scaphopods		Lamellibranchs	
<i>Cadulus austinclarki</i>	1 stat.	<i>Macoma siliqua spectri</i>	2 stat.
<i>Dentalium pretiosum berryi</i>	1 stat.	<i>Nuculana taphria</i>	1 stat.
<i>Siphonodentalium quadrifissatum</i>	1 stat.	Asterooids	
		<i>Astropecten ornatissimus</i>	1 stat.

Another 14 species of invertebrates were also taken alive in this environment, but were also taken at almost the same depths in the central and southern Gulf. None of the species were abundant as to numbers per station.

The dead shells collected from the basins and troughs are divided into

two groups. The first consists of a large number of local, shallow-water, sand and rock bottom species, which have either been transported into deep water through slumps or turbidity currents, or may actually live there because of high bottom-water temperatures. Probably most of this group was transported down the steep sides of the basins and channels through slumping. Some of these species are listed below, while all can be found in Table II of the appendix.

Gastropods		Lamellibranchs	
<i>Acmaea</i> , sp.	2 stat.	<i>Barbatia alternata</i>	1 stat.
<i>Fissurella</i> , sp.	1 stat.	<i>Barbatia baileyi</i>	1 stat.
<i>Diodora alta</i>	1 stat.	<i>Barbatia gradata</i>	1 stat.
<i>Diodora aspera</i>	1 stat.	<i>Anadara cepoides</i>	2 stat.
<i>Turbo</i> , sp.	1 stat.	<i>Glycymeris multicosata</i>	1 stat.
<i>Crucibulum scutellatum</i>	1 stat.	<i>Pecten vogdesi</i>	1 stat.
<i>Crepidula onyx</i>	1 stat.	<i>Cyclopecten peronius</i>	1 stat.
<i>Natica chemnitzii</i>	1 stat.	<i>Pododesmus cepio</i>	1 stat.
<i>Polinices otis</i>	2 stat.	<i>Crassinella varians</i>	1 stat.
<i>Cypraea annettae</i>	1 stat.	<i>Cardita megastropa</i>	1 stat.
<i>Ficus ventricosa</i>	1 stat.	<i>Trigoniocardia guanacastensis</i>	2 stat.
<i>Olivella</i> , sp.	1 stat.	<i>Ventricularia isocardia</i>	2 stat.
<i>Pyrene fuscata</i>	1 stat.	<i>Semele</i> , sp.	1 stat.
<i>Mitra crenata</i>	1 stat.	<i>Corbula marmorata</i>	1 stat.
<i>Hindsiclava andromeda</i>	1 stat.		
<i>Pleuroliria oxytropis</i>	1 stat.		

Scaphopods	
<i>Dentalium oerstedii</i>	2 stat.
<i>Dentalium vallicolens</i>	2 stat.
<i>Cadulus perpusillus</i>	4 stat.

Most of these species were found as shells at depths exceeding 300 meters, far below their living occurrence, since many of them live only intertidally to a few meters depth on the rocks which line these deep and very steep-sided channels.

The other group of dead shells is far more interesting and leads to considerable speculation as to how they got there. This assemblage of mollusks was so distinct that they formed one of the most clear-cut associations in the computer matrix. Of the nine species showing this strong association, only one was collected alive (once) in the northern basins, although three more were also taken alive on the upper slope in the Central Gulf. The nine species showing strong affinities for each other are listed here.

Gastropods		<i>Nuculana taphria</i>	5 stat.
<i>Turritella</i> , sp. (cf. <i>cooperi</i> )	6 stat.	<i>Cardita barbarensis</i>	13 stat.
<i>Nassarius miser</i>	8 stat.	<i>Lucina tenuisculpta</i>	10 stat.
		<i>Lucinoma annulata</i>	14 stat.
Lamellibranchs		<i>Nemocardium centifilosum</i>	20 stat.
<i>Nuculana hamata</i>	8 stat.	<i>Hiatella arctica</i>	6 stat.

Without exception, all have been taken off the California coast, most do not occur south of San Diego on the outer Pacific coast, and all are continental shelf species, seldom found living in depths of more than 180 meters. The stations which were held in close association by this peculiar assemblage of dead shells by computer analysis are located on fig. 26. The list of so-called "California shelf" species, and the number of station occurrences within the matrix stations is given below. The significance of this assemblage is discussed further on pages (123-125).

Gastropods		Lamellibranchs	
<i>Calliostoma gemmulatum</i>	1 stat.	<i>Acila castrensis</i>	5 stat.
<i>Calliostoma variegatum</i>	2 stat.	<i>Nuculana taphria</i>	4 stat.
<i>Margarites albolineatus</i>	1 stat.	<i>Nuculana hamata</i>	6 stat.
<i>Turcica coffea</i>	2 stat.	<i>Yoldia martyria</i>	1 stat.
<i>Turritella</i> , sp.	6 stat.	<i>Glycymeris corteziana</i>	2 stat.
<i>Pteryonotus carpenteri</i>	1 stat.	<i>Cyclopecten vancouverensis</i>	2 stat.
<i>Boreotrophon</i> , sp.	3 stat.	<i>Cardita barbarensis</i>	8 stat.
<i>Nassarius miser</i>	5 stat.	<i>Dimya californiana</i>	1 stat.
<i>Fusinus barbarensis</i>	1 stat.	<i>Lucina tenuisculpta</i>	6 stat.
<i>Antiplanes abarbarea</i>	1 stat.	<i>Lucinoma annulata</i>	6 stat.
		<i>Tellina carpenteri</i>	4 stat.
		<i>Tellina bodegensis</i>	2 stat.
		<i>Macoma planiuscula</i>	3 stat.
		<i>Hiatella arctica</i>	5 stat.

A few of the typical living and dead species of mollusks are shown on Plate VII. Many more are illustrated in KEEN (1958) and OLDROYD (1925-1927).

#### IX. Upper slope, central and southern Gulf, 121 to 730 meters.

The depths of between 121 and 730 meters south of the islands separating the Gulf provide a slightly different fauna from the northern basins, especially in the number of living invertebrate species. Much of this difference can be attributed to sampling technique, however. Twenty-four species were found to be common to both the northern and southern Gulf, and 31 species were collected alive from 14 stations located on fig. 26.

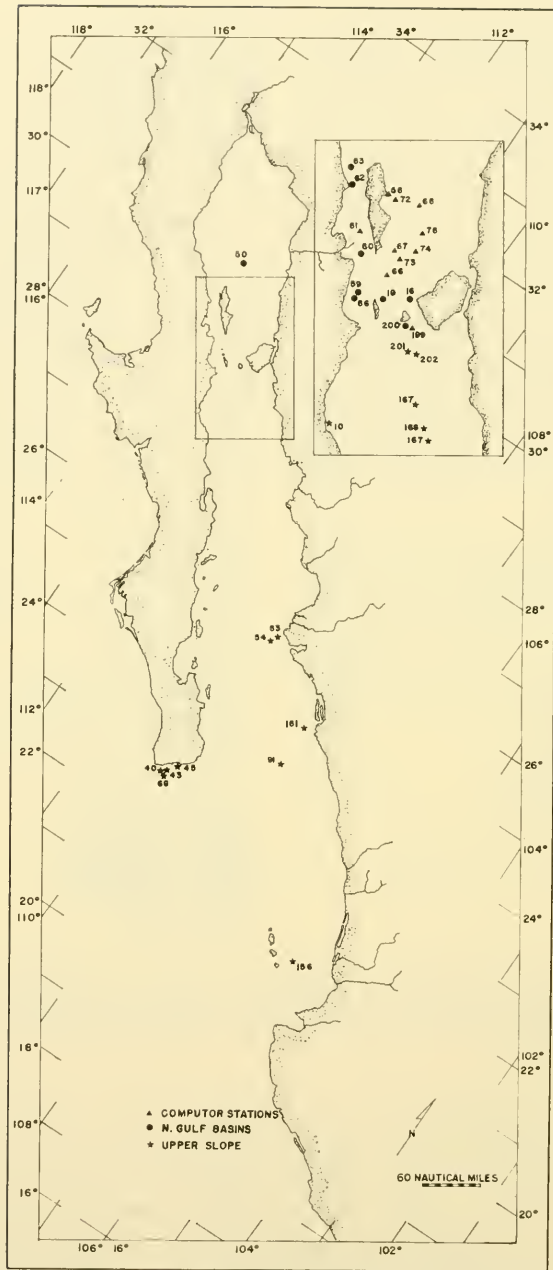


Fig. 26. Location of matrix-associated, plus all other stations, taken in the northern Gulf basin environment, and all stations occupied in the upper slope environment.

As in the northern Gulf basins, a considerable number of dead shallow-water mollusk shells were found on sand bottom. These arrived there either from slumping or as a result of lowered sea level during the Holocene. A list of both living and dead invertebrates from this environment can be found in Table I of the appendix, while the living species only (with number of station occurrences) from the 15 stations taken on the upper slope are listed below. Seven kinds of devices were used to establish this assemblage (Table III), with various small dredges predominating. They were: one orange peel grab, two rock dredges, three box dredges, five shell dredges, one 12-meter and two 3-meter otter trawls. It can be seen from this list that none of the species was taken frequently enough to appear in the contingency matrix analysis. Relatively few individuals were taken at any one station.

Sponges		<i>Amygdalum pallidulum</i>	1 stat.
<i>Pocillastra tricornis</i>	1 stat.	<i>Cyclopecten zaccæ</i>	1 stat.
Octocorals		<i>Corbula ventricosa</i>	1 stat.
<i>Anthomuricea</i> , sp.	1 stat.	<i>Pandora convexa</i>	1 stat.
Brachiopods		Pycnogonids	
<i>Terebratula obsoleta</i>	1 stat.	<i>Colossendeis bicincta</i>	1 stat.
<i>Argyrotheca lowei</i>	1 stat.	Crustaceans	
Amphineura		<i>Sicyonia ingentis</i>	1 stat.
<i>Lepidopleurus</i> (?)	2 stat.	<i>Heterocarpus vicarius</i>	2 stat.
Gastropods		<i>Pleuroncodes planipes</i>	3 stat.
<i>Emarginula velascoensis</i> (?)	2 stat.	<i>Paguristes holmesi</i>	1 stat.
<i>Solariella permabilis</i>	1 stat.	<i>Cancer porteri</i>	1 stat.
<i>Calliostoma</i> , sp.	1 stat.	<i>Stenocionops beebei</i>	1 stat.
<i>Polinices intemeratus</i>	1 stat.	<i>Ethusa ciliatifrons</i>	1 stat.
<i>Nassarius insculptus gordanus</i>	1 stat.	<i>Squilla</i> , sp.	3 stat.
<i>Nassarius miser</i>	1 stat.	Asteroids	
<i>Fusinus colpoicus</i>	1 stat.	<i>Astropecten californicus</i>	
<i>Cancellaria</i> , sp.	1 stat.	Fisher (adult)	1 stat.
<i>Clathurella thalassoma</i>	2 stat.	Holothurians	
Scaphopods		<i>Pseudostichopus mollis</i>	1 stat.
<i>Dentalium splendidulum</i>	1 stat.	Ophiuroids	
<i>Cadulus californicus</i>	1 stat.	<i>Schizoderma diplax</i> Nielsen	1 stat.
Lamellibranchs		<i>Amenichondrius granulatus</i>	
<i>Solemya valvulus</i>	1 stat.	Fisher	1 stat.
<i>Nucula cardara</i>	2 stat.		



One can also see from this list that the number of species living on the slope is sharply reduced from the number found on the shelf. One explanation for this, at least in the Gulf of California, is that these depths are located in the upper portion of the oxygen-minimum zone (fig. 9). Difficulty in sampling on the very steep slopes characteristic of this environment may also contribute to the lack of species in this collection. Some of the more characteristic mollusks are figured on Plates VII and IX, while others are illustrated in KEEN (1958).

#### X. Middle continental slope, 731 to 1,799 meters.

The middle continental slope, with its steep, dissected topography, is possibly the most difficult environment in the Gulf to sample adequately. Of the 12 stations taken in these depths, only four were occupied in the Gulf of California. Two more samples from slope depths were taken in the Sal Si Puedes Channel in the northern Gulf but were discussed under the basins and troughs environment. Since so few samples were taken in the Gulf proper, and the ecological conditions are so nearly uniform at these depths along the Pacific coast south of San Diego, all stations taken between 900 and 1,800 meters along the Middle American coast were included in the tabulations. These stations are: 39, 40, 84, 90, 127, 135, 138, 214, 215, 216, 221 and 273. Station locations and data can be found in the station data list in the appendix. The devices used for these 12 stations were: four 1/5 m<sup>2</sup> Petersen grabs, three deep diving dredge hauls, one 12-meter, one 10-meter and one 5-meter otter trawls and two rock dredges. Bottom water temperature values for the 12 stations ranged from 3° to 6°C., and thus could be considered lower bathyal in classification. Much of the middle slope region is also characterized by very low oxygen concentrations of .5 to .9 ml/L (fig. 9). Only 30 species of invertebrates have been identified from these 12 stations, six of them being found as dead shells only. Only three species of invertebrates were taken twice: the crustaceans, *Acantheephyra curtirostris* and *Paralomis multispina*; and the pelecypod, *Solemya agassizi*. The low oxygen concentrations and inadequate sampling of these depths probably accounts for the small number of invertebrates in this region. A complete list of the invertebrates is given below. A few of the mollusks are illustrated on Plate VIII.

Hexacorals  
*Cyathocerus*, sp. (dead)

*Stachytilum superbum*  
*Swiftia*, sp. (aff. *S. pacifica*)

Octocorals  
*Distichoptilum*, sp. nov.  
*Pennatula phosphorea californica*

Monoplacophorans  
*Neopilina galathea* (dead)

## Gastropods

*Solariella nuda**Turricula bairdii* (dead)*Cocculina diomedae* (dead)

## Lamellibranchs

*Solemya agassizi**Lucinoma*, sp. nov.*Vesicomys* (dead)

## Cephalopods

*Argonauta pacifica* (dead)

## Solenogasters

*Prochaetoderma*, sp. nov.

## Crustaceans

*Benthescymus tanneri**Heterocarpus affinis**Heterocarpus*, sp. nov.*Paracrangon areolata**Glyphocrangon spinulosa**Acanthephyra curtirostris**Axiopsis* (*Calocarides*), sp. nov.*Munidopsis*, sp.*Parapagurus pilasimanus**Neolithodes diomedae**Paralomis multispina**Paralithodes rathbuni**Gnathaphausia zoea*

## Holothurians

*Molpadia musculus* (*violaceum* type)*Molpadia musculus* (*musculus* type)*Synallactes ishikawa*

# XI. Abyssal southern borderland basins, and outer continental slope, 1,800 to 4,122 meters.

The abyssal region represents a complete change from the previously discussed deep-water environments, both in the diversity of fauna and the great abundance of individuals. Although only 15 stations were occupied at these depths, 186 species of benthic invertebrates have been identified, and many more are yet to be checked by specialists. Whereas in most of the shallower slope stations a species would be represented by only a few individuals, the species from the abyssal regions were extremely abundant, often comprising hundreds of individuals per station. The richness of fauna actually approaches that of the inner continental shelf.

Bottom-water temperatures within this environment range from 1.2° to 2.6°C. (fig. 11), which can be considered characteristic of true abyssal conditions. The oxygen values ranged from 1 to 2.8 ml/L., being high enough to support most forms of marine life. All stations except one were taken on pure silty clay bottom. The one exception was taken on clay with appreciable amounts of manganese crust. This environment differs from that of the middle continental slope in having lower bottom-water temperatures, much higher oxygen, and occurs on a relatively level, silty clay bottom, whereas the middle slope is characterized more by steep rocky and sandy bottom. Only five of the 86 species from the abyssal basin and slope environment were also found at middle slope stations. One species, the pelecypod, *Chlamys latiaurata monotimeris*, lives on kelp fronds, thus falls to the bottom wherever kelp drifts; one is a hermit crab,

*Parapagurus pilosimanus*, with a wide distribution; one a holothurian, *Molpadia musculus*, also with an extremely wide distribution in all seas; another is a bathypelagic shrimp, *Acanthophyra curtirostris*; and the fifth is the pelecypod, *Solemya agassizi*, which was rarely taken alive, and being very light (mostly peristacum) may possibly float some distance.

Although these stations, shown on fig. 3, were taken in abyssal depths, most of them were less than 100 nautical miles from land, as the shelf is very narrow along the Pacific coast of Mexico and deep basins lie very close to land. This proximity to land may well explain the richness of fauna, since upwelling and associated high surface productivity seem to be typical of most of the areas where trawling was carried out. This high surface primary production provides a rich accumulation of organic matter on the bottom, both in the borderland basins, and on the slopes which descend directly to the abyssal sea floor (PARKER, 1961). The majority of the invertebrates appear to be detritus or deposit feeders, which should thrive in the organic-rich bottoms. A complete list of the invertebrates identified so far from the 15 stations is given below. Of the 20 stations (successful and unsuccessful) taken at abyssal depths all but two (1/5 m<sup>2</sup> Petersen grabs) were made with various large trawling devices (Table III), similar to those used by the *Galathea* and *Albatross*. For this reason, few small animals were collected. These devices were: one mid-water trawl (on bottom), six deep diving dredges, three 3-meter Agassiz beam trawls, and of the one 12-meter, six 10-meter and one 5-meter otter trawls. The mesh size of the bags for all of the trawling devices, including deep diving dredge, was the same, as all net liners were made by the same men from the same bail of material, being about 1 cm. in diameter. Many of the typical mollusks are illustrated on Plate IX, X or can be seen in DALL (1908).

#### Octocorals

*Anthomastus ritteri*

*Thouarella*, sp.

*Scleroptilum* cf. *durissimum*

#### Hexacorals

*Caryophyllia diomedaea*

#### Polychaetes

*Maldane*, sp.

#### Brachiopods

*Macandrevia americana diegensis* 2

#### Pogonophora

*Galathealinum bruuni* (?)

#### Monoplacophorans

*Neopilina galathaea*

#### Gastropods

*Puncturella* cf. *expansa*

*Solariella ceratophora* (dead)

*Solariella equatorialis* 2

*chitonous trochids* (?)

*Fusinus rufocaudatus*

*Tractolira sparta*

## Gastropods (continued)

*Gemma*, n. sp. (aff. *G. exulans*) (dead)  
*Pleurotomella clarinda*  
*Steiraxis aulaca*

## Nudibranchs

*Bathydoris aioca*

## Scaphopods

*Dentalium megathyris* 5

## Lamellibranchs

*Solemya agassizi*  
*Nucula panamina*  
*Nuculana agapea*  
*Malletia truncata*  
*Tindaria compressa*  
*Arca corpulenta pompholynx*  
*Arca nucleator* 2  
*Limopsis compressus* 6  
*Chlamys latiaurata monotimeris* 2 (dead)  
*Cyclopecten*, n. sp.  
*Vesicomya*, sp. (dead)  
*Abra profundorum*  
*Cuspidaria panamensis* 2  
*Myonera garretti* 2  
*Poromya perla*

## Crustaceans

*Storthingura* aff. *pulchra*  
*Paropsurus giganteus*  
*Benthescymus altus* 2  
*Hymenopenaeus doris* 2  
*Sergestes phorcus*  
*Pandalopsis ampla*  
*Pontophilus occidentalis*  
*Glyphocrangon*, n. sp. (aff. *longirostris*)  
*Lebbeus*, sp. 2  
*Nematocarcinus* cf. *ensifer*  
*Acanthephyra brevirostris*  
*Acanthephyra curtirostris* 2  
*Acanthephyra*, n. sp. (aff. *sibogae*)  
*Munidopsis*, sp.  
*Munidopsis bairdii* 2  
*Parapagurus pilosimanus* 3  
*Paralomis verrilli*  
*Ethusina faxonii*

## Pycnogonids

*Colossendeis angusta* 2  
*Colossendeis bicincta*  
*Colossendeis colossea*  
*Colossendeis macerrima*  
*Pallenopsis californica* 2  
*Ascorhynchus agassizi*

## Holothurians

*Bathyplores*, sp.  
*Pseudostichopus mollis*  
*Oneirophonta mutabilis*  
*Peniagone*, sp.  
*Benthodytes sanguinolenta* 4  
*Psychropotes dubiosa*  
*Psychropotes raripes*  
*Abyssocucumis abyssorum* 3  
*Sphaerothuria bitentaculata*  
*Molpadia granulosa*  
*Molpadia musculus* forma *musculus*  
*Molpadia musculus* forma *spinosum*  
*Molpadia musculus* forma *violaceum*

## Echinoids

*Aporocidaris milleri* 3  
*Kamptosoma asterias*  
*Tromikosoma panamense* 2  
*Tromikosoma hispidum*  
*Urechinus loveni* 2  
*Brisaster latifrons*

## Asteroids

*Eremiacaster pacificus* (Ludwig)

## Ophiroids

*Ophiura irrorata* Lyman  
*Ophiomusium glabrum* Lütken and  
 Mortensen  
*Amphiura seminuda* Lütken and  
 Mortensen  
*Amphiodia digitata* Nielsen  
*Amphilepis patens* Lyman  
*Amphioplus hexacanthus* H. L. Clark  
*Ophiomusium lymani* Wyville Thomson  
*Ophiacantha setosa* Lyman

Numbers indicate number of station occurrences. Species without numbers were taken only once. Those taken dead only are indicated.

## XII. California borderland basins, 1,641 to 2,358 meters.

The California outer borderland basins are found in depths normally considered abyssal, but seem to have a fauna quite different from that of equivalent depths to the south. Although this area (fig. 3) is not within the strict area under consideration in this paper, it is important to indicate these differences, and to list the fauna found there. The author was fortunate to be consulted concerning fauna present in three areas along the California coast from Los Angeles to San Francisco, as part of a study of atomic waste disposal grounds, carried out by the Advanced Systems Division of the Pneumodynamics Corporation. Nine 5-meter otter trawl stations (Table III) were taken in depths of from 1641 to 2358 meters, four in the Santa Cruz Basin off Los Angeles, three in the Farallon Basin off San Francisco, and two in a small unnamed basin off Point Arguello. Although the trawls used in the California borderland basins were smaller than many of those used in the abyssal regions off Mexico, the inner liners of the nets were of same mesh size. Catches were of comparable size, and the individual animals were also of the same size in both regions. The basic composition of catches from the two regions were also similar, i.e., equal amounts of ophiuroids, asteroids, mollusks, polychaetes, etc. Temperatures ranged from about 2.5° to 4°C., and oxygen about 1 to 1.5 ml/L., while the sediments were all silty clay.

None of the basins was completely closed, such as those described by HARTMAN and BARNARD (1958), and seemed to be well-oxygenated and flushed by bottom currents. In configuration and environmental characteristics these three areas differed little from the basins studied in the deep borderland off Baja California, therefore it was somewhat surprising to find such a completely different fauna there. All three areas were very rich, both in species and in individuals. For instance, one short trawl with a small 15 foot "try" net, produced two large tubs of living animals, including hundreds of specimens of a small pecten, *Cyclopecten randolphi tillamookensis*. One surprising aspect of this basin fauna was its close affinity with bathyal and shelf fauna of the northern Pacific. Many of the species were formerly known only from the Gulf of Alaska, and in the vicinity of the Bering Sea and the Kamtchatka Peninsula. None of the animals was typical of those collected by the Albatross in Central American waters. This would suggest that there is some zoogeographic separation in the deep sea, which parallels geographic breaks along the shore. It also suggest that there is a migration south of many species



along the coast from Alaska terminating at San Diego. The flow of the California Current over this same region may influence this faunal distribution, although it is difficult to see how certain species of Buccinid gastropods could be distributed south by currents, as they have direct development from egg capsules, even though shallow-water Buccinid capsules often drift ashore.

Only three species of invertebrates, the shrimp, *Pandalopsis ampla*, the Galatheid shrimp, *Munidopsis bairdii*, and the kelp scallop, mentioned previously, occurred in both the northern and southern borderland. None of these species lives on or attached to bottom, so could be expected to occur anywhere. A large number of holothurians, asteroids, ophiuroids, sponges, polychaetes, sipunculids, anemones and pycnogonids were taken at these stations, but many were ashed before identification in order to test for radioactivity. The rest have not yet been identified by specialists. The remaining specimens have been deposited in the Invertebrate Collection at Scripps Institution. A complete list of the identified animals is given below. A few of the mollusks are illustrated on Plate VIII, but unfortunately the majority were ashed for remanent radioactivity studies.

#### Gastropods

*Margarites* cf. *beringensis*  
*Gaza rathbuni*  
*Solariella*, sp. (dead)  
*Buccinum diplodetum*  
*Ancistrolepis magnus*  
*Chrysodomus liratus*  
*Colus halidomus*  
*Colus hypolispis*  
*Colus trophius* 3  
*Cryptogemma adraestia*  
*Cryptogemma calypso*  
*Antiplanes vinosa* (dead)  
*Leucosyrinx erosina*  
*Leucosyrinx persimilis*

#### Scaphopods

*Dentalium* cf. *agassizi*  
*Dentalium* cf. *rectius*  
*Cadulus* cf. *tolmiei*

#### Lamellibranchs

*Solemya* cf. *johnsoni* 2  
*Nucula savatieri*

#### *Malletia faba* 2

*Chlamys* l. *monotimeris* (dead) 2  
*Cyclopecten* r. *tillamookensis* 2  
*Vesicomya stearnsi* 2  
*Cuspidaria* cf. *beringensis*  
*Dermatomya leonina*

#### Crustaceans

*Pandalopsis ampla* 3  
*Crago abyssorum* 3  
*Callianassa goniophthalma*  
*Munidopsis* cf. *bairdii*  
*Munidopsis verrilli*  
*Acanthalithodes hispidus*  
*Chionoecetes tanneri* 5

#### Sipunculids

*Phascalosoma*, sp. (?)

#### Crinoids

*Atelecrinus*, sp. (?)

## Holothurians

*Laetmophasma fecundum* (?)*Pannychia moseleyi* (?)

## Ophiuroids

*Ophiura lütkeni* (Lyman)*Amphiodia urtica* (Lyman)*Ophiacantha normani* (Lyman) 2

Numbers indicate number of station occurrences. Species without numbers were taken only once.

### Discussion

In order to provide explanations for the presence of distinct faunas in these 12 environments just described and shown areally in fig. 27, one must not only examine the physical characteristics of the environments, but also the geological history of the region and the biology of the species. The environmental boundaries are suggested both by the physical factors and the distribution and abundance of the more important index animals. One can readily see that a correlation is indicated between the distribution of certain physical factors, such as temperature, depth, sediment type, turbulence, oxygen and salinity, and the geographical limitations of most invertebrates, since the distributional patterns of both the species and physical factors coincide. On the other hand, the presence of some species or even whole assemblages may not be determined by the physical factors alone, but indirectly by biological factors, such as food preferences (which in turn are mainly determined by feeding mechanisms), competition for food, predator-prey relationships, reproductive capacity and larval development, commensal or parasitic relationships, etc.

One could gain an even better understanding of the organization of these aggregations of animals if it were possible to determine numbers and weights (biomass or standing crop) of the dominant and major subdominant organisms within the assemblage. For instance, if the percentages or biomass of animals involved in these various biological activities (feeding and reproduction) were known within each community, some idea of the energy relationships involved to sustain these communities could be ascertained. This achievement has rarely been achieved for one assemblage, except by SANDERS (1960), and no comparisons of this sort exist for a number of assemblages in a single region, or between assemblages from many regions. Unfortunately, standing crop and biomass figures are not available for this study.

Before discussing these various biological activities for each assemblage, it is first necessary to define the various terms used here. Feeding types of invertebrates have been defined time and time again, so that

there is some confusion existing between what is considered, for instance, a filter (and or) suspension feeder. Rather than give all of the previous definitions, most of which can be found in YONGE (1928) and JØRGENSEN (1955), only the ones which apply to this study are presented. The feeding types dealt with in the following discussion are 1) suspension feeders. These animals are those which both propel and filter their food from the surrounding waters, i.e. they may take food, both living and dead, from the water by bringing this water into contact with their feeding mechanisms, and often filtering out this food, passing the remaining water out of their systems. Their filters may be adjusted for various size food particles, or else, the water currents may be such that only large particles or larger animals are brought into contact with grasping mechanisms. Some of these suspension feeders may actually feed on deposits, or at least on soupy detrital material occurring just off the bottom, until unwanted particles tend to clog the filtering apparatus to such a degree that more energy is expended in getting rid of the unwanted material than in gaining food. For this reason, suspension feeders are at their best advantage in clear waters on a hard bottom. Type 2) discussed here is the deposit feeder. Deposit feeders gain their food directly from the bottom sediments or in the soupy organic layer on the surface of the sediments. In the rather limited number of species of lamellibranchs, they may use palps, which are highly developed sorting organs, or have long, prehensile inhalant siphons for picking up living and dead material from the sediments. Other invertebrates may be non-selective deposit feeders, such as holothurians and most polychaetes ingesting the whole sediment, extracting the food while the sediment is passing through the animal, and expelling the unused inorganic material. 3) Predators or carnivores are those animals which prey on or capture living food, particularly the more motile organisms. Many large gastropods, certain asteroids, many crustaceans, and even one group of lamellibranchs (*Cuspidaria*) fall into this group. 4) Algae feeders and/or browsers are, in this paper, those animals which are primarily herbivores, feeding either on diatom films, bryozoans, sponges, etc. on a rock or sandy surface, or feeding directly on attached vegetation. 5) The scavengers or carrion feeders feed primarily on dead flesh, although may also be predaceous when carrion is not available. Some animals which fall into this category are certain Buccinid snails and many crustaceans. Finally, there are the parasites, feeding directly on a host and eventually killing it, and commensal organisms, which may feed on or depend upon a host to get their food, without harming it. Other feeding types certainly do exist, but are modifications of the above types and are not discussed here.

Certain larval types are also mentioned in the following discussion, most of which are associated with molluscan development. It is within the mollusks that one of the greatest varieties of larval development is found; as most of the other invertebrate groups have a pelagic larval development, swimming about in the surface or surrounding waters for a considerable length of time (most echinoderms), or several successive larval stages, which may be free-swimming or passing part of their existence as parasites (most crustaceans, although not malacostracans). Lamellibranch species may have planktotrophic or pelagic larval development, where the veliger or trochophore larvae may spend anywhere from a few hours to several weeks swimming about in the water before settling. Others may have a lecithitrophic development, where the larva is furnished with considerable food in its egg and may either have a direct development from the egg without a pelagic existence, or else the pelagic existence is very short and the larvae does not feed before settling. Other lamellibranchs may even have brood protection, sheltering their young until they are ready to take up a direct development, without a trochophore stage. Gastropods have an even more varied larval development, ranging from those species which have trochophore larvae with pelagic stages lasting more than a month to those that lay relatively few large eggs from which young snails hatch and crawl away, or those that even bear living young in the image of the adult. An extensive discussion on reproduction and larval development of invertebrates can be found in THORSON (1950).

An examination of existing literature on present-day marine benthic communities, as well as many fossil assemblages, led to the conclusion that a basic organization of animals living together results from an interdependence of biological factors and an overall dependence upon the physical environment (see HESSE, ALLEE and SCHMIDT, 1951 and THORSON, 1950). The environmental extremes not only influences the physiological processes of the dominant or characteristic animals, but it may exert a control on the distribution and abundance of food, especially plankton and organic detritus. THORSON (1957) has proposed that parallel bottom communities, characterized by the same or closely related genera of dominants, exist wherever environmental conditions are similar. Perhaps these parallel communities are not so parallel in generic compositions as they are in the biological organization of the community as suggested in part by HESSE, ALLEE and SCHMIDT (1951). One type of community found in all waters with the same set of environmental conditions may be characterized by particular percentages of feeding types and dominated by animals with certain kinds of reproduction or larval development. It is



not necessary that the genera, or even families, are the same for the dominant organisms in these parallel communities, so long as the dominants perform the same function within the community. These "ecological parallel communities" have been designated "ISO-communities" by THORSON (1957, p. 504); although this concept has received earlier discussion by TISCHLER (1950, 1951) and CASPERS (1950). For this reason, a preliminary analysis of the feeding types (when known) of the characteristic animals of each environment was made, and a few conjectures as to the organization of the assemblages as to other biological factors are presented in the discussion of the results of this study. These assemblages have also been compared with similar assemblages or communities studied elsewhere in the tropics and sub-tropics, and in particular those described previously by the author from the Gulf of Mexico. Finally, an attempt is made to determine which of the environmental factors exerts the greatest influence upon the assemblage as a whole. The discussion of these assemblages follows in the same order as the earlier descriptoins.

### I. The Intertidal and Shallow Rocky Shores:

In all probability, the rocky shore habitat in the Gulf of California may offer one of the richest examples of this sort in the variety of species and numbers of individuals known in the world. The rocky shores of the temperate or boreal regions may be richer in numbers of individuals but there are far fewer species. The rocky shores of most tropical islands also seem to be relatively poor in numbers of species and individuals, at least from personal observations made on islands in the Indian Ocean, on Easter Island and in the Bahamas. LONGHURST (1958, pp. 54-59) cites relatively few intertidal rocky shore invertebrates in his discussion of the shallow, hard substrate community along the coast of Sierra Leone, West Africa. This would indicate that it is not the tropical climate alone which is responsible for the large number of species found on the rocky shores of the Gulf of California.

Although this assemblage of animals is found everywhere in the world where rocky shores exist, there was no exact counterpart in the Gulf of Mexico, with which this author is most familiar. The closest approximation to this assemblage off Texas is the fauna of the rock jetties at the major passes along the northern Gulf coast, described by WHITTEN, ROSENE and HEDGPETH (1950). There is little resemblance between their list and the one given here, except for a few mollusks. This is not surprising, since there are no natural rocky shores for the recruitment of the species adapted to this habitat along the coast of the northern Gulf of Mexico, while it is

the prevalent habitat for the major portion of the shoreline of the Gulf of California.

The rocky shore assemblage is entirely an epifaunal one, dominated by algae (or diatom film) and suspension feeders, plus a number of invertebrates which prey upon the others. Since a rock bottom is not conducive to the accumulation of detritus (except under the rocks), deposit feeders are virtually absent. SAVILOV (1961), in a similar study of feeding types in the Okhotsk Sea, states that sessile suspension feeders dominate the rocky shores. The majority of the gastropods are adapted to living in a rigorous environment, and nearly all of the lamellibranchs possess byssal threads by which they attach themselves firmly to the rocks. Some of the forms are thought to have a rather long planktonic development, permitting a wide dispersal over long stretches of coast line while many of the prosobranchs develop from egg capsules, which guarantee that they will be retained on the rocks and not swept into an unfavorable environment (THORSON, oral communication). According to THORSON (personal communication), many of the larvae of intertidal invertebrates also exhibit strong negative and positive phototropisms, which would facilitate settlement at the proper time during the tidal cycle, so as not to be swept off their selected place of attachment during early stages of settling. There is little doubt that the feeding habits and types of reproduction of the major components of this epifaunal community are similar on all rocky shores throughout the world. Many of the same characteristic genera (*Littorina*, *Ostrea*, *Mytilus*, *Fissurella*, *Balanus* and *Bugula*) occur nearly everywhere, although tropical shores are often characterized by many more genera and species and fewer individuals of each than temperate or boreal regions. The environmental factors exerting the most influence upon this assemblage are certainly rocky substratum, great turbulence, extreme range of water temperature, high oxygen and normal oceanic salinities.

Most of the fossil assemblages studied in the Baja California region and in the Gulf of California are of Pliocene to Pleistocene age. All of them are composed of a mixture of intertidal rocky shore and nearshore shelf assemblages. Discussions of these deposits can be found in HERTLEIN and EMERSON (1959), EMERSON (1956 and 1960a), and ADDICOTT and EMERSON (1959). Only two recent papers describe fossil assemblages from the Gulf of California proper, one by EMERSON (1960a) on the Pleistocene invertebrates of Cerralvo Island, and the other by HERTLEIN and EMERSON (1959) on the Pleistocene fauna of the Tres Marias Islands. An earlier review of the paleontology of the Gulf of California can be found in DURHAM (1950). Of the 34 species of invertebrate fossils from Cerralvo Island listed by





Fig. 27. Areal distribution of the Gulf of California environments. Distribution of the intertidal environments is shown on figure 14. Stippled area near the head of the Gulf was not sampled adequately enough to designate environments and thus does not represent any specific environment.

EMERSON, only 12 can be considered part of the rocky shore assemblage. Two corals were also cited which are now living at Maria Cleophás Island and Cape San Lucas. The rest of the fossil mollusks from Ceralvo Island belong to the shallow, nearshore shelf environment, and as Emerson states, it is a mixed fauna resulting from the reworking of the attached and non-attached elements of that region. The Pleistocene fauna from Maria Cleophás Island (HERTLEIN and EMERSON, 1959) is primarily a level-bottom fauna. Of the 28 species found at this locality, only eight were attaching forms usually found on intertidally exposed rocks. This seems somewhat surprising, since most of the present shoreline of Maria Cleophás is rocky, and the surrounding shelf is very narrow, providing little level bottom for the majority of these species which prefer this habitat. This very narrow shelf was observed personally in a survey around the island in 1959 (FOOSE, 1962). Few of the rocky shore animals cited in the present survey are listed from the fossil deposits in northwestern Baja California, although the majority of the fossils are rock-living species normally found on the California coast (EMERSON, 1956; ADDICOTT and EMERSON, 1959; and EMERSON and ADDICOTT, 1958). A discussion of the fossil corals from the Gulf of California, some of which were taken intertidally in the present study, can be found in SQUIRES (1959).

## II. Intertidal Sand Beach and Sand-Flats to 10 Meters:

This assemblage is quite similar in composition throughout all warm-temperate to tropical regions of the world where sand-flats and beaches exist (PEARSE, HUMM and WHARTON, 1942, SCHUSTER, 1956, and GAULD and BUCHANAN, 1956). For instance, a comparison of the surf-zone and inner shelf, sand bottom assemblages of the northern Gulf of Mexico (PARKER, 1960, pp. 320-321) with its equivalent in the Gulf of California reveals a great many similarities, especially at the subgeneric level of mollusks and crustaceans. For nearly every species of mollusk, crustacean and echinoderm listed for the Gulf of Mexico nearshore sand-bottoms, there is an equivalent species in the same environment in the Gulf of California. Many of the species from both Gulfs can be considered twin species, with common ancestors in the Miocene and Pliocene of Panama and Columbia (OLSSON, 1961), which at that time was an open seaway between the Caribbean Sea and the Pacific Ocean. This phenomenon has been discussed at length for several invertebrate groups and fish by EKMEN (1953, pp. 30-38). The principal difference between the two regions is that there were many more species in this environment in the Gulf of California, even though sand beaches are the dominant feature of the coast

of the Gulf of Mexico and constitute less than half of the shoreline of the Gulf of California. The great variation in the size and sorting of sand particles along the coast of the Gulf of California, as compared to only very fine, well-sorted sands which are found along the northern Gulf of Mexico coast, may account for the greater diversity of animals in this environment in the Gulf of California. A greater range of water temperature ( $0^{\circ}$  to  $+40^{\circ}\text{C.}$ ) in the northern Gulf of Mexico, as opposed to only  $15^{\circ}$  to  $30^{\circ}\text{C.}$  in the Gulf of California may offer an even better explanation for lower species diversity in the Gulf of Mexico.

BUCHANAN (1958) and BASSINDALE (1961) investigated the inshore sand-bottom community in the tropics off Accra, Ghana, which is in the same temperature province as the Gulf of California. BUCHANAN reports two species of *Donax*, one of *Tivela*, a *Bulla*, a *Terebra* and an *Olivella* from the surf zone, the same genera which are common to the surf zone from somewhat deeper water in 6 to 15 meters on fine sand, which also contains the same components as the inshore sand bottom community in the Gulf of California. A complete list of these sand beach and sand flat species of invertebrates off Ghana can be found in BUCHANAN (1958, pp. 19-21) and BASSINDALE (1961, pp. 500-507). LONGHURST (1958) in his study of bottom communities off Sierra Leone, just north of BUCHANAN's region, designated the shallow, nearshore sand-flat assemblage as the *Tellina* iso-community. The dominant animals of LONGHURST's *Tellina* iso-community are *Donax* (= *Tellina*), *Terebra*, and a suspension feeding polychaete, *Spio*, sp. The less abundant members are a polychaete (*Sigalioi*), an amphipod (*Urothoe*), a Hippid crab (*Albunea*) and another species of the gastropod, *Terebra*.

One region of nearshore sea bottom in the tropics which seems to be quite different from those discussed previously is located on the Malabar coast of India. SESHAPPA (1953) collected a number of grab samples in this region in depths to about 10 meters. The bottom temperature range was from  $26^{\circ}$  to  $30^{\circ}\text{C.}$  (similar to that off Mazatlan), but because of the Monsoons, salinities fluctuated widely from season to season ( $16\text{‰}$  to  $35\text{‰}$ ). Seshappa's nearshore sand community bore little resemblance to either its counterpart in the Gulf of California or those studied off West Africa. A polychaete, *Prionospio*, was the only dominant, and *Lucina* was the only genus of nine molluscan genera found there that was also represented in an equivalent environment in the Gulf of California.

It is impossible to obtain a quantitative conception of this assemblage in the Gulf of California, since so many of the shallower samples from the surf zone were taken by hand collecting. It was observed, however, that

within the surf zone, *Heterodonax* was exceedingly abundant in certain localities and large handfuls could be taken easily at the water's edge. Various species of *Donax* were abundant as dead shell, but very few living specimens were observed at any time. Great numbers of *Turritella* shells were observed in freshly-deposited strand lines along the shore, but none were collected alive, not even by means of grab samples taken fairly close to shore. EMERSON and STILLMAN BERRY (personal communication) reported abundant living populations of *Turritella* just outside the surf zone in the Puerto Peñasco and Guaymas regions. BUCHANAN (1958) found *Turritella* in large numbers at the shelf edge, while *Turritella* is found at intermediate shelf depths in European boreal waters (THORSON, 1957). The most abundant living gastropods were the Olivellas, Olivas and Terebras.

Eight bottom grab samples were taken in depths of 5 to 11 meters on sand bottom, using a small 1/20 square meter Van Veen grab. The living mollusks found in these stations (shown below) give an idea of the relative abundance and diversity of animals which can be found in small samples from this environment.

Station Number	Number of Individuals	Species	
4	1	<i>Nuculana elenensis</i>	(P)
	1	<i>Lucina cancellaris</i>	(P)
	1	<i>Ctena clarionensis</i>	(P)
	1	<i>Transenella puella</i>	(P)
	Total 4		
5	3	<i>Nucula declivis</i>	(P)
	9	<i>Tellina felix</i>	(P)
	2	<i>Tagelus politus</i>	(P)
	Total 14		
6 (296)	2	<i>Laevicardium elenense</i>	(P)
	1	<i>Megapitaria squalida</i>	(juv.) (P)
	Total 3		
7	1	<i>Kellia suborbicularis</i>	(P)
	1	<i>Tellina felix</i>	(P)
	Total 2		
11	1	<i>Terebra variegata</i>	(G)
	2	<i>Laevicardium elenense</i>	(P)
	2	<i>Tivela delesserti</i>	(P)
	1	<i>Tellina amianta</i>	(P)
	Total 6		

Station Number	Number of Individuals	Species
111	None living	
113	Total 1	<i>Olivella anazora</i> (G)
114	1	<i>Olivella fletcheriae</i> (G)
	1	<i>Megapitaria aurantiaca</i> (P)
	1	<i>Transenella puella</i> (P)
	3	<i>Macoma</i> , sp. (juv.) (P)
	<hr/> Total 6	

P = Pelecypod - G = Gastropod.

Only 36 living specimens of mollusks were taken in these eight small-sized samples: no other groups have been identified yet from these stations. If these samples cover  $1/20 \text{ m}^2$  each or a total of  $2/5 \text{ m}^2$  the average number of animals per square meter is roughly 90. This figure is not too reliable, since not only is the total area sampled insufficient, but the distribution of animals is very patchy in this environment. This can be seen by the variation in the number of individuals in the eight stations. The majority of the living individuals of mollusks from these stations were very small, and almost juvenile in size.

A preliminary appraisal was made of the feeding types among the invertebrates of the near shore, sand-bottom assemblage. The dominant feeding type among the lamellibranchs appears to be suspension feeding, which was also observed by SANDERS (1958), SAVILOV (1961) and McNULTY, WORK and MOORE (1962). This would seem logical, since the nearshore zone is characterized by continual turbulence and longshore current transport, bringing in an abundant supply of suspended organic matter and living organisms held in suspension. The abundance of light in this zone also produces a large supply of phytoplankton, one of the principal sources of food for suspension feeders. Predators comprise the greatest proportion of gastropods, and as such they are probably dependent upon the large lamellibranch population.

The relatively few deposit-feeding mollusks can be attributed to the probable lack of organic detritus, which is not apt to collect in the continuously agitated and well-sorted sand, so typical of this environment. Most of the lamellibranch larval shells examined indicated that the majority of species have a pelagic development while many of the very large proso-branch gastropods have large, egg-capsuled produced larvae which can probably withstand the turbulence so typical of these waters. The fact that so many of the inhabitants of the sand-flat environment are very active animals and have a long pelagic development may explain the great



uniformity of this assemblage over long stretches of coast line, even where there are considerable portions of rocky coast separating the beaches.

This environment provides the most useful tools for the interpretation of the Recent geological history of any continental shelf. Many sturdy mollusk species are confined to this depth, and are thus excellent indicators of sea level. Presence of members of this assemblage as dead shell on deeper parts of any continental shelf is usually an indication of previously lowered sea level unless transported by ice. The presence of submerged shorelines resulting from the last glaciation was substantiated and dated in the Gulf of Mexico by using typical mollusk shells of intertidal and nearshore shelf species (CURRAY, 1960 and PARKER, 1960). Time and again, many of the Gulf of California species typical of this environment appeared as dead shell on portions of the middle and outer continental shelf off San Blas and Hermosillo. They were almost always associated with sand deposits at preferred depths or on slight topographic highs, which could have resulted from a once lowered sea level (VAN ANDEL, *et al.*, in press). Since many of the mollusk species in this habitat are subjected to the pounding of the surf, most of them are quite sturdy and resistant to abrasion. They are, therefore, the most likely species to remain in place and undamaged over long periods of geological time. This observation is substantiated by their abundance in Tertiary fossil localities. Lists of mollusks from unconsolidated sand and sandstone deposits from the Gulf of California, compiled by EMERSON (1960a) and HERTLEIN and EMERSON (1959), and presumed to be of Pleistocene age, are dominated by the sand-flat species, most of which were in a good state of preservation.

### III. Low Salinity Lagoons and Mangrove Swamps:

This assemblage, with its abundant populations of oysters, *Rangia*, Mytilids, Corbiculids and Penaeid shrimp, closely resembles the low-salinity, river-influenced assemblage of the northern Gulf of Mexico coasts (PARKER, 1959). The presence of the immense Arcid, *Anadara tuberculosa*, the large Corbulas, and many more species of corbiculids in the Gulf of California lagoons, constitutes the principal difference between the Gulf of Mexico and Gulf of California faunas. Otherwise, 11 of the 19 listed species for the Gulf of California lagoons have their exact counterparts in the Gulf of Mexico. Many of the same genera and sub-genera of mollusks frequenting these low-salinity areas are also known from similar regions in South America, Africa and tropical, sub-humid Asia.

It is difficult to determine the dominant feeding type or usual form of larval development for the low-salinity lagoon assemblage, as so little is



known concerning the biology and life history of the common inhabitants of this environment. It was impossible to determine from the literature, the type of feeding or development from the Corbiculids, *Mytilopsis* or *Rangia*, although it is suspected that all may be suspension feeders, specialized to select lighter organic material from the more dense inorganic particles by some sort of ciliary mechanisms. Of the 18 genera listed for this environment in the Gulf of California, 55% are probably suspension feeders. However, about half of these are adapted to high turbidity waters, such as oysters and *Rangia*, which can function in high concentrations of inorganic material, and are in reality feeding upon the deposits. Of the remaining, 22% are herbivores, 14% are predators or scavengers, and *Melampus* can be considered a terrestrial herbivore. No estimate can be made of the usual mode of larval development, except that virtually all of the large lamellibranchs have planktonic larvae, which are thought to settle rather rapidly in response to tidal and discharge changes in the estuaries. Less is known for the gastropods, although *Melampus* is known to take up an aquatic existence only to reproduce, the juveniles soon creeping out of the water to live under damp vegetation along the shore.

The environmental factors limiting this assemblage have been discussed at length by PARKER (1956, 1959 and 1960) for its counterpart in the Gulf of Mexico. Salinity certainly has a limiting effect in this environment, since many species die or fail to reproduce whenever salinities rise above 10 or 15‰. The extreme range of water and air temperatures encountered in these shallow waters may serve to exclude many other invertebrate species which might compete with the lagoonal species which are adapted to changes of up to 30°C. between minimum and maximum. Sediment is limiting, only when it is too soft to support the populations of oysters and possibly *Anadara*. It is known that pH or hydrogen-ion concentrations are lower in the lagoons and estuaries than in the open sea, but it is not known whether these low pHs have any effect on estuarine faunas.

This assemblage is relatively uncommon in the fossil deposits surrounding the Gulf of California, but it comprises a large percentage of shell middens of the prehistoric peoples in the southern part of the Gulf. The species typical of low-salinity lagoons are valuable in paleoecological interpretations, since they are excellent indicators of climatic change (dry to wet or vice-versa) and as in the previous assemblage, good shoreline indicators. Since they thrive only in waters of low to medium salinity, it is unlikely that they will be found living in open sounds, gulfs or oceans. In order for low salinity conditions to be maintained in areas where these mollusks live, there should be little connection with the open sea. There-

fore, lagoonal areas must be part of the shoreline or allied with the terrestrial environment. The occurrence of estuarine shells at the shelf edge off San Blas (VAN ANDEL, *et al.*, in press) constitutes excellent proof that a shoreline existed there at one time.

Although not investigated at all in the Gulf of California, the inlet environment should not be completely neglected, since the very existence of lagoons and estuaries along the Gulf of California coast means that inlets or access to these lagoons from the Gulf must also exist. The inlets were a very distinct and characteristic habitat for the Gulf of Mexico lagoons and sounds as pointed out in PARKER (1955, 1956 and 1959). The physical factors which set this environment apart from other lagoon or open ocean areas are: first of all, two-layered, strong tidal currents which generally sweep the bottom clean creating either a shell-gravel or hard sand bottom, variable salinities and temperatures, generally in the upper range of the climate in which they are located, and finally a continual supply of nutrients, both from the estuarine side and open Gulf or ocean side.

A few observations were made in the inlet into Mazatlan harbor in April, 1959. One species of mollusk, *Atrina* (probably *maura*), certainly must have been abundant, as native divers were harvesting them in large numbers and have been doing so for years. This has proved to be one of the index mollusks for the inlet environment on the Gulf of Mexico coast also (PARKER, 1956 and 1959). Bottom samples were difficult to obtain as the bottom was too hard, but a few small Van Veen samples did produce a number of living *Olivella*, *Tellina*, *Crepidula* and small Venerids. All of these genera were found to be very characteristic in the Gulf of Mexican inlets as well and seem to be a typical *ISO-Tellina* community. The stations from this inlet are: 11, 112, 113, 114, all taken with a 1/20 m<sup>2</sup> Van Veen grab.

No other comparable studies of inlets as distinct habitats for macro-invertebrates are known to the author, although HENNING LEMCHE (personal communication) has recognized that the conditions which characterize inlet environments usually produce a rich nudibranch population, as well as a rich growth of algae, bryozoans, hydroids and turbellarians. Investigations of similar environments in other parts of the world produced many of the same characteristic organisms, with the exception of those mollusk genera which are exclusively tropical, such as *Pinna* and *Atrina*.

#### IV. Nearshore Sand to Sand-Mud, 11 to 26 Meters.

This environment corresponds closely to the shallow or nearshore shelf environment off the Mississippi Delta (PARKER, 1960), and portions of both

the nearshore and intermediate shelf off Texas (PARKER, 1960). A comparison of the common animals from these three regions shows an almost identical generic composition, which substantiates THORSON's (1951) concept of parallel communities. For instance, in the check list of common invertebrates for this environment (2 to 24 meters) off the Mississippi Delta, 8 of the 11 gastropod species have their exact counterparts (even to subgenus) in the nearshore, 11 to 26 meter environment in the Gulf of California. Fifteen of the 22 pelecypods, all of the echinoderms, and a large number of crustaceans are also represented by closely related species. Most of these twin species were found too in the same depths and bottom type off Texas. There was no doubt as to similarity of the assemblages between the Gulf of California and Gulf of Mexico, although it is surprising that no exact generic counterparts have been described previously, since this assemblage undoubtedly exists elsewhere in the world. Three other regions have been studied in tropical latitudes, but the environmental factors are much more extreme and variable than those in the Gulf of California. These are Madras, India in the Bay of Bengal, the Persian Gulf, and off Ghana, West Africa. None of these regions was characterized by the diversity of animals found in the American Gulfs, nor was there much similarity in the dominant groups. However, the fluctuation of environmental parameters in these regions, undoubtedly contributes to less diversity.

SAMUEL (1944) published a few observations on benthic communities in similar depths off Madras, India. She found that the primitive chordate, *Branchiostoma*, was the most abundant animal on sand bottom between 18 and 30 meters. Two echinoids, including *Lovenia* (which also occurs in the same environment in the Gulf of California) were the next most abundant animals. Only two mollusks, a *Marginella* and *Glycymeris* were common. No others were taken more than once. Except for the presence of *Lovenia*, there seems to be little resemblance between the Madras community and the one found at similar depths and on the same sediment in the Gulfs of California and Mexico. A slightly different community was found on clay bottom in these depths off Madras. An Anomuran crab and several other decapod crustaceans were the dominant animals. The only common mollusks were the gastropods, *Oliva*, *Cantharus* and *Murex*, which were also found at similar depths in both Gulfs, but occupied no position of importance within the community.

THORSON (1957) mentioned several communities from the Persian Gulf, in depths ranging from two to 60 meters on sand and shelly sand bottom. Only the dominants were given, none of which corresponded to the dominants of the American communities or assemblages at these depths.

This is not surprising, as the Persian Gulf is noted for its extremely high temperatures and also hypersalinity. These extremes may be limiting to a large number of invertebrate species. One community on shell gravel was characterized by a species of *Branchiostoma* (thus paralleling Samuel's community off Madras), a species of *Venus*, a *Glycymeris* and a polychaete, *Temnopleurus*. A *Branchiostoma* community may exist in the Gulf of California from preliminary observations, but was not sampled. The only other community described by Thorson from the Persian Gulf in shallow depths and on sand bottom was the *Xenopthalmus pinnotheroides* crab community. The community was completely dominated by this small crab, accompanied by a few polychaetes of no quantitative significance. Apparently, there was nothing like the diversity of species found in the Gulf of California in either the Persian Gulf or Bay of Bengal.

BUCHANAN (1958, p. 21-23) describes an "inshore fine sand community" from depths of six to 15 meters off Accra, Ghana on the West African coast. In overall aspect, the fine sand community was characterized by two animals, the pelecypod, *Cultellus tenuis* (related to *Ensis*), and the polychaete worm, *Diopatra neopolitana*. Within the major structure of this community, three smaller communities were found which he called: (1) the *Owenia* beds, (2) the Accra Bay silt patch (*Macoma* bed), and (3) the *Dentalium* zone. The distribution of these small communities within the six to 15 meter depths off Accra is reproduced in fig. 28. This picture is quite similar to that shown in fig. 16 for the pattern of distribution of the computer-designated groups of species in similar depths in the Tiburón region. Buchanan attributed much of the patchiness of these communities to small differences in grain size, organic matter content, and possibly wave action. However, he found that there was nothing to distinguish the environment of the *Owenia* beds from the rest, unless larval settlement of the dominants had been influenced by the direction of the prevailing current. Similar invertebrate species are also found in the Tiburón near-shore sand bottoms, such as *Ensis*, *Tagelus*, several species of *Tellina* and *Macoma*, and many tube-forming polychaetes, not yet identified. There are minute differences in sediment types in this area, even though sands predominate throughout (fig. 8). The group "7" assemblage, using *Laevicardium elenense* as the key species, seems to be confined more to the silty-sand portion of this environment, while the *Chlamys circularis* group is more closely allied with shell-sand and shell-gravel sediments at slightly greater depths. Mollusks were the typical components of these groups, with pelecypods outnumbering the gastropods. The other index groups contained more gastropods or crustaceans. The minute differences of environmental factors within the major environments have yet to be



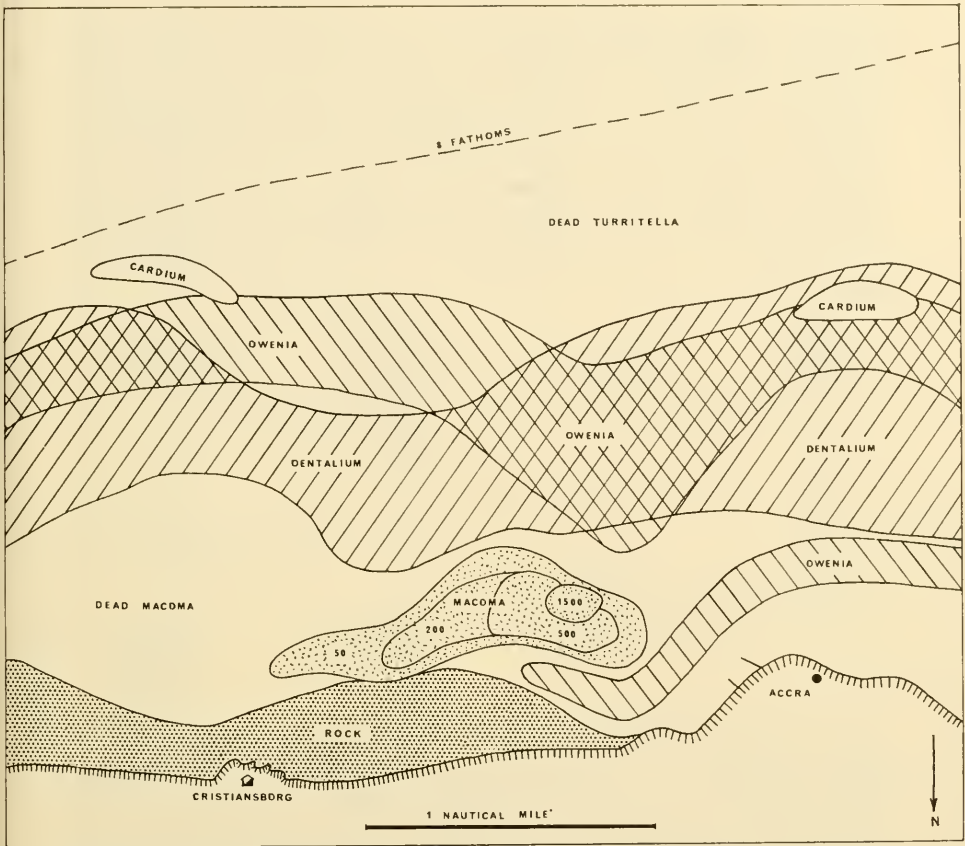


Fig. 28. Illustration of the patchiness of community distribution in the nearshore "fine sand" community off Accra, Ghana, from BUCHANAN (1958).

studied in detail, especially where salinities, temperatures, and bottom types appear fairly uniform. It is possible that here the biological factors, such as competition, feeding types, larval development, etc. are more important in limiting the composition of small communities than the physical-chemical factors.

The nearshore, 11 to 26 meter region, with its almost uniform sand bottom, provided an opportunity to check the effectiveness of the grab sampler as opposed to the shell dredge in appraising the quantitative aspect of bottom communities. As mentioned previously, the depths of between 11 to 26 meters appear to be the most prolific in species of all environments studied in the Gulf of California, resembling somewhat the *Venus* community of British and Danish waters (FORD, 1923). Whether this diversity compares quantitatively with other regions in the world

remains to be investigated in detail. It was possible to obtain some quantitative figures for the nearshore sand bottom environment from eight stations taken with a  $1/20 \text{ m}^2$  Van Veen grab which only totaled  $2/5 \text{ m}^2$ , insufficient for strict square meter comparisons with other regions. An average of 2.6 living individuals and 2.1 living species of animals was taken from these eight samples using a 1 mm. diameter screen. Most of the stations were taken in the southern Gulf, and the data for these stations can be found in the appendix. The results of this survey are shown in a table below.

Station Number	Number Living Species	Number Dead Species	Number Living Individuals
1	0	22	0
8	4	20	4
9	3	38	3
16	3	5	3
21	0	0	0
22	2	9	2
24	3	18	4
26	2	0	4
Average 2.1/station		14/station	2.6/station or $52/\text{m}^2$

Five  $1/10 \text{ m}^2$  Petersen Grab samples were taken in one spot, within this same environment, off Topolabompo near Los Mochis. Table VII gives one an idea of how diverse this region is in respect to species, and also the relatively low standing crop of animals which was found. These five samples may offer the only valid comparison in this study with other benthic studies, although the total area is still less than one half a meter. Inspection of the species composition of these stations (Table VII) indicate that they represent a rather good *Tellina* community, similar to those described by THORSON (1957). Cumulative curves of these five samples, as well as cumulative species curves for the eight Van Veen samples listed above are given in fig. 29. These cumulative curves are based upon the appearances of new species in successive samples as the area is also increased. Fig. 29A gives first the cumulative curves for the eight samples listed above in the 11 to 36 meter depth ranges, and secondly the curve for equal-sized samples taken in the 1 to 10 meter depths. One can easily see that the diversity is about the same in both environments. Fig. 29b gives the cumulative curve for nine nearly successive shell dredge samples in the same region, also as area is increased. Both in 29A and 29B, plots of the total number of species taken in each sample is given, in order to demonstrate the relative uniformity of catch effort. Finally, in fig. 29D,



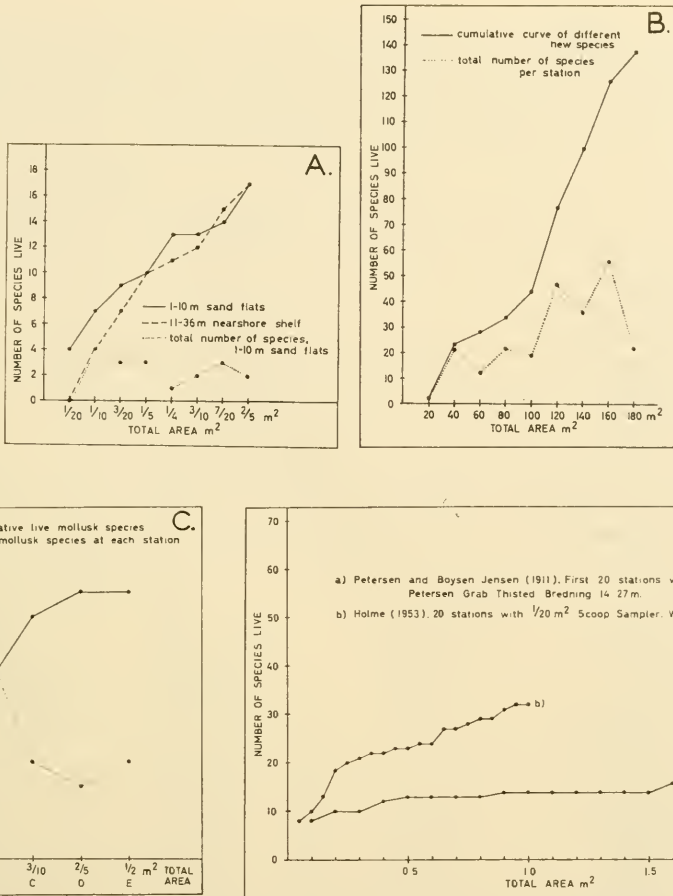


Fig. 29. Cumulative curves of appearances of new species in successive samples from various localities in the Gulf of California and northwestern Europe.

- A. Curves of  $\frac{1}{20} m^2$  VAN VEEN samples in two shallow environments in the southern Gulf of California region.
- B. Curve of 9 successive samples from the northern shelf region, taken with a small shell dredge, covering roughly  $20 m^2$  per sample.
- C. Curve of mollusk species only from 5 equal-sized samples in one spot off Topalobompo, Mexico, in a depth of 17 meters, using a  $\frac{1}{10} m^2$  PETERSEN Grab.
- D. Cumulative curves of species diversity in 20 consecutive stations each from a) Denmark and b) England.

cumulative curves for successive samples in boreal waters are reproduced from HOLME (1953) for Whitsand Bay, England, and from PETERSEN and BOYSEN JENSEN (1911) from Danish waters. There is no doubt concerning the great diversity of Gulf of California waters as compared to boreal waters when comparing this series of graphs. All of the Gulf of California curves reach toward the asymptote, with little indication of

Table VII.

Analysis of numbers of individuals and species of living and dead invertebrates from five successive Petersen Grab samples at Station P 51, depth 16 meters, fine sand bottom.

Species	Samples				
	A.	B.	C.	D.	E.
<i>Oliva incrassata</i> .....	1				
<i>Nassarius pagodus</i> .....	2				
<i>Architectonica placentalis</i> .....	1				
<i>Natica caneloensis</i> .....	2				
<i>Terebra malonei</i> .....	1				
<i>Phos articulatus</i> .....	1				
<i>Eulima varians</i> .....	1				
<i>Balchis</i> , sp.....	1				
<i>Pyramidella conica</i> .....	1				
<i>Terebra variegata</i> .....			2		
<i>Polinices intemerata</i> .....			1		
<i>Philine</i> , sp.....		1			
<i>Nuculana</i> , sp.....		1			
<i>Chione mariae</i> .....		1			
<i>Corbula</i> , sp.....		6			
<i>Tellina felix</i> .....		2	2	2, 10	1
<i>Lucina approximata</i> .....		1			
<i>Pitar concinnus</i> .....		1, 3		1, 7	
<i>Pandora</i> , sp. (juv.).....		1			
<i>Periploma</i> , sp. (juv.).....		1			
<i>Chione</i> , sp. (juv.).....		1			
<i>Tagelus politus</i> .....			1	1, 3	
<i>Anadara perlabiata</i> .....					1
<i>Corbula luteola</i> .....					1
<i>Cyclinella</i> , sp.....					1
polychaetes.....	5+	5+	5+	5+	5+
Total species living.....	4	6	5	4	1
Total species dead.....	6	6	—	3	4
Total individuals, living.....	8	10	11	9	5
Total individuals, dead.....	8	14	—	20	4
1 = living					
1 = dead					

levelling off. On the other hand, both curves from boreal waters level off after a few samples, and virtually no new species are added after the fourth or fifth sample. Each new Gulf of California sample produces nearly a whole new set of species.

The nine stations used in fig. 29C were taken by a small shell dredge, one half a meter wide, towed for five minutes at about one quarter of a knot. This method covered about 20 square meters per sample, if the dredge was kept constantly on the bottom. All samples were taken in the Tiburón region in about the same environment as the eight grab samples tabulated above. The overall catch was far greater with the shell dredge than with the Van Veen, being at least ten times more productive in each case, averaging 26 species and 87 individuals per station. Because the area covered by the shell dredge was far greater than that for the grab samples, an entirely different picture is obtained for the kind of animals living there. If the shell dredge samples are equated on a square meter basis, they produced only an average of 4.4 individuals per square meter, roughly 15 times less than that computed for the Van Veen samples. It would seem, therefore, that the shell dredge is completely ineffective for quantitative studies, although it certainly produces a much greater variety of animals, especially from groups seldom taken with bottom grabs (see THORSON, 1957, pp. 473-476). The following table gives the figures for the shell dredge catches.

Station Number	Number Living Species	Number Dead Species	Number Living Individuals
178	1	2	2
181	22	18	67
183	12	11	19
184	21	35	48
190	19	12	68
194	46	48	197
195	36	37	63
196	56	73	253
208	22	17	63
Average 26/station		28/station	87/station or 4.4 m <sup>2</sup>

The figures for the number of identified species in the small dredge samples gives some conception of how prolific this environment can be in diversity of species, living and dead. The total average number of living and dead species for all nine stations is 54 per station, while the greatest number is 129. It should also be mentioned that many of the shells of species recorded were those taken alive at other stations or in different years. Although the majority of the Van Veen grab samples were taken to the south of the shell dredge samples, two grab samples (Stations 24 and 26) collected within the shell dredge sampling region, produced the same

number of species there as in the southern Gulf. Small trawl samples were also taken in the southern section of this environment, and if anything, the diversity of species was even greater than that produced by the shell dredge. Although the species are not listed for the above two grab sample stations, only one species was taken more than once, equalling the diversity found in the grab sample survey of the shallow, sand-flat environment.

Either invertebrate distribution is extremely patchy on the continental shelf of the Gulf of California, or each population of species is spread very thinly over the bottom. Since the species composition is fairly similar in the nine stations cited above, the latter alternative is probably the correct one. Certainly, there is no apparent dominance of macro-invertebrate species indicated here, similar to the boreal region studied by PETERSEN (1911–1915), THORSON (1957) or SANDERS (1956 and 1960) although such a small bottom area was sampled quantitatively that valid comparisons are impossible. Animals of the size studied by SANDERS were not identified in this study, although everything was saved which could be retained in 1 mm. screens. It was observed that relatively few polychaetes, amphipods or copepods were collected from these sediment samples. This same lack of dominance of any one species of invertebrate, large or small, was also observed on the fine sandy bottoms of the northern Gulf of Mexico (PARKER, 1956a and 1960). Few quantitative benthic invertebrate studies have been undertaken in the tropics and sub-tropics, with the exception of THORSON's (1957 and personal communication) in the Persian Gulf (which being hypersaline and very hot is on the whole a rigorous and unfavorable environment), BUCHANAN's (1958) off Ghana, and LONGHURST's (1957 and 1958) off Sierra Leone, Africa. For this reason it is difficult to make comparisons of standing crop and species diversity between the tropics and the more well-known boreal regions. SPÄRCK (1931) discussed the quantitative aspect of benthic populations as deduced from a small number of samples in the Mediterranean. Although the waters sampled for this study are generally warm, some of the species taken may also occur in Boreal regions. Only a few very abundant species occurred in these samples, paralleling the Danish communities of PETERSEN (1911–1915). Although there seems to be no dominance of particular species of invertebrates in the American sub-tropical regions, there is certainly dominance in the Gold Coast area of West Africa (BUCHANAN, 1958) and off Sierra Leone to the north (LONGHURST, 1957 and 1958). In each of Buchanan's five communities, lying roughly parallel to each other in descending depth, there are about ten moderately abundant species, and at least one or two very abundant species of invertebrates. No mention was made of the

number of rare species taken at each station or the total number of species occurring at any one station. LONGHURST (1958) found no relationship between the distribution of communities and depth, except for a change at about 80 meters, with two communities inshore (a shelly-sand and mud community), and one on the outer shelf and slope. The inshore communities range into the estuaries and do not exactly correspond to any of the Gulf of California communities. Relatively few species were given in Longhurst's synopsis, but upon further appraisal of the discussions of the various communities, there appears to be a much greater diversity. There is no doubt, however, that both Buchanan's and Longhurst's communities have a structure similar to those of Petersen, Thorson and Sanders. The question then arises, how are the Ghana, Sierra Leone and Persian Gulf regions different from the Gulf of Mexico and Gulf of California, the former being characterized by a group of dominant animals, and the latter, though having no dominant species, seems nevertheless to have similar physical conditions? At least they are more similar to each other in mean temperatures, than they are to Danish or Massachusetts waters. The most important difference is probably in the extreme of physical factors.

This lack of species dominance in the American waters, may well have several explanations, both geological and biological. The great diversity of level-bottom species in the tropical and sub-tropical Americas has not been confined to Recent geological times. DALL (1890b-1903) described a large number of molluscan species from what is at present called the Pliocene of Florida, and 312 species of mollusks from a small horizon in the Miocene of Tampa, Florida (DALL, 1915). Similar very large lists of mollusk species have been described from other Tertiary deposits in North and South America (GARDNER, 1926-1947; WOODRING, 1925, 1928, 1957 and 1959; and OLSSON, 1922). It is difficult to determine from fossil deposits how many species may have been living at any one time in one spot, but it cannot be denied that there was as much diversity in the molluscan fauna during the middle and late Tertiary as there is today in the warmer waters of the Americas. On the other hand, a check of the molluscan fauna of the Middle Atlantic Miocene (DALL, 1904) or Danish Miocene (SORGENFREI, 1958), which were warm temperate to Boreal in climate, shows a very small number of species as compared to tropical Miocene formations.

Although there was a great diversity of marine mollusks in the northern Gulf of Mexico (over 1,000 species on level-bottoms), the diversity is far greater in the Gulf of California, where at least 1,400 level-bottom species



are known (KEEN, 1958), and possibly another 1,500 are yet to be described. One explanation for the great variety of mollusks within the Gulf of California may be found within its geological history. In middle Tertiary times, the relatively deep marine connections between the Caribbean Sea and Pacific Ocean permitted a mixing of the two faunas, the greater part of the migration taking place from east to west (EKMAN, 1953). A large number of new species were added to an already abundant, partly endemic eastern Pacific fauna from the Caribbean. There has also been a continual renewal of species from the Indo-Pacific region. Many western and southern Pacific species are transported first to islands such as the Galapagos, Cocos and Clipperton Islands, and eventually to the mainland (ROSENBLATT, 1959; and WALKER, 1960). During the Pleistocene, it seems that there was also a southern migration of some California province species. Aside from this recruitment of species from outside, the evolution of new species has also certainly occurred. With the high primary productivity of the Gulf as a basis for high benthic production plus the great variety of habitats available for mollusk species, virtually all species from these various zoogeographic regions can be successfully maintained in various parts of the Gulf. Since no very drastic seasonal environmental changes occur, and salinities remain constant and optimum for marine animals, most species may only be eliminated by predation or competition for food. SPÄRCK (1926) suggested that both water temperature and availability of food may affect the diversity and abundance of marine populations, although this was implied indirectly. Through a series of tank experiments, Spärck showed that a lack of food would tend to eliminate a large number of invertebrate species growing and reproducing in cold waters, especially those with high metabolic requirements. When the food supply was reduced, only those with low energy requirements would remain, and these could then become the dominant organisms in the environment. On the other hand, a lack of food in warm (20°C.) waters had little effect on most of the species adapted to these waters, since their metabolism would be lower, and thus would need less food to survive. The population would then consist of many species with relatively few individuals of each species.

There is yet another theoretical explanation for lack of dominance in most of the Gulf of California assemblages. The majority of mollusks, and perhaps other invertebrates, may have a very short life span of one to two years, leading to an alternation of species in any one spot. During the course of a year, one group of invertebrate larvae may settle in a particular part of an environment, live and reproduce there, while the larvae of this generation may settle elsewhere (see THORSON, 1950). The adults may also

prey upon the larvae of their own kind as they settle if the population of adults is dense enough (URSIN, 1960). The parents may die in a relatively short time, and a new group of species may then re-occupy the habitat of the first group. One observation substantiating this surmise is that on the shallow, sandy bottoms from 11 to 26 meters, there is one very large assemblage of both living and dead mollusks, occurring either living or dead at most of the stations. One group of stations may contain a number of living species found only at these stations, although these same species may also be found dead at another group of stations. The latter stations in turn contain a different set of living species, which may be found dead among the living population of the first set of stations. One argument against this premise, is that environmental conditions seem to be very uniform throughout the area where the 11 to 26 meter assemblage is found. Salinities are constant, sediment-size is relatively uniform, and temperature variations are not too great at these depths. If the environmental conditions are constant, then larval settlement should be more or less random and periodical. The strong tidal currents, which sweep back and forth between the northern and central Gulf constitutes one factor which does not remain uniform. If larval settlement should take place when the currents are sweeping north, certain species may tend to settle only in the northern part of the environment. Alternatively, if larvae are produced during the southern trend of the tidal currents, settlement may only take place to the south although these intervals may be too short to be effective.

Of the 21 species of mollusks which were significantly found together in this environment (Table IV), 12 species or 57% are suspension feeders, 4 or 20% are predators, 3 or 14% are deposit feeders, and 2 or 9% are believed to be scavengers. As could be predicted in this environment, the abundant animals (qualitatively) are suspension feeders, well-adapted to the hard sand substratum which contains relatively little interstitial organic matter. A preliminary analysis of probable feeding types for all of the living mollusks taken at the computer-paired stations (fig. 17) gave the following organization: 40 species or 45% are suspension feeders, 26 species or 30% are predators, 17 or 19% are deposit feeders, 4 or approximately 4% are algae feeders, and 2 or about 2% are possibly parasitic or commensal. These percentages are not too meaningful, since the samples were not quantitative. Again the suspension feeders predominate. The fact that intensive upwelling takes place nearby and occasionally high inshore surface productivity (fig. 10) occurs in this area where these typical stations were taken (fig. 17), may also account for the high per-

centage of suspension feeders, which could take advantage of these plankton blooms. Analyses of feeding types of the dominant members of benthic communities has seldom been attempted, although SANDERS has done so in both Long Island Sound (SANDERS, 1956) and in Buzzards Bay, Massachusetts (SANDERS, 1958, 1960), and apparently by SAVILOV (1961) and TURPAEVA (1957), which were not available in their entirety to this author. For instance, in Buzzards Bay, SANDERS (1960) indicates that in the silty-clay, *Nephtys incisa*-*Nucula proxima* community, the most abundant three species are selective and non-selective deposit feeders, the fourth ranked species is probably a carnivore, and the fifth a suspension feeder. Of the 30 most abundant (by number, but not necessarily by weight) species of invertebrates in this community, 10 or 33% are selective deposit feeders, 8 or 26% are non-selective deposit feeders, 4 or 14% are suspension feeders, 6 or 20% are carnivores, and the remaining 7% are scavengers and one specialized deposit feeder (*Turbonilla*). Earlier, SANDERS (1958) remarked that in Buzzards Bay, 80 to 99% by number of benthic fauna comprised the primary consumers, i.e. herbivores and detritus feeders. The filter or suspension feeders made up the majority of the fauna of sandy sediments, while deposit feeders dominated the fauna on clay bottom. In the sand-bottom *Ampelisca* community, suspension feeders constituted two-thirds of the population by number, while 80% of the fauna of the silty clay, *Nephtys*-*Nucula* community are deposit feeders. This same relationship between fine sediments and feeding types was also found by SANDERS to exist in Long Island Sound (SANDERS, 1956, 1958). Sanders results are therefore in relatively close agreement with those found in the present study for the shallow waters of the Gulf of California. McNULTY, WORK and MOORE (1962), in a study of level bottom communities of south Florida in somewhat comparable depths, but carbonate rather than terrigenous sediments, offered several generalizations regarding the relationship between feeding type and sediment size. Since terminology differs from that used here, direct comparisons are difficult. They found that detritus feeders predominate in the finest sediments, and deposit and filter feeders at intermediate size grades. However, their sediment data indicates that on the whole, grain size is much larger in Biscayne Bay, Florida than in the nearshore environments of the Gulf of Mexico.

Two thirds of the index or characteristic 21 species for this environment most likely have planktonic larval development, while the other third could have non-planktonic development. Since nothing was known concerning the exact reproduction of many of the Gulf of California species of mollusks under discussion, larval development types were often hypo-

thesized from what was found in the literature concerning closely-related sub-tropical and tropical species. It must be realized, however, that it is known that development can differ radically within the same genus of mollusks. For this reason, 40 species of important lamellibranchs were examined by the author and W. K. Okkleman as to prodissoconch type.

#### V. Intermediate Shelf, 27 to 65 Meters:

The assemblage characterizing this environment actually becomes important as a distinct entity at about a depth of 39 meters, especially in the southern Gulf. In the northern Gulf, the change is more gradual. Although 10 stations were taken in depths of 27 to 38 meters, only 38 species were found, none being confined to these depths. Nineteen of these species were more abundant in the shallower waters, while 19 were more commonly taken in the deeper waters. This overlap in depth ranges plus the lack of large numbers of individuals and species indicates that there is a transition zone between the major assemblages of the nearshore and intermediate shelf depths. This transition zone was more distinct in the southern Gulf, as the sediments were much finer than those inshore or offshore, ranging from silty sand to silty clay. Reduced wave action permits the accumulation of finer sediments along with greater amounts of organic matter within the sediments. The larger amounts of organic matter can apparently support a large population of Penaeid shrimp, since the 27 to 38 meter depth zone is the primary inshore shrimp grounds for both the Gulfs of Mexico and California. The shrimp and the more common invertebrates found at these 10 stations, the echinoid, *Lovenia cordiformis*, the scaphopod, *Cadulus perpusillus*, and the pelecypod, *Nuculana elenensis*, are all deposit feeders, well adapted to feeding in this habitat.

This same transition zone was also observed in the northern Gulf of Mexico, wherever fine sediments occurred inshore of major sand bottom areas resulting from lowered sea level (PARKER, 1960; and CURRAY, 1960). As in the Gulf of California, the northern Gulf of Mexico intermediate shelf assemblage was most distinct in depths of 39 to 65 meters on the relict sand deposits. Only off Texas where deposition has been more rapid, and fine sediments occur uninterrupted across the shelf, was the intermediate shelf assemblage continuous from 20 to 65 meters. The assemblage in this clayey zone in the Gulf of Mexico was also characterized by uncommon and widely-dispersed deposit feeders. The number of living animals in 1/5 m<sup>2</sup> Van Veen samples from this transition environment off Rockport, Texas averaged only 2.2 individuals per station or about 12



per square meter (PARKER, 1960, p. 326). Five Van Veen ( $1/20 \text{ m}^2$ ) samples were also taken at the same depths in clayey sediments in the Gulf of California. They averaged 6.3 individuals per sample, or 126 animals per square meter, a much higher population than for the equivalent environment in the Gulf of Mexico. This may not be a valid comparison, as the total area sampled this way was so small. These higher numbers might be representative for the Gulf of California, since this zone is very narrow, receiving a steady influx of animals from inshore and offshore. In the Gulf of Mexico this zone is 10 to 20 miles wide, receiving little recruitment from the other zones, at least in the central portion.

BUCHANAN (1958) also found a benthic community in more or less equivalent depths of from 8 to 20 fathoms (15 to 36 meters) off Ghana, which he called the "sandy-silt community". His community bears little resemblance to the association of animals found in this study, except for the presence of *Penaeus duorarum*, one of the dominant shrimp in the inshore shrimp grounds (HILDEBRAND, 1954) on the coast of the northern Gulf of Mexico. He also found very large populations of living and dead *Turritella annulata* Kiener. This genus did not appear in abundance alive, either in the Gulf of Mexico or Gulf of California. The dominant mollusks of Buchanan's sandy-silt community were also deposit feeders, although the dominant gastropod is a herbivore, which was said to feed on the algae growing on the *Turritella* shells.

As indicated by a prolific and indicative fauna, the waters in depths ranging from 39 to 65 meters constitute the most distinct portion of this environment. However, many of the species found there still range into shallower water, and dead shells can often be found along the shore. In the previous description of the assemblages, the fauna of this zone was divided into a northern and southern portion. The northern assemblage was taken on sand bottom, while the southern assemblage is more confined to clayey bottom. The northern assemblage, as revealed by the computer associated *stations* was found exclusively on sand bottom resulting from reworked old delta deposits presumably laid down during lowered sea level and more pluvial periods (VAN ANDEL, *et al.*, in press). This assemblage and its equivalent on sand bottom to the south of San Blas are remarkably similar to that found on relict delta sand deposits off the Texas coast in 36 to 63 meters (20 to 35 fathoms) (PARKER, 1960, pp. 322-23). Again many of the mollusks from this environment are represented by twin species from both oceans, which probably had common origins in the Miocene and Pliocene shallow seas across Middle America. A few of the Gulf of Mexico species of mollusks and their equivalents from the Gulf of California intermediate shelf are listed below.



Gulf of Mexico  
Scaphopods

*Dentalium gouldii*  
*Cadulus carolinensis*

Gastropods

*Calyptrea centralis*  
*Natica floridana*  
*Strombus alatus*  
*Semicassis granulatus*  
*Ficus carolae*  
*Murex recurvirostris rubidus*  
*Nassarius ambiguus*

Pelecypods

*Chlamys gibbus gibbus*  
*Pecten ravenelli*  
*Crassatella speciosa*  
*Crassinella martinicensis*  
*Lucina sombreroensis*  
*Trigoniocardia media*  
*Papyridea soleniformis*  
*Laevicardium laevigatum*  
*Microcardium tinctum*  
*Gouldia cerina*  
*Chione clenchi*  
*Tellina tayloriana*  
*Tellina lintea*  
*Tellina squamifera*  
*Macoma extenuata*  
*Solecortus cumingianus*

Gulf of California  
Scaphopods

*Dentalium oerstedii*  
*Cadulus perpusillus*

Gastropods

*Calyptrea mamillaris*  
*Natica idiopoma*  
*Strombus gracilior*  
*Semicassis centriquadrata*  
*Ficus ventricosa*  
*Murex r. recurvirostris*  
*Nassarius pagodus*

Pelecypods

*Chlamys circularis*  
*Pecten vogdesi*  
*Crassatella gibbosa*  
*Crassinella pacifica*  
*Lucina excavata*  
*Trigoniocardia biangulata*  
*Papyridea aspersa*  
*Laevicardium elatum*  
*Microcardium pazianum*  
*Gouldia californica*  
*Chione mariae*  
*Tellina inaequistriata*  
*Tellina reclusa*  
*Tellina fluctigera*  
*Macoma siliqua*  
*Solecortus guaymasensis*

There are many more mollusks and other invertebrate species in this environment in both gulfs, which are identical in appearance, and which give similar aspects to both areas. The geological occurrences of most of the pelecypods taken in the Gulf of California in this study can be found in OLSSON (1961). A surprising number of the species were found to occur in middle Tertiary formations. Likewise, the twins of these species in the Gulf of Mexico or their precursors have also been described from Tertiary deposits of Florida (DALL, 1890b-1903) and the Caribbean (WOODRING, 1925, 1928). Many of these twin species have identical depth, temperature and sediment "preferences" today in both oceans. It is therefore possible that large portions of the Central and South American Mio-Pliocene seaways may have been represented by sand bottom at about these depths. Here then, is another instance of the importance of the geological setting influencing the composition of assemblages or communities. Tectonic

events during the Tertiary of Middle America furnished the setting for the recruitment of this multitude of Caribbean species into Pacific coastal community complexes.

BUCHANAN (1958) describes a community in similar depths off Accra, Ghana which he terms the "silty-sand community", occurring in from 36 to 45 meters (20-25 fathoms). This community is characterized by a giant Foraminifera, which so far has not appeared in shallow water in the eastern Pacific. The only important molluscan species were a *Cardium* and a *Phos*, while the crustaceans consisted of several species of decapod shrimp. Most of the macro-invertebrate species also ranged into the off-shore "coarse-sand community" to depths of about 90 meters (50 fathoms). As can be seen, the kinds of animals in BUCHANAN's community bear little resemblance to those found in equivalent depths in the Gulf of Mexico or Gulf of California although water temperatures are slightly lower off Ghana. LONGHURST (1958) in his discussion of benthic communities off Sierra Leone, West Africa gives no list of invertebrates restricted to intermediate shelf depths, but rather finds strict dependence upon sediment size and estuarine influence. It is evident from his data, that relatively few invertebrate species live in depths of 27 to 65 meters compared to the number of species living in similar depths in the Gulf of California. In a discussion of the quantitative aspects of his study, LONGHURST (1957) did find that there was a decrease in number of species and individuals with increasing depths. He also stated that there was little difference between his region and similar depths in temperate, boreal and Arctic waters in terms of the biomass, and individuals and species per square meter. He reported that 800 species of animals were taken by grab and dredge off Sierra Leone, which differed only slightly from JONES (1951) list of 757 species from the Isle of Man in the British Isles, although comparisons of this sort are not too meaningful as the level of systematic knowledge of the two areas are quite different.

Almost equal numbers of suspension, deposit and carnivorous feeders were produced from a preliminary analysis of the feeding types of the mollusks and a few other invertebrates found in the northern sand-bottom, intermediate shelf assemblage. Of the 68 species selected for his survey, 17 are probably deposit feeders, 16 are suspension feeders, 15 are predators, 2 scavengers, 3 are algae feeders, and the rest are unknown as to feeding habits. Although a sand bottom is usually characterized by an excess of suspension feeders, these sands are at greater depths and less affected by turbulence than most sandy areas, possibly allowing more organic matter to accumulate on the bottom. The alternating strong currents which sweep

through the channel between Tiburón Island and the mainland, lose their strength in the center of the distinct area confirmed by the matrix south of Tiburón, and thus may begin to drop their load of silt and organic material which become inter-bedded with the sand. Examination of the prodissoconchs of the characteristic pelecypods from this environment indicated that the majority of species have a pelagic larval development.

The second association within the intermediate shelf environment was found in the southern Gulf. As in the northern region, nearly half (11 of 23) of the index species from the matrix-associated stations proved to be crustaceans. The principal environmental difference between the northern and southern associations is that the majority of the 11 stations were located on clayey bottom. Temperatures are much higher and have a smaller range, thus permitting a larger number of tropical species to survive there. Waters are also clearer and plankton blooms less common.

As in the northern region, the southern portion of the intermediate shelf is characterized by a fauna with a strong resemblance to that found on the intermediate shelf of the Gulf of Mexico (PARKER, 1960, pp. 322-23). The major difference between the two Gulfs is the fact that the genera confined to clay bottom in the Gulf of Mexico are also found on sand bottom in the southern portion of the Gulf of California. Many of the species on the intermediate shelf of the Mazatlan region are also twins of the Gulf of Mexico species found in similar ecological conditions. In fact, the number of twin species is even greater in the southern than in the northern Gulf of California. This is not surprising, since the ecological conditions in the San Blas to Mazatlan region more closely resemble those of the northwestern Gulf of Mexico shelf than those of the Tiburón region.

A survey of feeding types of the mollusks collected alive from the two southern stations taken on sand bottom showed a predominance of predators and suspension feeders. Of the 61 species of mollusks taken alive at these two stations, 34 are most likely predators, 15 are suspension feeders, 6 are probably deposit feeders, 4 algae feeders and 2 may be scavengers. The feeding-type composition of the species is more normal for a sand bottom than that found on equivalent sand bottoms in the northern region. Eleven stations and 37 species of living mollusks were taken on clayey bottoms in the southern Gulf. A breakdown of probable feeding types for this assemblage produced: 12 suspension feeders, 17 predators, 6 possible deposit feeders, and 2 probable algae feeders. The majority of the crustaceans can also be considered as scavengers and predators. It was observed that the species with the greatest number of individuals were the deposit feeders. The large number of predators are accounted for by the fact

that most of the southern stations were taken with an otter trawl, the best method for collecting the more mobile animals which comprise most of the predators. According to a survey of prodissocochns by the author, most of the lamellibranch species have a planktotrophic larval development. Perhaps 40% of the gastropods have a pelagic stage, but it is almost impossible to be sure, since the gastropod survey was based on probable development from related species. Thorson (personal communication) states that within only a very few families of prosobranchs is there strict uniformity in larval development. The high percentage of species with pelagic development seems reasonable, since this environment in the southern Gulf is one of the largest in areal extent and possibly the most uniform. Planktonic larvae should therefore settle with a fairly high degree of success in this region.

#### VI. Outer Shelf, 66 to 120 Meters, Clay Bottom, Southern Gulf:

The animals found on the outer shelf in the Gulf of California, especially on clayey bottom, are very similar to those taken in equivalent depths in the Gulf of Mexico. The large number of equivalent or twin species in this environment, as in the previous one, suggest that clay bottoms to depths of 100 meters may also have existed across Central and South America during Tertiary periods. Of the 21 typical species taken in from 70 to 120 meters in the Gulf of Mexico (PARKER, 1960), 13 had their exact equivalents in the Gulf of California in the same depths, and an additional 6 species were taken at slightly different depths. It is virtually impossible to separate most of these "twin" species from the two gulfs without identifying labels. One is also struck by the amazing similarity of trawl and dredge hauls from the clayey bottoms of the two Gulfs. The twin species constitute the largest populations, so that a preliminary appraisal of unlabelled samples would give very little indication of which Gulf the samples originated from. To demonstrate the close similarities of this assemblage in both gulfs, a list of species from both areas is appended.

Gulf of Mexico (PARKER, 1960,  
pp. 323-4) 75-120 Meters

Gulf of California (Tables in  
Appendix) (40-65 Fathoms)

#### Pelecypods

*Anadara baughmani* Hertlein, 1951  
*Cuspidaria ornatissima* (Orbigny, 1846)  
*Eucrassatella speciosa* (A. Adams, 1852)  
*Laevicardium fiski* Richards, 1954

#### Pelecypods

*Anadara mazatlanica*  
*Cuspidaria pectinata*  
*Eucrassatella gibbosa rudis* (*Crassatella*)<sup>1</sup>  
No equivalent at this depth<sup>2</sup>

<i>Lyropecten subnodosus</i> (Linné, 1758)	No equivalent at this depth <sup>2</sup>
<i>Microcardium transversum</i> Rehder and Abbott, 1951	<i>Nemocardium centifilosum</i> ( <i>Microcardium</i> )
<i>Nuculana jamaicensis</i> (Orbigny, 1842)	<i>Nuculana laevis</i> <i>radius</i>
<i>Pecten papyraceus</i> (Gabb, 1873)	No equivalent in eastern Pacific
<i>Pitar cordata</i> (Schwengel, 1951)	<i>Pitar catharius</i>
<i>Poromya granulata</i> Nyst and Westendorp, 1839	<i>Cyathodonta dubiosa</i> ?
<i>Solecurtus sanctaemarthae</i> (Orbigny, 1853)	<i>Solecurtus broggii</i> Pilsbry and Olsson, 1941 <sup>1</sup>
<i>Trigoniocardia media</i> (Linné, 1758)	No equivalent at this depth <sup>2</sup>
<i>Verticordia ornata</i> (Orbigny, 1846)	No equivalent at this depth <sup>2</sup>
Gastropods	Gastropods
<i>Conus clarki</i> Rehder and Abbott, 1951	<i>Conus arcuatus</i>
<i>Distorsio mogentyi</i> Puffer and Emerson, 1956	<i>Distorsio constrictus</i>
<i>Muricopsis hexagona</i> Lamarck, 1822	<i>Ocenebra slooti</i>
<i>Polystira albida</i> (Perry, 1811)	
(= <i>Pleuroliria</i> )	<i>Pleuroliria oxytropis</i>
<i>Sconsia striata</i> (Lamarck, 1816)	No equivalent in eastern Pacific
<i>Turritella exoleta</i> (Linné, 1758)	No equivalent at this depth <sup>2</sup>
Echinoderms	Echinoderms
<i>Astropecten duplicatus</i> Sladen	<i>Astropecten californicus</i>
Crustaceans	Crustaceans
<i>Rhaninoides louisianense</i> Rathbun	No equivalent at this depth <sup>2</sup>

<sup>1</sup>) These species were collected alive from this environment in a series of samples collected by JOSEPH R. CURRAY in November, 1961. All were analyzed, but not included in computer data.

<sup>2</sup>) The twin of the Gulf of Mexico species was taken in either slightly less or slightly greater depths.

It is significant that the major offshore shrimp grounds (HILDEBRAND, 1954) are located on silty clay bottom in depths of 75 to 126 meters (40 to 65 fathoms) in both Gulfs. Preliminary observations of the shrimp grounds in the Gulf of Thailand (JØRGEN KNUDSEN, personal communication) also indicated about the same invertebrate composition for similar depths. In all probability, shrimp (Penaeid) grounds in sub-tropical and tropical regions throughout the world have a similar composition where the invertebrate genus or sub-genus is concerned.

Most of the lamellibranch species found on the clayey bottoms of the outer shelf are thought to be deposit feeders or suspension feeders subsisting upon organic material occurring close to the bottom. The majority of the gastropods are predators. Those species which are not predators are in the family Calyptraeidae, and are epifaunal in habitat. The feeding type



composition is therefore exactly as suspected for a deep water fine sediment bottom and as found by SAVILOV (1961). The majority of the mollusks examined from this habitat were found to have a pelagic larval development, which would tend to produce a rather widely dispersed population over this uniform environment.

#### VII. Outer Shelf, 66 to 120 Meters, Sand Bottom, Northern Gulf:

BUCHANAN (1958) described an outer shelf community, designated as the "offshore coarse sand community", which in terms of environmental factors and faunal composition is quite similar to the Gulf of California outer shelf sand bottom environment. While in the Gulf of California, the sand-sized particles are mostly of terrigenous origin, BUCHANAN's coarse sand deposits are calcareous in nature. Both sand deposits are probably end results of the Holocene lowered sea level. Buchanan's characteristic and abundant animals, a solitary coral, *Caryophyllia*, large numbers of small tectibranchs, and another large Foraminifera, are either very rare or not found at all in the equivalent Gulf of California environment. Some of the rather scarce mollusks which Buchanan found in the coarse sand community do have their equivalents in the Gulf of California at the same depths. He found *Eucrassatella*, *Phos*, *Cardium*, two species of *Corbula*, *Nassarius*, two species of *Calliostoma*, *Pleuroliria*, *Pitar*, *Nuculana*, and a species of *Pecten*, all of which closely resemble the species of the same genera found on the outer shelf of the Gulf of California. Temperatures for these depths off Accra, Ghana are from 14° to 16°C. — about the same as those for equal depths in the Gulf of California. Since both sediment type and bottom temperature range are similar in depths of about 65 to 120 meters in both regions, it is not too surprising that there is such a similarity of faunas as well.

No exact counterparts of this assemblage is known from other parts of the world, since uniform terrigenous sand deposits are relatively uncommon, except where deposition has been slow for a long time, and sands remain uncovered at fairly great depths. The composition of the fauna in this environment is very patchy (unlike the populations on the southern clayey bottoms), and few mollusk species were taken more than twice out of 18 stations. The crustaceans were by far the most abundant invertebrates and many were taken at four or five stations. Unfortunately, most of the crustaceans were also collected at depths both offshore and inshore of the outer shelf region, and thus are poor indicator species. In many ways, the Tiburon outer shelf region is a transition area rather than a

distinct entity. The breakdown of the thermocline in this environment because of intense turbulence and upwelling may contribute substantially to the transitional nature of this assemblage. The majority of pelecypod species are suspension feeders, while 80% of the living gastropods are predators. A few of the gastropods species and about half of the lamelli-branches seem to have a pelagic larval development, which again is transitional in larval development types between shallow and deep waters.

#### VIII. Northern Gulf Basins and Troughs, 230 to 1,500 Meters:

No detailed studies have previously been carried out in any other region with these peculiar environmental characteristics. Somewhat similar environments may exist elsewhere, for instance the Red Sea, with its great depths and warm bottom temperatures (21 to 23°C.) and high bottom oxygen. However, apart from FUCHS' (1901) discussion of the "Pola" expedition, the present author knows of no comprehensive study of the fauna of the deeper parts of the Red Sea. Surprisingly, the benthic fauna from 300 to 2,190 meters in the Red Sea was composed of typical bathyal species resembling those found in the southern Gulf of California. Since bottom temperatures are so high in the deep parts of the Red Sea, there seems to be little reason for vertical stratification of animals. The lack of at least some shallow-water species at these depths is also puzzling. One also wonders how these typical bathyal species of invertebrates and fish were able to cross the shallow entrance to the Red Sea from the Indian Ocean. This may be one instance of pressure being a limiting factor to distribution. BALDI (1961) has described a Miocene fauna from Hungary which he presumes had lived in an environment similar to that found in the Gulf of California northern basins and troughs. A few of the genera reported by Baldi, such as *Surcula*, "*Gemmula*", *Amusium*, a giant *Dentalium* and *Bathytoma* (?) do occur at bathyal depths elsewhere and appear to superficially resemble those mollusks taken at bathyal depths in the Gulf of California. It may be hazardous, however, to state that Baldi's *Nassa-Pleurotoma* clay represents the same environment as the northern Gulf basins. More likely equivalents may appear in the Southern California and Venezuelan Tertiary basins.

It is significant that none of the living species of mollusks from the northern basins, and especially those from the 1,500 meter deep channels, have ever been found as part of the lower bathyal or abyssal fauna elsewhere. None of these species can be considered deep water species, the majority having been found previously in shelf depths. Additional species of mollusks were taken from the deep channels by DURHAM (1950) on the

"E. W. Scripps" cruise in 1941. The majority of DURHAM's collection consisted of either new species (not taken alive) or were considered as fossils. Even though the depths of these channels are thought of as abyssal, none of the mollusk species collected in this or DURHAM's study were listed in CLARKE's (1962) tabulation of abyssal mollusks of the world.

The problem of explaining the presence of the Californian Province mollusks, cited previously for the northern Gulf basins, is a difficult one, although a hypothesis is presented here. Most of these cold, shallow-water species were actually collected from several shelly-sand layers in large-diameter piston cores which were taken from the center of Tiburón basin. Present bottom water temperatures in this basin range from 11 to 14°C. These temperatures are about the same as those found during most of the year on the continental shelf off California. Some of these same species were also collected as sub-fossils in between 200 and 800 meters off Cape San Lucas, Baja California. It is possible that these cold, shallow-water species of mollusks entered the Gulf of California around Cape San Lucas during the colder parts of the Pleistocene and during lowered sea level. A few shallow-water (although more tropical) species of shells were dredged at the edge of the shelf off San Blas, Nayarit in 110-115 meters (62 fathoms). These shells were dated by the C-14 method by GEORGE BIEN of Scripps Institution. They gave ages between 17,000 and 19,000 years B.P. (CURRAY, 1962). These dates furnish some proof that sea level was at least 100 meters lower than at present in the Gulf of California. If the sea level were to be lowered 100 meters in the Gulf of California at the present time, there would be virtually no continental shelf up to Tiburón Island. However, a shelf with depths of 15 to 150 meters would exist in the northern Gulf. During early Holocene times, the northern Gulf would have provided the primary environment for the settlement of any California shelf species which might have invaded the Gulf during lowered sea level migrating slowly northward on what narrow shelf areas that may have existed. Since the northern Gulf deep-water bottom temperatures are now approximately the same as those that might have existed in shallow-water during the Pleistocene, and equal to those now present on the shelf off California, a number of cold-water mollusk species could survive. The fact that some of these cold-water species were taken alive during this study substantiates this hypothesis. The majority of the Pleistocene populations perished, contributing to the shelly deposits now buried under a few feet of recently-deposited clay in the northern Gulf.

Owing to the peculiar physical conditions in the northern deep basins

and troughs, the analysis of the feeding types of the animals living in this environment is of some interest. As there were so few living species collected, it will be difficult to give a true assessment of the dominant feeding types. All of the pelecypod species are deposit feeders, the single gastropod is a predator, the two echinoids are non-selective deposit feeders, the three scaphopods are deposit feeders and the eight coral species are probably predaceous suspension feeders. The feeding types among the shallow-water dead shell species found in the deep troughs consisted entirely of suspension and algae feeders—the dominant feeding type found on the intertidal rocky shores at the edges of these channels. The California Province mollusks found as dead shell in the basins consisted of 80% deposit feeders, and 12% were designated suspension feeders, giving some indication that they must have lived in a detritus-rich clay bottom environment.

#### IX. Upper Slope, Central and Southern Gulf, 121 to 730 Meters:

The list of invertebrates for this environment is typical of bathyal depths, and two species of mollusks found in this study, the pelecypod, *Nucula cardara*, and the scaphopod, *Cadulus californicus*, were even reported from abyssal depths in a list of all known abyssal mollusks compiled by CLARKE (1962). Bottom water temperatures in this portion of the Gulf are normal for bathyal depths, ranging from 11° or 12°C. in the upper parts to about 4° or 5°C. in the lower or deeper portions. Oxygen concentrations are very low at these depths in most of the Gulf (fig. 6), ranging from 1 ml/L. in the shallower portions to less than .05 ml/L. in the 300 to 500 meter zone, increasing slightly to .5 ml/L. at depths of 700 to 800 meters. Very few living organisms were taken in the low-oxygen portions of the upper slope, and several regions were completely devoid of life, even though trawls and dredges brought up large amounts of wood and undecayed organic matter (GOLDBERG and PARKER, 1960). The only animals which could be considered at all common in this zone were several species of Stomatopod shrimp (*Squilla*), and at times tremendous numbers of *Pleuroncodes planipes* and *Munida*, both Galatheid shrimp. It is suspected that all of these shrimp are probably carrion feeders and thus should find food plentiful in this region where organic decay is very slow. It is of interest that VINOGRADOV (1953) stated that both *Squilla* and *Pleuroncodes* are high in phosphate content, especially in the form of the mineral, apatite, the principal mineral found in phosphatized wood taken in this



environment (GOLDBERG and PARKER, 1960). Not only is oxygen almost non-existent in portions of the upper slope environment, but phosphate concentrations are exceedingly high, reaching saturation point. This correlation between high phosphate in the organisms and the environment is therefore not too surprising.

Two other invertebrates were abundant in the upper portions of the "oxygen-minimum" zone off Baja California in the Pacific Ocean, a gastropod, *Nassarius miser*, and a holothurian, *Cucumaria chilensis*. *Pleuroncodes* occurred in such abundance at these localities that they created the effect of a red sea at night. Trawling beneath these large surface concentrations of *Pleuroncodes* produced an abundance of casts and partially decayed individuals (BOYD, 1963). It is possible that the decay of these tremendous populations of Galatheids depletes the oxygen in this zone and also provides the organic matter for the large numbers of *Nassarius* and holothurians on the bottom.

There are no comparable studies of the bathyal assemblage as a whole in the literature, although bathyal invertebrates have been collected by many expeditions and discussed in monographs for almost every phylum. DALL (1886, 1889, 1890 and 1908) discussed at great lengths the mollusks collected from both bathyal and abyssal depths along the Atlantic and Pacific coast of the Americas. There are also many papers in existence on other invertebrate groups from bathyal depths, resulting from the various cruises of the American fisheries vessel, Albatross. It is too difficult, at the moment, to attempt a compilation of all the species by station, in order to determine the assemblages or communities found. This same drawback applies to the "Challenger", "Siboga" and other major deep sea expeditions. Even EKMAN's (1953) discussion of the bathyal fauna gives little indication of the association of animals to be found. He also confined his treatment to north Atlantic depths, where the fauna has little resemblance to that found in tropical bathyal regions. SPÄRCK (1951) took several quantitative grab samples at lower bathyal to abyssal depths off West Africa but did not list the species.

Even though the majority of the species of animals in this environment are deposit feeders or scavengers (on the basis of anatomy), 26% of the species can be classified as suspension feeders, a rather high percentage for these depths. This relatively high percentage of suspension feeders probably subsist on the rain of organic matter resulting from the high primary production in the surface waters of this zone. The high primary production on the surface seems to be one of the major causes of the "oxygen-minimum" zone, since blooms are often found overlying strong



thermoclines, which often follow a period of intense upwelling. Dissolved oxygen in the water column below the thermocline is rapidly depleted by the oxidation of the organic debris (resulting from the death of the bloom) as it falls to the bottom. Even so, much of the organic matter does reach the bottom unchanged, thereby providing food for the detritus feeders and scavengers living there.

Virtually nothing is known concerning the larval development and reproduction of the mollusks living in the upper bathyal regions. A preliminary examination of the prodissoconchs of some of the lamellibranchs by W. K. OCKELMANN and the author indicated that at least some of them have a lecithitrophic development and probably no pelagic veliger or feeding stage. OCKELMANN (1958 pp. 243-45) has shown that the number of non-pelagic larval species of lamellibranchs increase rapidly from Boreal to Arctic waters, while THORSON (1944) indicated that none of the species of prosobranch gastropods investigated by him in the Arctic had a pelagic development. According to a preliminary analysis of the Gulf of California data, a similar phenomenon occurs in the Gulf where the number of species of mollusks having a pelagic larval development decreases with increasing depth. Similar observations were also reported by THORSON (1950, pp. 26-28). Since bottom water temperatures approach Arctic values as one descends into abyssal depths, and food becomes less plentiful, it would seem that temperature and availability of food may influence the distribution of mollusk species with non-pelagic larval development.

#### X. Middle Continental Slope, 731 to 1,799 Meters:

The mid-slope assemblage is a typically deep-sea one, composed entirely of lower bathyal and upper abyssal fauna. Three of the eight species of mollusks taken in this environment were listed as abyssal by CLARKE (1962) and all of the genera are primarily abyssal in distribution. Bottom water temperatures (3 to 6°C.) are partly in the abyssal range, according to the description of the abyssal environment given by MADSEN (1961). There seems to be no real dividing line between abyssal and bathyal, based on depth or temperature alone. Whether a fauna in any region is bathyal or abyssal depends upon many circumstances. For instance, depth is not a valid limiting factor, when one considers the fauna of the deep isothermal basins, such as the Red Sea, Ballenas Channel in the Gulf of California, and the Sulu Basin. These areas have what have been called abyssal depths, but are characterized by high outer shelf temperatures at the bottom. Likewise, the Arctic and Antarctic regions have abyssal

temperatures of  $1^{\circ}$  to  $2^{\circ}\text{C}$ ., but in many places depths of much less than 2,000 meters. If depth or pressure were the determining factor, then animals normally found in the middle continental slope environment depths should also occur at similar depths in the northern basins of the Gulf of California. On the contrary, a fauna of much shallower water but known previously from equivalent bottom temperatures was found. If temperature is the primary limiting factor, why do many of the Arctic and Antarctic bottom faunas remain mostly near the poles? Relatively few Arctic species are ever found on the abyssal sea bottom, south of  $30^{\circ}$  north latitude, nor are Antarctic species found north of  $30^{\circ}$  south latitude, even though bottom temperatures typical of shallow polar waters extend over most of the abyssal sea floor.

No community or ecological studies concerned primarily with this particular environment are known from the literature. Numerous collections have been taken on the slope and many species have been described from these depths, but as in the upper slope environment, a synthesis of this material is difficult. The best descriptions of partial assemblages of the middle continental slope environment can be found in the narratives of the Challenger (MURRAY, 1895, and MOSELEY, 1880), Albatross (TOWNSEND, 1916), Siboga (WEBER, 1902), Swedish Albatross (NYBELIN, 1951), and Galathea (BRUUN, GREVE and SPÄRCK, 1956, and MADSEN, 1961) Expeditions.

All but five of the mollusk species collected alive from this environment are deposit feeders. The four octocorals may be considered suspension feeders, although the term predator might be a better classification. No attempt was made to classify the crustaceans as to feeding types, although the shrimp living just off the bottom and the large decapod crabs are probably predators or scavengers. The fact that some suspension feeders exist at these relatively great depths is not too surprising, since surface production is still rather high over this portion of the slope, at least along the Middle American coast. No estimate can be given of the larval development of the mollusks taken in this environment. NATLAND (1933) described a Pliocene deep sea fauna from southern California Tertiary basins. A few mollusk species related to those occurring in this assemblage have been found in Miocene and Pliocene formations of the West Coast of North America (GRANT and GALE, 1931), and the Pliocene of Costa Rica and Panama (OLSSON, 1942), so that this assemblage may still have some use in paleoecological interpretations, even though this environment is considered too deep for most geological formations containing abundant fossil material.

# XI. Abyssal Southern Borderland Basins and Outer Continental Slope, 1,800 to 4,122 Meters:

This is not only the deepest of environments studied in the Gulf of California and along the West Mexican coast, but it is also one of the most fascinating especially with regard to the types of creatures living there. The majority of deep-sea expeditions have concentrated on the more accessible upper slope regions, or the true abyssal sea floor and deep trenches. For instance, the Galathea Expedition (BRUUN, 1959) concentrated on the deeper parts of the oceans, particularly the trenches and the abyssal and hadal depths below 6,000 meters. The Russian expeditions, using the Vityaz and Ob (FILATOVA, 1959; ZENKEVITCH, *et al.*, 1959; and ZENKEVITCH and BELJAEV, 1955) also carried out most of their sampling on the great abyssal plains or at hadal depths in the trenches. The American Albatross concentrated more on slope than did any of the other expeditions, since they were originally interested in marine resources which were close enough to shore to be utilized by man.

Even though the lower portions of the continental slope off most continents are characterized by so-called abyssal depths and temperatures (2,000 to 4,000 meters, and 1° to 2.5°C.), the richness and complexity of the faunas are not duplicated anywhere else in the deep sea, and in many cases not even on the continental shelf. An example of the richness of fauna from the continental slope region off Central America is given by WOLFF (1961) in a partial list of one trawl haul taken off Panama and Costa Rica. This was the richest deep sea haul ever made, although similar rich hauls were taken with smaller gear by the present author off Mexico. Several of these hauls produced almost as many individuals and were of nearly the same composition as Galathea Station 716. For instance, two 3-meter Agassiz beam trawl hauls were taken during this study in from 2,000 to 4,000 meters off Baja California in June, 1961, and each contained between 100 and 300 kilograms (200 to 600 pounds) of one species of Macrourid fish alone. Plates XI–XV illustrate the benthic life in the region within a few miles of the Beam Trawl stations of the present study. On the average, otter trawls taken on the lower slope off Mexico produced much larger catches per hour on the bottom, than trawls taken with the same gear in depths of 50 to 100 meters.

There are several reasons why the standing crop of benthic invertebrates and probably vertebrates is so high on the lower continental slope and borderland basins. One of these is that the slope is, morphologically, closely associated with the continental land masses and thus still close enough to shore to be affected by coastal surface productivity. Many of

the deep coastal basins are beneath major upwelling areas, with their high surface production and associated great accumulation of bottom organic matter. Continental shelves along the west coast of the Americas are very narrow and, because the continental slope drops off very sharply, numerous slumps and turbidity currents occur which transport shelf organic debris to abyssal depths.

It was hypothesized by PARKER (1961) that the competition and evolution of many new forms during the early Tertiary forced many of the older forms of animal life deeper down into the newly-formed trenches and borderland basins which were as yet unoccupied by present-day animal life. It is suspected that present day forms were absent from these great depths at that time, because recent geological and geophysical evidence suggests that many of the present deep ocean basins are relatively young, and most of the major trenches of the world are thought to have been formed only since early Tertiary times (PARKER, 1961). The major abyssal plains of the central Pacific are still comparatively devoid of animal life (FILATOVA and LEVENSTEIN, 1961; and AGASSIZ, 1905), which may also be related to the virtually barren surface waters over these basins. The relative youth of the trenches is substantiated by the fact that each trench seems to have its own endemic fauna (ZENKEVITCH and BIRSTEIN, 1960), most of which have evolved either from Tertiary shallow water forms, or have differentiated rather recently from older animals which had already migrated on to the continental slope prior to the Tertiary.

In WOLFF's (1961) paper on the description of the animals from one *Galathea* station (716) off Costa Rica in 3,570 meters depth, he lists 54 species of invertebrates. From a composite of stations taken in equivalent depths between Baja California and Guatemala during this study, 86 invertebrate species have been identified (pages 186-87). A number of faunal groups were identified in WOLFF's paper, but were not identified in this study and vice-versa. Although sponges, actinarians, polychaetes, asteroids and ophiuroids (identified in WOLFF's paper) were taken in large numbers in this study, most have not yet been identified by specialists. Likewise, WOLFF has not yet received identifications for brachiopods and soft corals which were identified in the present list. Only twelve species of invertebrates were taken in common by both sampling programs, of which five were mollusks, two pycnogonids, two holothurians, one ophiuroid and two echinoids. WOLFF reports one species of fish from Station 716 and indicates that other species were also taken. Fish were abundant in the present samples, most of which have been identified by CARL L. HUBBS and RICHARD ROSENBLATT of Scripps Institution. Other descriptions of



abyssal fauna on a single catch basis can be found in MURRAY (1895), WEBER (1902), NYBELIN (1951), ZENKEVITCH, *et al.* (1955), BRUUN (1957), SUEHIRO, *et al.* (1960) and WOLFF (1960).

As is to be expected, the majority of the species of animals living in the abyssal borderland and slope environment are deposit feeders, most of which are mollusks and echinoderms. Nothing is known concerning reproduction of these species. Further research on deep sea animals should now be concentrated on the biology of these animals, rather than zoo-geography, but this will necessitate far more sophisticated sampling techniques than are now available.

A check was made as to the abyssal character of the molluscan species taken in this environment, by using CLARKE's (1962) compilation of abyssal mollusk records from the literature. Altogether, 27 species of mollusks were identified from the lower slope and southern borderland. Of these, 18 were listed as abyssal by Clarke. Those species not considered new have also been taken in slightly shallower depths, but farther north, and would still be considered abyssal on the basis of temperature. The majority of the other invertebrates have been collected only in abyssal depths, indicating the true abyssal character of this assemblage.

Surprisingly enough, elements of this same abyssal assemblage have been reported from Pliocene sediments in Costa Rica, Panama and Ecuador (OLSSON, 1942). Typical abyssal and bathyal genera, sub-genera and species of mollusks, directly related to forms taken in depths of between 500 and 3,000 meters on the adjacent slope were well-preserved in dark shales and sandstones, which must have been uplifted several thousand feet.

## XII. California Borderland Basins, 1,641 to 2,358 Meters:

As mentioned previously, the differences in the fauna of the northern basins along the California coast seem to be sufficient to constitute a different assemblage, partly abyssal in nature. Of the mollusks found in this environment, CLARKE (1962) reports only 8 of the 25 species as being abyssal. The rest have been reported as either bathyal or as Arctic shelf species. It was also observed that most of the fish taken from the California borderland region were either shallower water species or had previously been taken on the continental shelf of the northern and north-western Pacific (HUBBS, personal communication).

It is puzzling as to why the California borderland basin assemblage is so different from that found at equivalent depths to the south, since temperature, oxygen and sediment conditions are similar in both areas. The only feasible explanation for this separation of faunas is that the



California basins (probably formed during the middle Tertiary [EMERY, 1960]) have been occupied by a northern rather than a southern migration of benthic animals. The Mexican basins and slope, on the other hand, seem to have been occupied by a migration to the north from the Tropics. Barriers separating the northern and southern borderland exist as shallow ridges cutting transversely across the slope into Baja California (KRAUSE, 1961 and in press). These ridges may serve to separate the migration of animals from both directions. There is also some evidence from unpublished deep current studies that the bottom waters along the coast of California may move in a general southern direction, thus inhibiting larval transport on the bottom from south to north. A thorough study of the oceanography, geology and a summary of the biology of the Southern California borderland basins can be found in EMERY (1960). HARTMAN and BARNARD (1958) have written a more detailed study of the faunas of the somewhat shallower borderland basins, which are quite different from those studied in this paper. The inner basins have very shallow sills, which severely limit the bottom oxygen concentrations, thus benthic invertebrates are often lacking or very scarce. None of the benthic species of invertebrates found by Hartman and Barnard in the inshore basins were taken in this present study, even though some of their samples were taken in over 1,000 meters.

An analysis of feeding types produced a predominance of deposit feeders and scavengers, as should be expected at these depths. Of the 37 species of invertebrates identified and listed previously in the discussion of the assemblages, 15 are deposit feeders, five probably scavengers, 14 are mobile predators, two are considered suspension feeders and one a fixed predator. The feeding composition, then, is about the same as that determined for the abyssal assemblage to the south. The majority of the gastropods from this environment are Buccinids, which are known to have direct development from egg capsules, and all but one of the lamellibranch species seem to have a lecithitrophic or non-pelagic development as well.

### Summary and Conclusions

The data obtained in this study have made it possible to describe some of the major benthic invertebrate communities or assemblages on the continental shelf of an unusual subtropical to tropical region and have also provided information as to the composition of some deep sea assemblages. Seldom before, has there been an opportunity to investigate the degree of association between such a large number of species (1,150) and stations (272) for such a great variety of marine environments. The existence of a

large body of data for a number of ecological factors has enabled the author to explain some of the vagaries of faunal distribution within this interesting region, based both on the distribution of the abundant animals and the boundaries of the physical-chemical factors. The biology (development and feeding habits) of some of the components of these assemblages has been superficially investigated, offering a few more parameters to help explain marine invertebrate distribution. Finally, various events in the past (the geological factors) have afforded yet a few more explanations for the "whys" of animal zoogeography.

In all, 12 distinct assemblages of benthic invertebrates, based on the close association of the most numerous and characteristic species, and also representing 12 environments or major habitats, were found in the area included in this study. This region encompassed the west American coast from San Francisco, California to Guatemala, and included the entire Gulf of California. These 12 assemblages have a few abundant species but were generally characterized by a great diversity of species and relatively few individuals of any one species. The 12 environments which have distinctive assemblages of invertebrates are:

- I. Intertidal rocky shores.
- II. Intertidal sand-beach and sand-flats to 10 meters.
- III. Low-salinity lagoon and mangrove mud flats.
- IV. Nearshore, sand and sand-mud bottom, 11 to 26 meters.
- V. Intermediate shelf, 27 to 65 meters.
- VI. Outer shelf, 66 to 120 meters, clay bottom, southern Gulf.
- VII. Outer shelf, 66 to 120 meters, sand bottom, northern Gulf.
- VIII. Northern Gulf basins and troughs, 230 to 1,500 meters.
- IX. Upper slope, central and southern Gulf, 121 to 730 meters.
- X. Middle continental slope, 731 to 1,799 meters.
- XI. Abyssal southern borderland basins and outer continental slope, 1,800 to 4,122 meters (limits of sampling depths).
- XII. California borderland basins, 1,641 to 2,358 meters.

Many of these environments and their assemblages have counterparts in other parts of the world, although few benthic ecological studies have been carried out in tropical and sub-tropical areas of comparable richness. Those environments investigated elsewhere are: the intertidal rocky shore; intertidal sand flats; low-salinity lagoons; nearshore shelf, intermediate shelf, outer shelf on clay and sand bottom, upper slope, middle slope and abyssal slope. Those with no exact known counterparts in the world are: the northern Gulf basins and California borderland environ-

ments. A diagram illustrating the relationship of these assemblages to the geomorphology of the sea bottom and surrounding land masses is shown in fig. 27.

The average standing crop of benthic invertebrates for the inshore assemblage appears low as compared to that found for quantitative studies carried out in temperate or boreal regions. Since so few quantitative studies have been made elsewhere in the tropics and the area covered quantitatively in this study is so small, a comparison between the Gulf of California and other tropical regions is difficult.

Evidence was produced from a comparison of shelf assemblages found off the Pacific coast off Mexico and in the Gulf of Mexico that a large number of twin or allopatric species of mollusks are present at certain preferred depths and on specific sediment types. These almost indistinguishable "twin" species are presumed to have descended from single common species which moved freely between the Atlantic and Pacific Oceans across submerged portions of Middle and South America during Miocene and Pliocene times. Since the "twin" species now occupy exactly the same environment on each side of the Middle American land mass, it is hypothesized that the original Mio-Pliocene species also lived in similar environments. This phenomenon is most evident in the intermediate shelf sand bottom, 27 to 65 meters, and outer shelf, clay bottom, 66 to 126 meters environments. For this reason, it is suspected that at some time the marine connections across Middle America must have been in depths of at least 27 to 120 meters, with certain areas covered continuously with sand and others with silty clay. Few "twin" species were found below 120 meters, although a number of cosmopolitan deep-water species were taken at depths below 1,000 meters.

An analysis of feeding types (mostly of mollusks) for the various assemblages indicated a close relationship between feeding type and bottom character, as well as other factors in the marine environment. In general, a larger number of suspension feeders, along with an equally large number of predators, are found on well-sorted sands and silts, especially in the shallower waters. The deposit feeders and scavengers usually outnumbered other types on poorly-sorted sandy mud and deeper silty clay sediments. Certain areas below the euphotic zone were still occupied by fairly large numbers of suspension feeders. These areas are also characterized by very high surface plankton production and at times considerable turbulence. These factors may allow suspension feeders to utilize as food, the suspended organic matter resulting from the high surface production.

Finally, this study has produced a few more parameters for paleoeco-

logical interpretation, especially the deeper environments. These criteria may be useful in interpreting the environments of deposition of ancient basins and continental slopes. The living assemblages found both in the shallow and deeper waters closely resemble those found in Tertiary deposits around the Gulf of California, in Central America and in the Caribbean region. The use of computer filing and analysis as used in this investigation may facilitate the interpretation of modern as well as ancient environments.

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### Appendix: List of Stations

Stat. No.	Date	Time + 7 from to	Depth m. from to	Latitude	Longitude	Temp. °C.	Oxyg. ml/L	Sed. type	Device
1	2/ 3/59	1940	15	23°12.8'	106°29.7'	15.0	3.0	1	57
2	7/ 3/59	1829	45	24°18.0'	107°50.0'	15.0	3.0	75	52
3	8/ 3/59	0535	2710	23°58.4'	108°59.5'	2.0	2.0	72	82
4	10/ 3/59	2100	4 7	24°13.5'	110°18.5'	22.0	3.0	1	59
5	13/ 3/59	1200	4 7	25°21.3'	108°51.7'	24.0	3.0	1	57
6	17/ 3/59	2133	68	26°32.2'	109°36.8'	12.0	3.0	1	59
7	22/ 3/59	1200	7 9	25°52.5'	109°27.5'	24.0	5.0	71	52 59
8	25/ 3/59	1109	23	27°06.0'	112°00.0'	22.0	4.0	1	57 59
9	26/ 3/59	1805	13	27°20.5'	112°16.0'	22.0	3.0	1	59
10	30/ 3/59	1830	135 183	27°42.0'	112°37.5'	13.0	3.0	1	59
11	31/ 3/59	1425	11	27°46.4'	112°42.1'	22.0	4.0	1	59 57
12	31/ 3/59	1746	73 78	27°54.5'	112°45.2'	22.0	3.0	1	59
13	1/ 4/59	0245	33	28°25.0'	112°03.1'	11.0	3.0	1	59 57
14	1/ 4/59	0510	13	28°31.5'	111°54.0'	15.0	4.0	1	57
15	1/ 4/59	1455	13	28°11.7'	112°48.2'	22.0	4.0	1	57
16	1/ 4/59	1645	22	28°18.0'	112°52.0'	22.0	4.0	1	57
17	1/ 4/59	2142	31	28°43.5'	112°18.0'	15.0	3.0	1	52 59
18	2/ 4/59	1954	402	28°51.0'	112°37.2'	12.0	3.0	1	51 59
19	2/ 4/59	2210	421	28°44.2'	112°48.5'	8.0	2.0	1	51
20	3/ 4/59	1430	735	28°08.1'	112°16.0'	4.0	.5	1	52
21	5/ 4/59	1410	25	28°56.0'	113°33.8'	22.0	4.0	1	57 59
22	6/ 4/59	1145	13	29°16.0'	113°17.0'	15.0	2.3	1	57 59
23	6/ 4/59	1707	92	29°32.7'	112°45.1'	16.0	2.4	1	59
24	6/ 4/59	1855	23	29°39.2'	112°34.5'	16.0	2.5	1	57 59
25	8/ 4/59	0453	33	30°19.3'	112°54.3'	19.0	4.0	1	51
26	8/ 4/59	2310	23	30°56.0'	113°16.8'	20.0	4.7	75	57
27	9/ 4/59	0030	64	30°52.0'	113°26.0'	22.0	3.6	73	51
28	9/ 4/59	1020	25	30°05.2'	114°36.0'	21.0	3.3	1	51 57
29	10/ 4/59	1010	27	31°07.1'	114°38.2'	20.0	4.2	74	57 59
39	20/ 3/59	1710	1828	22°48.1'	110°11.2'	2.0	2.0	4	77
40	21/ 3/59	2100	1340 366	22°48.2'	109°47.4'	2.3	2.5	77	63
41	22/ 3/59	0712 0845	2790 2817	22°32.2'	109°43.0'	1.5	2.0	72	74
42	26/ 3/59	0840 1400	2622 2715	22°35.6'	110°06.5'	1.5	2.0	72	74
43	27/ 3/59	0600 0700	366 212	22°48.0'	109°44.5'	11.0	1.0	5	78
44	27/ 3/59	1500 1630	366 512	22°51.5'	109°41.3'	10.0	.5	77	78
45	28/ 3/59	1131 1254	330 340	23°00.1'	109°35.7'	12.0	2.5	6	78
46	28/ 3/59	1745 1750	54	23°48.0'	109°40.5'	21.0	3.0	1	68

(continued)

## Appendix: List of Stations (continued)

Stat. No.	Date	Time +7 from to	Depth m. from to	Latitude	Longitude	Temp. °C.	Oxyg. ml/L	Sed. type	Device
47	29/ 3/59	0750 0810	64	24°09.5'	109°48.0'	21.0	3.0	12	68
48	31/ 3/59	2300	2	24°41.5'	110°22.6'	23.0	4.0		79
50	1/ 4/59	0710 0715	92 119	25°26.0'	109°24.0'	10.0	2.0	72	68
51	1/ 4/59	1900	17	25°31.5'	109°13.5'	24.0	3.0	1	77
52	2/ 4/59	0110 0230	2141 2251	25°22.0'	110°00.0'	2.0	1.0	72	74
53	2/ 4/59	1034	920 272	25°31.8'	109°22.8'	12.0	2.0	71	78
54	2/ 4/59	1205	165 137	25°29.3'	109°24.3'	9.0	2.0	72	68
55	4/ 4/59	0115 0125	37	27°45.0'	112°38.5'	18.0	3.0	1	68
56	4/ 4/59	0125 0135	69	27°45.0'	112°38.5'	15.0	3.0	1	68
57	4/ 4/59	0135 0145	64	27°45.0'	112°38.5'	18.0	3.0	1	68
58	5/ 4/59	1240	460	28°37.2'	113°02.5'	13.0	1.4	10	63
59	6/ 4/59	0904 1014	595 515	28°39.7'	113°02.5'	13.0	1.3	10	63
60	6/ 4/59	1200	1182	28°55.2'	113°12.4'	12.0	1.6	2	51
61	7/ 4/59	1340	662 405	29°04.7'	113°20.1'	12.0	.9		78
62	8/ 4/59	1245 1330	532 625	29°18.0'	113°39.9'	12.0	1.0	1	63
63	8/ 4/59	1605 1800	549	29°25.4'	113°45.0'	14.0	1.0	1	78
64	8/ 4/59	1025	92	29°30.5'	113°27.0'	19.0	3.0	1	71
65	9/ 4/59	0145	320	29°28.0'	113°02.0'	12.0	1.9	4	74
66	9/ 4/59	0730	420	28°53.8'	112°54.8'	11.0	1.1	1	53
67	9/ 4/59	1900	396	29°06.1'	112°57.5'	11.0	1.5	1	53
68	9/ 4/59	2255	119	29°24.3'	113°19.0'	19.0	1.9	1	68
69	9/ 4/59	2340	119	29°34.3'	113°19.0'	19.0	1.9	1	77
70	10/ 4/59	0110 0125	229 110	29°24.3'	113°19.0'	19.0	1.9	1	68
71	10/ 4/59	0200 0215	73	29°20.0'	113°00.2'	13.0	2.3	12	68
72	10/ 4/59	0320 0335	132	29°24.6'	113°19.0'	12.0	2.3	12	68
73	10/ 4/59	0745	397	29°04.5'	112°54.2'	11.0	1.2	1	53
74	10/ 4/59	0900	269	29°10.8'	112°48.3'	11.0	2.3	1	53
75	10/ 4/59	1205	232	29°19.0'	112°51.8'	12.0	2.4	5	53
80	18/ 4/59	0712 1700	430	30°01.0'	113°31.0'	11.0	1.9	1	63
81	25/ 4/59	1430 1525	1433	28°40.1'	113°01.9'	11.0	1.4	6	51
82	28/ 4/59	0807 2015	109 111	30°32.0'	113°26.0'	14.0	2.0	75	63
83	28/ 4/59	1330 1500	130	29°21.0'	112°42.0'	16.0	2.4	1	63
84	9/ 5/59	2145 0400	1410 1420	22°47.5'	106°52.0'	4.0	.5	70	74
85	9/ 5/59	1121 1245	435	22°44.0'	106°33.5'	4.0	.5	72	74
86	9/ 5/59	2100 2225	2030	22°38.5'	107°08.0'	2.0	1.0	72	77
87	10/ 5/59	1545 1635	57 44	23°56.6'	107°21.8'	24.0	3.0	72	72
88	10/ 5/59	1839 1935	77 88	23°50.5'	107°22.6'	24.0	3.0	72	72
89	11/ 5/59	0015 0115	109 128	23°47.3'	107°26.0'	12.0	1.5	70	72
90	11/ 5/59	0742 1240	1370 1382	23°38.9'	107°55.8'	4.0	.5	72	72
91	11/ 5/59	1600 1715	724 738	23°54.7'	108°09.5'	5.0	.5	72	72
92	12/ 5/59	0900 0915	88	24°06.2'	107°49.1'	14.0	3.0	71	68
93	12/ 5/59	1030 1500	95	24°05.0'	107°49.2'	13.0	3.0	71	63
94	13/ 5/59	0040 0200	40 44	23°33.5'	106°50.7'	24.0	3.0	71	72
95	13/ 5/59	0220 0300	44 48	23°35.2'	106°53.5'	26.0	3.0	71	72
96	15/ 5/59	0015 0635	3001 2988	22°11.2'	107°46.1'	2.0	2.0	72	72
97	18/ 5/59	1910 2010	55	21°50.0'	106°09.4'	26.0	3.0	72	72
98	18/ 5/59	2240 2340	37 47	21°48.0'	105°51.0'	14.0	3.0	72	72
100	31/ 9/58	0900 1600	0	31°05.0'	114°45.0'	24.0	4.9	1	76
101	23/ 3/59	0900 1600	0	22°45.0'	109°40.0'	30.0	5.0	10	76
102	26/ 3/59	0900 1600	2	22°45.0'	109°40.0'	30.0	5.0	1	76
103	28/ 3/59	0900 1600	0	23°33.0'	109°23.0'	30.0	3.0	10	76
104	29/ 3/59	0900 1600	0 9	24°10.0'	109°50.0'	25.0	3.0	10	66 76
105	1/ 4/59	0900 1600	0	25°25.0'	109°25.0'	28.0	3.0	10	76

(continued)

## Appendix: List of Stations (continued)

Stat. No.	Date	Time + 7 from to	Depth m. from to	Latitude	Longitude	Temp. °C.	Oxyg. ml/L	Sed. type	Device
106	5/ 4/59	1200	0	28°32.0'	112°45.0'	21.0	3.0	1	76
107	5/ 4/59	1200	0	28°32.0'	112°45.0'	21.0	3.0	10	76
108	5/ 4/59	1400	3	28°32.0'	112°45.0'	11.0	3.0	10	66
109	7/ 4/59	0900 1030	0	28°55.0'	113°31.0'	21.0	3.0	77	76
110	9/ 4/59	2300	0	29°20.0'	113°15.0'	19.0	1.9	1	79
111	5/ 5/59	1500	5	23°10.7'	106°25.8'	14.0	4.0	1	57
112	5/ 5/59	1630	2	23°12.2'	106°25.6'	30.0	3.0	1	75
113	5/ 5/59	1100	7	23°11.2'	106°25.9'	30.0	4.0	1	57
114	5/ 5/59	1730 1745	7	23°11.1'	106°26.0'	30.0	4.0	1	57
115	6/ 5/59	0900 1600	0	23°13.9'	106°28.9'	24.0	3.0	77	76
116	6/ 5/59	0900 1600	0	23°14.0'	106°28.2'	24.0	3.0	1	76
117	7/ 5/59	1600	0	23°15.0'	106°28.8'	30.0	4.0	1	76
118	17/ 5/59	0630 1730	0 5	21°14.0'	106°20.0'	30.0	4.0	14	75 57
119	20/ 5/59	1430 1630	3	20°35.0'	105°15.0'	30.0	4.0	14	66
125	17/11/58	0420 0450	238	15°45.0'	95°40.5'	14.0	.1	72	74
126	18/11/58	0855 1130	220 238	15°17.5'	95°53.5'	14.0	.1	72	74
127	18/11/58	2056 0343	1006 1135	15°38.0'	95°18.5'	8.0	.1	72	74
128	18/11/58	1500 1625	3529 3557	14°28.0'	95°09.0'	1.5	2.0	72	74
129	20/11/58	1510 1610	320 305	14°31.0'	93°09.2'	11.0	.1	72	74
130	20/11/58	1330 1520	403	14°24.0'	93°03.0'	10.0	.1	72	74
131	21/11/58	1520 1920	3596 3642	12°20.0'	91°51.0'	1.5	2.0	72	74
132	27/ 1/59	1200	20 22	32°35.0'	117°11.1'	10.0	3.0	1	74
133	27/ 1/59	1400 1500	92	32°31.9'	117°17.5'	9.0	2.0	3	74
134	28/ 1/59	1405 1700	2013	32°39.2'	118°09.0'	2.5	1.3	10	74
135	29/ 1/59	0515 0650	1190	32°36.6'	117°35.2'	6.0	1.8	72	74
136	12/ 2/60	1940 2130	183 458	31°38.3'	116°51.4'	10.0	.5	10	63
137	13/ 2/60	1530 1700	2068 2086	31°16.4'	117°34.2'	2.5	1.3	81	71
138	15/ 2/60	2245 0100	875 1281	30°11.9'	117°37.7'	4.0	.9	5	63
139	15/ 2/60	1702 2315	2708 2763	29°40.2'	117°06.6'	2.0	2.0	8	71
140	16/ 2/60	0638 0815	549 732	29°30.8'	117°16.8'	8.0	.3	10	63
141	17/ 2/60	0926 1700	3009 3989	29°03.5'	116°41.5'	1.5	1.8	72	71
142	18/ 2/60	0430	567	29°37.0'	116°31.0'	8.0	.3	10	63
144	10/ 3/60	0050 0415	915 1858	33°36.3'	119°26.8'	2.5	1.0	72	70
145	11/ 3/60	0050 0510	1880 1936	33°40.5'	119°29.3'	2.5	1.0	72	70
146	11/ 3/60	0720 0800	1918 915	33°39.9'	119°28.2'	2.4	1.5	72	67
147	15/ 3/60	2100 2200	92 84	23°10.9'	106°35.5'	14.0	2.0	72	69
148	16/ 3/60	0945 1035	18	24°09.4'	107°25.1'	30.0	3.0	1	69
149	17/ 3/60	1100 1200	11	24°13.0'	107°26.5'	30.0	3.0	75	69
150	16/ 3/60	2015 2100	33 36	24°32.6'	108°03.0'	18.0	2.0	71	69
151	16/ 3/60	2215 2230	430 455	24°39.5'	108°01.0'	18.0	1.0	71	79
152	11/ 3/60	1026	116	22°06.7'	106°17.2'	9.0	.9	12	78
153	17/ 3/60	0200	40	24°56.0'	108°33.5'	24.0	3.0	71	78
154	17/ 3/60	0515	40	25°04.0'	108°47.5'	11.0	1.5	71	78
155	17/ 3/60	0636	33	25°07.5'	108°54.5'	11.0	2.0	72	78
156	8/ 3/60	2200 0200	236 403	21°35.0'	106°06.6'	13.0	1.0	70	69
157	9/ 3/60	2115 0100	13 22	21°46.4'	105°45.2'	30.0	3.0	13	69
158	10/ 3/60	2245 0200	53 61	22°09.0'	106°08.0'	20.0	3.0	12	69
159	11/ 3/60	2200 0220	46 57	22°30.8'	106°01.2'	20.0	3.0	1	69
160	20/ 3/60	0900 1600	0	21°55.0'	106°37.0'	24.0	3.0	1	76
161	17/ 3/60	1125	55	25°24.5'	109°18.5'	11.0	2.0	72	63
162	20/ 3/60	1200	2	28°23.8'	111°29.8'	20.0	4.0	1	76
163	20/ 3/60	1730	0	28°26.8'	111°38.7'	20.0	4.0	1	76
164	21/ 3/60	0100 0200	75 64	28°13.8'	111°46.7'	14.0	2.0	2	69

(continued)

## Appendix: List of Stations (continued)

Stat. No.	Date	Time +7 from to	Depth m. from to	Latitude	Longitude	Temp. °C.	Oxyg. ml/L	Sed. type	Device
165	21/ 3/60	1030	7 9	28°22.0'	111°31.5'	20.0	3.0	1	63
166	21/ 3/60	1415	84	28°11.5'	111°40.0'	14.0	3.0	1	63
167	21/ 3/60	1920 1930	320 310	28°02.0'	111°47.2'	11.0	.5	1	69
168	22/ 3/60	1000	201	28°10.8'	111°49.0'	11.0	1.0	1	68
169	22/ 3/60	1038	84	28°12.6'	111°47.3'	14.0	1.0	1	68
170	22/ 3/60	1515	61	28°16.0'	111°44.8'	14.0	3.0	12	68
171	22/ 3/60	1600	42	28°19.3'	111°42.3'	14.0	3.0	12	68
172	22/ 3/60	1730	13	28°23.3'	111°39.8'	20.0	3.0	12	68
173	22/ 3/60	2000	7 9	28°25.3'	111°39.0'	20.0	3.0	1	79
174	23/ 3/60	1535	61	28°11.3'	111°37.0'	14.0	3.0	1	68
175	23/ 3/60	2040	26	28°31.0'	112°04.2'	13.0	1.2	2	68
176	23/ 3/60	2155	82	28°27.8'	112°08.8'	13.0	1.2	1	68
177	24/ 3/60	0130 0145	68 70	28°25.5'	112°06.1'	13.0	1.2	1	63
178	24/ 3/60	0300	22	28°26.8'	112°00.9'	18.0	3.0	2	63
179	24/ 3/60	0900 1245	0	28°41.4'	111°55.0'	20.0	4.0	1	76
180	24/ 3/60	1430	9	28°40.5'	111°55.2'	20.0	3.0	1	76
181	24/ 3/60	1815	16	28°30.0'	111°59.5'	18.0	3.0	1	68
182	24/ 3/60	1830 1900	18	28°30.0'	111°59.5'	15.0	2.5	1	69
183	24/ 3/60	2240	18	28°30.8'	111°53.6'	15.0	3.0	1	68
184	25/ 3/60	0005	15	28°26.0'	111°55.4'	18.0	3.0	12	68
185	25/ 3/60	0100	57	28°20.9'	111°58.0'	13.0	2.4	1	68
186	25/ 3/60	0140	60 66	28°17.5'	112°00.1'	13.0	2.4	1	68
187	25/ 3/60	0230 0310	292 320	28°12.9'	112°03.2'	11.0	.3	1	68
188	25/ 3/60	0755	42	28°10.0'	111°55.2'	13.0	3.4	2	68
189	25/ 3/60	0925	28	28°20.5'	111°50.0'	14.0	3.0	1	58
190	25/ 3/60	1010	13	28°24.6'	111°48.0'	18.0	3.0	1	68
191	25/ 3/60	2100 2200	35 26	28°41.0'	112°06.0'	15.0	3.0	4	69
192	24/ 3/60	2300	15	28°49.5'	112°00.1'	18.0	3.0	1	76
193	26/ 3/60	2200	6	28°51.3'	111°58.0'	20.0	3.0	1	79
194	27/ 3/60	0822	13	28°54.9'	112°14.0'	20.0	3.0	2	68
195	27/ 3/60	0915	22	28°50.5'	112°11.0'	18.0	3.0	2	68
196	27/ 3/60	1100	24	28°45.8'	112°04.0'	16.0	3.0	1	68
197	27/ 3/60	1145	24	28°43.8'	112°09.1'	16.0	3.0	77	63
198	27/ 3/60	1335	92	28°41.6'	112°11.0'	14.0	1.5	12	68
199	27/ 3/60	1450	278	28°39.2'	112°26.4'	12.0	1.6	6	63
200	27/ 3/60	1555	298	28°39.5'	112°29.0'	11.0	1.6	78	63
201	27/ 3/60	1700	230	28°30.0'	112°22.0'	11.0	1.2	1	68
202	27/ 3/60	1800	187	28°31.1'	112°17.9'	11.0	2.0	4	68
203	27/ 3/60	1840	128 119	28°30.0'	112°16.2'	11.0	1.4	1	63
204	27/ 3/60	2010	77	28°36.6'	112°05.0'	14.0	1.3	1	63
205	28/ 3/60	0930	6	28°41.4'	111°55.9'	18.0	3.0	1	76
206	29/ 3/60	0930 1645	0	28°56.0'	112°14.1'	20.0	4.0	1	76
207	29/ 3/60	1950	7	29°16.5'	112°24.1'	18.0	3.0	1	79
208	30/ 3/60	1345	13	29°53.8'	112°45.5'	19.0	2.6	1	68
209	30/ 3/60	1515	73	29°51.8'	112°46.8'	14.0	2.6	1	68
210	30/ 3/60	1550	73 77	29°50.9'	112°49.0'	15.0	2.6	1	68
211	30/ 3/60	1945 2045	110 108	29°54.3'	113°03.2'	15.0	2.0	1	69
212	31/ 3/60	2340 0040	67 57	30°20.5'	113°20.5'	14.0	1.9	75	69
213	9/ 4/60	1913 2055	366 238	28°57.0'	113°22.0'	12.0	2.0	5	63
214	29/ 5/60	0905	1089	32°44.5'	117°43.0'			4	77
215	29/ 5/60	1026	1080	32°44.0'	117°43.0'			4	63
216	29/ 5/60	1700	1107	32°51.5'	117°16.3'			2	77
217	30/ 5/60	0803	115	32°51.7'	117°16.2'			2	77

(continued)



## Appendix: List of Stations (continued)

Stat. No.	Date	Time + 7 from to	Depth m. from to	Latitude	Longitude	Temp. °C.	Oxyg. ml/L	Sed. type	Device
218	30/ 5/60	0836	231	32°51.2'	117°16.3'			75	77
219	30/ 5/60	0924	318	32°52.2'	117°16.7'			1	77
220	30/ 5/60	1030	415	32°53.4'	117°18.7'			4	77
221	30/ 5/60	1600	1043	32°45.7'	117°38.7'			79	77
222	8/ 3/60		31	32°33.4'	117°13.2'			2	74
223	9/ 3/60		220	31°04.5'	116°29.5'			72	74
224	30/ 5/60	1328	628	32°54.8'	117°24.7'			2	77
255	6/11/60	1815 2215	1903	33°38.0'	119°28.0'			72	70
256	9/11/60	0500 0745	1669 2198	34°56.0'	121°49.5'			72	70
257	11/11/60	0415 0720	1830	37°35.7'	123°15.2'			72	70
258	30/ 3/60	0445 0525	906	37°34.0'	123°16.0'			72	70
259	31/ 3/60	0350 0715	2028	37°34.5'	123°16.7'			72	70
260	1/ 4/60	0435 0815	1980	37°34.3'	123°18.8'			72	70
261	30/11/60	2100 2220	106	26°01.7'	112°57.5'	13.0	.1	72	70
262	1/12/60	0045 0135	103	25°52.3'	112°49.2'	12.9	.2	1	80
263	2/12/60	0227 0403	42	26°24.8'	113°00.5'	17.0	3.0	4	69
264	2/12/60	1230 1350	183 292	26°04.5'	113°34.0'	11.0		1	69 80
265	3/12/60		292	28°36.0'	115°34.5'	11.0		72	69
266	3/12/60	2045 2135	101	29°07.8'	115°23.2'	13.0	.1	7	69
267	4/12/60	0753 0840	118	30°17.2'	116°03.2'	10.2	.1	72	69
268	2/12/60	0840 0915	92 82	26°12.5'	113°18.2'	13.3	2.1	72	80
269	30/ 5/60	1200	42	32°51.5'	117°16.0'			1	77
270	9/ 3/59	1816	9	24°51.7'	108°14.3'	24.0	4.0	1	59
271	10/11/60	1800 2300	2380	37°36.5'	123°18.5'			72	70
272	7/11/60	0100 0530	1907	33°36.4'	119°30.0'			72	70
273	9/11/60	0130 0445	1630	34°46.0'	121°46.6'			72	70
274	28/ 4/61	2205 0245	1986 1975	30°52.0'	116°53.0'	2.5	1.3	4	71
275	29/ 4/61	0835 1345	2782 2779	29°59.5'	116°33.2'	2.0	2.0	72	71
276	29/ 4/61	2200 0550	4062 4050	28°57.8'	116°39.0'	1.5	2.0	72	71
277	1/ 5/61	1040 1720	3547 3450	24°45.0'	113°27.0'	1.6	2.0	72	73
278	2/ 5/61	0420 0530	40 43	25°57.7'	112°19.8'	13.0	1.1	72	80 70
279	2/ 5/61	0725 0805	73 80	25°54.3'	112°32.0'	12.0	.6	72	70
280	2/ 5/61	1000 1050	121 116	25°43.0'	112°51.4'	12.0	.6	72	70
281	2/ 5/61	1215 0200	147 163	25°42.8'	112°55.0'	11.0	.5	72	70
282	2/ 5/61	1410 1500	190 218	25°43.0'	112°59.9'	10.0	.4	72	70
283	2/ 5/61	1510 1550	201 164	25°43.0'	113°02.5'	10.0	.4	72	70
284	2/ 5/61	1700 1938	274 293	25°30.0'	112°56.6'	10.0	.4	72	70
285	3/ 5/61	0845 1530	3481 3518	23°59.5'	113°11.9'	2.5	2.8	72	73
287	6/ 5/61	1635 0040	4191 4163	27°20.0'	115°23.1'	1.2	2.9	72	73
288	12/ 3/60	1211	11	22°41.0'	105°53.8'	30.0	3.0	73	59
289	12/ 3/60	1250	17	22°39.7'	105°56.7'	30.0	3.0	12	59
290	3/ 3/59	0020	168	23°23.5'	106°45.5'			72	53
291	4/ 2/59	2227	888	28°29.4'	112°44.3'			72	53
292	16/ 1/58	1200 1600	24	16°38.0'	99°58.0'	30.0	2.0	4	66
293	21/ 6/59	1100 2200	1190	32°35.5'	117°28.5'	6.0	1.8	72	81
296 A	18/ 3/59	1020	11	26°16.5'	112°38.2'	22.0	5.0	1	59 57
297 A	24/ 3/59	0900 1600	18	22°45.0'	109°40.0'	30.0	5.0	10	66
296 B	11/62		18	22°54.8'	106°08.0'				
297 B	11/62		62	22°21.2'	106°08.5'				
298	11/62		57	22°22.0'	106°05.3'				
299	11/62		53	22°23.2'	106°02.0'				
300	11/62		48	22°24.4'	105°59.0'				
301	11/62			22°26.5'	105°52.2'				

(continued)

## Appendix: List of Stations

Stat. No.	Date	Time + 7 from to	Depth m. from to	Latitude	Longitude	Temp. °C.	Oxyg. ml/L	Sed. type	Device
302	11/62		22	22°27.7'	105°49.0'				
303	11/62		13	22°12.0'	105°42.5'				
304	11/62		68	22°01.0'	106°14.3'				
305	11/62		71	21°52.0'	106°11.8'				
306	11/62		53	21°53.0'	106°09.8'				
307	11/62		62	21°43.4'	106°12.8'				
308	11/62		71	21°42.0'	106°15.5'				
309	11/62		115	21°41.0'	106°17.5'				
310	11/62		104	21°40.6'	106°15.0'				
311	11/62		78	21°43.0'	106°16.0'				
312	11/62		90	21°43.4'	106°16.4'				
313	11/62		59	21°12.5'	105°25.5'				
314	11/62		83	21°04.3'	105°27.5'				

Key to Code Numbers used under Sediment Type and Device Headings  
in Station Data Table

Sediment Type Code		Sample Device Code	
Code Number	Sediment Type	Code Number	Device
1	sand	51	Gravity Core
2	muddy sand	52	PBS Core
3	sandy mud	53	Piston Core
4	mud	57	Van Veen Grab
5	gravel	58	Snapper Grab
6	gravel and sand	59	Orange Peel Grab
8	hard clay	63	Rock or Chain Dredge
10	rock	66	Diving
11	shell	67	Plankton Net
12	shelly sand	68	Shell Dredge
13	shelly mud	69	10' Otter Trawl
14	coral	70	16' Otter Trawl
70	clay	71	30' Otter Trawl
71	clayey silt	72	40' Otter Trawl
72	silty clay	73	10' Beam Trawl
73	sand-silt-clay	74	Deep Diving Dredge
74	clayey sand	75	Mini-dredge
75	silty sand	76	Hand Collecting
77	sand and rock	77	1/10 m <sup>2</sup> and 1/5 m <sup>2</sup> Petersen Grab
78	shell-mud-sand	78	Box or Pipe Dredge
79	sandy silt	79	Dipnet
81	silty clay and rock	80	Closing Dredge
		81	Isaak's Fish Trap
		82	Mid-water Trawl

### Explanation of Table I

1. Under list of species: Series of numbers preceeding every species name is the IBM code number for that species, and identifies that species on the IBM species-data cards. These numbers can be referred to for any future programs which might be carried out utilizing the data in this study.
2. The systematic arrangement of species in this list follows a number of authorities including KEEN (1958), MORTENSEN's "Monograph of the Echinoidea", JOHN GARTH's various papers on Decapod crustacea of the eastern Pacific, HYMAN's volumes on the invertebrates: Protozoa through Echinoderms, and various other monographic series. Specialists may not always agree completely as to the systematic arrangement, but an attempt was made to consult with leading specialists in each group of invertebrates.
3. Species names are not italicized, as the list of names were printed-out by an IBM machine which has only one kind of type.
4. The station numbers which are *underlined* are those stations at which living animals were found for that species.
5. Depth ranges are given in fathoms, since the original data had been plotted in fathoms, and time did not permit a complete conversion to meters.
6. Living depth ranges are given by a solid line, while distribution of dead shell or tests is given by dotted lines.
7. The code numbers (Roman numerals) under the Environment column correspond to the numbers of the environments given throughout the text.

TABLE I  
SYSTEMATIC LIST OF SPECIES

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TABLE I  
(CONTINUED)

## STATION NUMBERS

## DEPTH RANGE IN FATHOMS

## ENVIRONMENTS

[illegible]



STATION NUMBERS

[illegible]





TABLE I (CONTINUED)	SYSTEMATIC LIST OF SPECIES	STATION	NUMBERS
------------------------	----------------------------	---------	---------

[illegible]







## Appendix: Table II. Supplemental Lists of Invertebrate Species from Various Gulf of California Environments<sup>1</sup>

### I. Intertidal Rocky Shores:

Living only.

Anthozoa  
*Pocillopora porosa*  
Amphineura  
*Acanthochitona angelica*  
*Acanthochitona exsquisita*  
*Chiton articulatus*  
*Chiton goodalii*  
*Callistochiton gabbi*  
*Lepidozona clathrata*  
*Lepidozona subtilis*

#### Prosobranchiata

*Acmaea discors*  
*Acmaea fascicularis*  
*Acmaea mitella*  
*Acmaea semirubida*  
*Patella mexicana*  
*Nomeopelta dalliana*  
*Nomeopelta mesoleuca*  
*Fissurella longifissa*  
*Fissurella rugosa*  
*Diodora alta*  
*Tegula globulus*  
*Tegula ligulata*  
*Turbo fluctuosus*  
*Nerita scabricosta*  
*Nerita funiculata*  
*Littorina aspersa*  
*Littorina conspersa*  
*Littorina dubiosa pencillata*  
*Littorina pullata*  
*Vermicularia pellucida*  
*Petalochonchus macrophyllum*  
*Cerithium sculptum*  
*Cerithium stercusmuscarum*  
*Thais biseriatis*

*Acanthina lugubris*  
*Acanthina tuberculata*  
*Morula ferruginosa*  
*Purpura patula pansa*  
*Pyrene fuscata*  
*Cantharus macrospira*  
*Marginella californica*  
*Crassispira nympha*  
*Conus purpureus*

#### Pulmonata

*Siphonaria maura maura*  
*Onchidiella binneyi*

#### Lamellibranchiata

*Barbatia illota*  
*Barbatia reeveana*  
*Arcopsis solida*  
*Brachidontes multiformis*  
*Isognomon chemnitzianus*  
*Cardita affinis californicus*

#### Crustacea

*Grapsus grapsus*

#### Holothuroidea

*Brandtothuria impatiens*  
*Athyone glanelli*

#### Asteroidea\*

*Oreaster occidentalis* Verrill  
*Linckia columbia* (Gray)

#### Echinoidea

*Diadema mexicanum*

Abundant, but not living at time of collection.

#### Prosobranchiata

*Fissurella virescens*  
*Diodora saturnalis*  
*Turbo squamiger*  
*Neritina luteofasciata*  
*Petalochonchus contortus*  
*Hipponix antiquatus*  
*Cypraea annettae*  
*Trivia californiana*  
*Jenneria pustulata*  
*Cymatium gibbosum*

*Pyrene strombiformis*  
*Nassarius tiarula*

#### Lamellibranchiata

*Arca pacifica*  
*Barbatia alternata*  
*Ostrea conchaphila*  
*Anomia adamas*  
*Anomia peruviana*  
*Pseudochama inermis*

<sup>1</sup> This list contains all living, identified species from all significant stations for environments, whenever these lists are not in the main body of the text.

\* Added after Table I was prepared.



## 11. Intertidal Sand Beaches and Sand-Flats to 10 Meters:

Living only.

Prosobranchiata	<i>Tellina felix</i>
<i>Cerithium maculosum</i>	<i>Macoma pacis</i>
<i>Cerithidea albonodosa</i>	<i>Heterodonax bimaculatus</i>
<i>Strombus gracilior</i>	
<i>Oliva spicata</i>	Crustacea
<i>Olivella anazora</i>	<i>Clibanarius digueti</i>
<i>Bulla gouldiana</i>	<i>Neopanope peterseni</i>
	<i>Ocyode occidentalis</i> Stimpson <sup>1</sup>
Scaphopoda	<i>Uca crenulata</i>
<i>Cadulus austinclarki</i>	
	Holothuroidea
Lamellibranchiata	<i>Selenkothuria lubrica</i>
<i>Cardita grayi</i>	<i>Thyone parafusus</i>
<i>Cardita megastropa</i>	<i>Neothyone gibbosa</i>
<i>Codakia distinguenda</i>	
<i>Transanella puella</i>	Echinoidea
<i>Pitar lupanaria</i>	<i>Eucidaris thouarsi</i>
<i>Megapitaria squalida</i>	<i>Echinometra vanbrunti</i>
<i>Anomalocardia subimbricata tumens</i>	<i>Brissus laticarinatus</i>

Abundant, but not living at time of collection.

Prosobranchiata	<i>Papyridea aspersa</i>
<i>Neritina luteofasciata</i>	<i>Tivela byronensis</i>
<i>Turritella gonostoma</i>	<i>Pitar concinna</i>
<i>Turritella leucostoma</i>	<i>Megapitaria squalida</i>
<i>Cerithium uncinatum</i>	<i>Dosinia dunkeri</i>
<i>Cypraea arabicula</i>	<i>Dosinia ponderosa</i>
<i>Strombus granulatus</i>	<i>Chione californiensis</i>
<i>Cassis coarctata</i>	<i>Chione compta</i>
<i>Nassarius angulicostis</i>	<i>Chione picta</i>
<i>Nassarius tiarula</i>	<i>Anomalocardia subimbricata</i>
	<i>Protothaca metaodon</i>
Lamellibranchiata	<i>Protothaca grata</i>
<i>Anadara multicostata</i>	<i>Anatina undulata</i>
<i>Anadara labiosa</i>	<i>Mulinia pallida</i>
<i>Glycymeris delessertii</i>	<i>Tellina erythronotus</i>
<i>Atrina maura</i>	<i>Donax assimilis</i>
<i>Cardita grayi</i>	<i>Donax californicus</i>
<i>Cardita laticostata</i>	<i>Donax carinatus</i>
<i>Cardita radiata</i>	<i>Donax punctostriatus</i>
<i>Diplodonta subquadrata</i>	<i>Tagelus affinis</i>
<i>Diplodonta sericata</i>	<i>Semele guaymasensis</i>
<i>Trachycardium procerum</i>	<i>Pholas chiloensis</i>

## IV. Nearshore Shelf, Sand Bottom, 11 to 26 Meters, Northern Gulf:

Living only.

Hexacorallia	Prosobranchiata
<i>Heterocyathus aequicostatus</i>	<i>Calliostoma bonita</i>
<i>Astrangia cortezi</i>	<i>Niso excolpa</i>
<i>Astrangia pedersonii</i>	<i>Turritella leucostoma</i>

<sup>1</sup>) Seen on beaches, identified in Scripps Institution collections from Gulf of California, but not collected as part of this study.

## Prosobranchiata (continued)

*Architectonica nobilis*  
*Calyptraea conica*  
*Calyptraea mamillaris*  
*Calyptraea subreflexa*  
*Crepidula arenata*  
*Crepidula excavata*  
*Crepidula incurva*  
*Crepidula perforans*  
*Crucibulum scutellatum*  
*Crucibulum serratum*  
*Crucibulum spinosum*  
*Polinices reclusianus*  
*Strombus gracilior*  
*Hexaplex erythrostomus*  
*Eupleura muriciformis*  
*Anachis adelinae*  
*Anachis varia*  
*Strombina solidula*  
*Cantharus pallidus*  
*Phos articulatus*  
*Nassarius pagodus*  
*Nassarius versicolor*  
*Fusinus ambustus*  
*Oliva incrassata*  
*Oliva spicata polposta*  
*Olivella dama*  
*Olivella fletcheriae*  
*Olivella gracilis*  
*Mitra hindsi*  
*Lyria cummingii*  
*Cancellaria balboae*  
*Cancellaria cassidiformis*  
*Cancellaria decussata*  
*Cancellaria obesa*  
*Clavus roseolus*  
*Clavus pembertonii*  
*Clavus unimaculatus*  
*Clathrodrillia pilsbryi*  
*Crassispira nephele*  
*Crassispira tabogensis*  
*Crassispira xanti*  
*Hormospira maculosa*  
*Pleuroliria picta*  
*Conus perplexus*  
*Conus scalaris*  
*Terebra armillata*  
*Terebra malonei*  
*Terebra specillata*  
*Terebra tuberculosum*  
*Terebra variegata*  
*Pyramidella adamsi*

## Scaphopoda

*Dentalium oerstedii*  
*Dentalium inversum*  
*Cadulus perpusillus*

## Lamellibranchiata

*Nuculana acrita*  
*Nuculana costellata*  
*Nuculana elenensis*  
*Nuculana fastigata*  
*Nuculana impar*  
*Adrana exoptata*  
*Adrana penascoensis*  
*Adrana tonosiana*  
*Anadara obesa*  
*Lioberus salvadoricus*  
*Pecten sericeus*  
*Chlamys circularis*  
*Crassatella gibbosa*  
*Trachycardium panamense*  
*Laevicardium elatum*  
*Laevicardium elenense*  
*Pitar concinnus*  
*Pitar newcombianus*  
*Megapitaria aurantia*  
*Megapitaria squalida*  
*Chione compta*  
*Chione mariae*  
*Cooperella subdiaphana*  
*Tellina amianta*  
*Tellina arenica*  
*Tellina iris*  
*Tellina tabogensis*  
*Macoma siliqua*  
*Donax gracilis*  
*Ensis californicus*  
*Corbula luteola*  
*Corbula nasuta*  
*Corbula ovulata*  
*Pandora claviculata*  
*Lyonsia gouldii*

## Crustacea

*Balanus trigonus*  
*Balanus concavus mexicanus*  
*Munida tenella*  
*Euceramus transversilineatus*  
*Minyocerus kirkii*  
*Porcellana cancrisocialis*  
*Dardanus sinistripes*  
*Paguristes digueti*  
*Paguristes praedator*  
*Pagurus benedicti*  
*Pagurus gladius*  
*Petrochirus californiensis*  
*Pylopagurus varians*  
*Parapylocheles glasselli*

## Echinoidea

*Arbacia incisa*  
*Encope micropora*  
*Clypeaster, sp.*

## Echinoidea (continued)

*Mellita*, sp.  
*Lovenia cordiformis*  
*Brissopsis pacifica*  
*Moira clotho*

## Ophiuroidea\*

*Amphiodia occidentalis* (Lyman)

## IV. Nearshore Shelf, Sand Bottom, 11 to 26 Meters, Southern Gulf:

## Hexacorallia

*Astrangia conferta*<sup>1</sup>

## Prosobranchiata

*Architectonica placentalis*<sup>1</sup>  
*Calyptrea mamillaris*  
*Crepidula aculeata*  
*Crepidula incurva*  
*Natica broderipiana*  
*Natica chemnitzii*<sup>1</sup>  
*Natica othello*<sup>1</sup>  
*Polinices intemerata*  
*Polinices uber*  
*Sinum debile*<sup>1</sup>  
*Sinum sanctijohannis*<sup>1</sup>  
*Ficus ventricosa*  
*Distorsio decussatus*<sup>1</sup>  
*Bursa nana*  
*Eupleura muriciformis*  
*Typhis cummingii*<sup>1</sup>  
*Strombina hirundo*  
*Cominella subrostrata*<sup>1</sup>  
*Cantharus capitaneous*  
*Nassarius pagodus*  
*Oliva incrassata*  
*Olivella anazora*<sup>1</sup>  
*Olivella fletcherac*  
*Mitra hindsii*  
*Cancellaria exopleura*<sup>1</sup>  
*Hormospira maculosa*  
*Conus perplexus*  
*Terebra armillata*  
*Terebra variegata*

## Lamellibranchiata

*Nucula declivis*  
*Nuculana elenensis*  
*Anadara concinna*  
*Anadara nux*<sup>1</sup>  
*Anadara*, sp.  
*Atrina maura*  
*Chlamys circularis*  
*Chlamys tumbezensis*<sup>1</sup>

*Lucina cancellaris*  
*Ctena clarionensis*  
*Trachycardium panamense*  
*Transanella puella*  
*Pitar concinnus*  
*Pitar frizzeli*<sup>1</sup>  
*Megapitaria squalida*  
*Dosinia dunkeri*  
*Chione gnidia*  
*Chione*, sp.  
*Mulinia bradleyi*<sup>1</sup>  
*Tellina cognata*<sup>1</sup>  
*Tellina felix*  
*Macoma*, sp.  
*Tagelus politus*  
*Corbula nasuta*  
*Corbula ovulata*  
*Pandora claviculata*  
*Abra palmeri*<sup>1</sup>  
*Lyonsia gouldii*  
*Periploma*, sp.

## Crustacea

*Balanus trigonus*  
*Euceramus panatellus*<sup>1</sup>  
*Dardanus sinistripes*  
*Paguristes praedator*  
*Pagurus gladius*  
*Pagurus smithi*<sup>1</sup>

## Echinoidea

*Moira clotho*  
*Brisaster townsendi* (A. Agassiz)

## Asteroidea\*

*Astropecten californicus* Fisher (juv.)

## Ophiuroidea

? *Amphiura seminuda* Lütken and Mortensen.

<sup>1</sup>) These species confined primarily to the southern Gulf.

\* Added after completion of Table I.

## V. Intermediate Shelf, Sand Bottom, 27 to 65 Meters, Northern Gulf:

Living only.

Hexacorallia  
*Heterocyathus aequicostatus*

Prosobranchiata  
*Calliostoma nopheloide*  
*Solariella triplosthephanus*  
*Calyptrea mamillaris*  
*Crepidula excavata*  
*Crepidula striolata*  
*Crucibulum concameratum*  
*Crucibulum scutellatum*  
*Natica grayi*  
*Cassia centricaudatum*  
*Ficus ventricosus*  
*Murex recurvirostris*  
*Strombina gibberula*  
*Nassarius pagodus*  
*Nassarius versicolor*  
*Fusinus colpoicus*  
*Fusinus dupetitthouarsi*  
*Olivella fletcheriae*  
*Mitra sulcata*  
*Lyria cummingii*  
*Knefastia tuberculifera*  
*Clavus melca*  
*Clavus pallidus*  
*Crassispira ericana*  
*Hindsiclava dotella*  
*Turricula armilda*  
*Pleuroliria albicarinata*

Lamellibranchiata  
*Anadara cepoides*  
*Anadara nux*  
*Anadara obesa*  
*Lioberus salvadoricus*  
*Chlamys circularis*  
*Crassatella gibbosa*  
*Trigoniocardia biangulata*  
*Laevicardium elatum*  
*Nemocardium pazianum*  
*Transanella puella*  
*Pitar newcombianus*  
*Chione mariae*  
*Tellina inaequistriata*  
*Macoma medioamericana*  
*Macoma siliqua*  
*Macoma undulata*  
*Pandora granulata*  
*Plectadon scaber*

Crustacea  
*Balanus concaus mexicanus*  
*Balanus trigonus*

*Munida tenella*  
*Pleuroncodes planipes*  
*Porcellana cancrisocialis*  
*Dardanus sinistripes*  
*Paguristes bakeri*  
*Paguristes praedator*  
*Pagurus benedicti*  
*Pagurus californicus*  
*Pagurus gladius*  
*Pagurus smithi*  
*Pylopagurus varians*  
*Hypoconcha lowei*  
*Calappa saussurei*  
*Hepatus lineatus*  
*Randallia americana*  
*Randallia ornata*  
*Lithadia cummingii*  
*Cancer amphioctus*  
*Portunus iridescent*  
*Portunus minimus*  
*Portunus pichilinguei*  
*Micropanope polita*  
*Mesorhea belli*  
*Collodes tenuirostris*  
*Euprognatha bifida*  
*Paradasygus depressus*  
*Podochela hemphilli*  
*Pyromaia tuberculata*  
*Stenocionops ovata*  
*Cymopolia fragilis*  
*Cymopolia zonata*  
*Clythrocerus laminatus*  
*Ethusa lata*  
*Pseudorhombila xanthiformis*  
*Pinnotheres, sp.*

Echinoidea  
*Arbacia incisa*  
*Clypeaster europacificus*  
*Clypeaster, sp.*  
*Lovenia cordiformis*  
*Agassizia scrobiculata*  
*Brissopsis pacifica*  
*Meoma grandis*

Asteroidea\*  
*Luidia columbia* Lütken  
*Astropecten californicus* Fisher (juv.)

Ophiuroidea  
*Amphigyptis perplexa* Nielsen

\* Added after completion of Table I.

## V. Intermediate Shelf, Sand Bottom, 27 to 65 Meters, Southern Gulf:

Living only, sand bottom.

## Hexacorallia

*Heterocyathus aequicostatus*<sup>1</sup>

## Prosobranchiata

*Calliostoma bonita**Astele rema**Archilectonica placentalis**Calyptrea conica**Crucibulum scutellatum*<sup>1</sup>*Crucibulum spinosum**Natica broderipiana**Natica colima**Natica grayi**Polinices otis**Polinices uber**Sinum pazianum**Distorsio decussatus**Bursa caelata**Bursa nana**Murex elenensis**Murex recurvirostris**Hexaplex brassica**Ocenebra perita**Ocenebra cf. vitatta**Eupleura muriciformis**Coralliophila hindsii**Cosmiocoeloma cf. palmeri**Strombina marksii**Cantharus capitaneus**Phos articulatus**Hindsia acapulcana**Nassarius pagodus**Nassarius versicolor**Latirus hemphilli**Fusinus centrifugus**Fusinus colpoicus*<sup>1</sup>*Fusinus dupetitthouarsi*<sup>1</sup>*Mitra erythrogramma**Mitra hindsii**Gemmula hindsiana**Knefastia walkeri**Clavus roseolus**Clavus walkeri**Clathrodrillia alcestris**Hindsiclava andromeda**Turricula fusinella**Pleuroliria albicarinata*<sup>1</sup>*Pleuroliria picta**Terebra specillata*

## Scaphopoda

*Dentalium oerstedii oerstedii*<sup>1</sup>*Dentalium oerstedii numerosum*

## Lamellibranchiata

*Nuculana eburnea**Nuculana morella**Glycymeris multicostata**Glycymeris tessellata**Atrina, sp.**Chlamys circularis*<sup>1</sup>*Plicatula inezana**Cardita spurca beebei**Trachycardium belcheri**Lophocardium cummingii**Nemocardium pazianum*<sup>1</sup>*Chione mariae**Tellina pristophora**Semele paziana*

## Crustacea

*Balanus concavus mexicanus*<sup>1</sup>*Porcellana cancrisocialis*<sup>1</sup>*Clibinarius, sp. indet.**Dardanus sinistripes*<sup>1</sup>*Paguristes digueti**Paguristes praedator*<sup>1</sup>*Pagurus gladius*<sup>1</sup>*Pylopagurus varians*<sup>1</sup>*Parapylocheles glasselli**Hypoconcha lowei*<sup>1</sup>*Calappa saussurei*<sup>1</sup>*Hepatus kossmanni**Iliacantha hancocki**Persephona townsendi**Randallia bulligera**Lithadia cumingii*<sup>1</sup>*Portunus acuminatus**Portunus affinis**Euphyllax robustus**Medaeus lobipes**Leilolambrius punctatissimus**Heterocrypta macrobrachia**Solenolambrus arcuatus**Collodes gibbosus**Collodes tenuirostris*<sup>1</sup>*Euprognatha bifida*<sup>1</sup>*Paradasygius depressus*<sup>1</sup>*Pyronaia tuberculata*<sup>1</sup>*Stenorhynchus debilis**Notolopus lamellatus**Ethusa lata**Ethusa mascrone americana**Oediplax granulata**Chasmophora macrophthalmia**Prionoplax cf. ciliata*<sup>1</sup>) Indicates the same species found within the same depth range in the northern Gulf also.



## V. Intermediate Shelf, Clay bottom, 27 to 65 Meters, Southern Gulf:

Living only, clay bottom.

## Prosobranchiata

*Architectonica nobilis*  
*Crepidula arenata*  
*Crepidula excavata*<sup>1</sup>  
*Crucibulum lignarium*  
*Crucibulum spinosum*  
*Xenophora robusta*  
*Natica broderipiana*  
*Natica elenae*  
*Polinices uber*  
*Distorsio constrictus*  
*Distorsio decussatus*  
*Bursa nana*  
*Murex recurvirostris*  
*Ocenebra*, sp.  
*Cantharus capitaneus*  
*Fusinus depetithouarsi*<sup>1</sup>  
*Harpa crenata*  
*Hormospira maculata*  
*Conus arcuatus*  
*Conus perplexus*  
*Conus recurvus*  
*Conus scalaris*

## Scaphopoda

*Dentalium oerstedii oerstedii*<sup>1</sup>

## Lamellibranchiata

*Noetia delgada*  
*Glycymeris tessellata*  
*Chlamys circularis*<sup>1</sup>  
*Plicatula inezana*  
*Plicatula penicillata*  
*Anodontia edentuloides*  
*Pseudochama saavedrai*  
*Trachycardium belcheri*  
*Pitar catharius*  
*Megapitaria squalida*

*Chione kelletti*

*Chione mariae*<sup>1</sup>

*Semele paziana*

## Crustacea

*Balanus concavus mexicanus*<sup>1</sup>  
*Porcellana cancrisocialis*<sup>1</sup>  
*Clibinarius panamensis*  
*Dardanus sinistripes*<sup>1</sup>  
*Paguristes praedator*<sup>1</sup>  
*Pagurus gladius*<sup>1</sup>  
*Pagurus smithi*<sup>1</sup>  
*Petrochirus californiensis*  
*Pylopagurus varians*<sup>1</sup>  
*Hypoconcha lowei*<sup>1</sup>  
*Calappa saussurei*<sup>1</sup>  
*Cycloes bairdii*  
*Hepatus kossmanni*  
*Iliacantha hancocki*  
*Persephone townsendi*  
*Randallia bulligera*  
*Portunus acuminatus*  
*Portunus affinis*  
*Portunus asper*  
*Euphyllax robustus*  
*Medaeus lobipes*  
*Leilolambrus punctatissimus*  
*Collodes gibbosus*  
*Collodes tenuirostris*<sup>1</sup>  
*Collodes tumidus*  
*Paradasygius depressus*<sup>1</sup>  
*Pyromaia tuberculata*<sup>1</sup>  
*Stenorhynchus debilis*  
*Ethusa lata*  
*Oediplax granulatus*

## Holothuroidea

*Thyonaeta mexicana*

## VI. Outer Shelf, Clay bottom, 66 to 120 Meters, Southern Gulf:

## Prosobranchiata

*Architectonica nobilis*  
*Calyptrea conica*  
*Crepidula excavata*  
*Crepidula incurva*  
*Crucibulum serratum*<sup>\*</sup>  
*Crucibulum*, n. sp.<sup>\*</sup>  
*Distorsio constrictus*  
*Distorsio decussatus*  
*Ocenebra sloati*, n. ssp.  
*Strombina clavulus*  
*Strombina*, n. sp.<sup>\*</sup>

*Cantharus capitaneus*  
*Cantharus*, n. sp.<sup>\*</sup>  
*Phos cococensis*  
*Phos*, n. sp.  
*Nassarius cattalus*  
*Clathrodrillia*, sp.  
*Hormospira maculosa*  
*Pleuroliria oxytropis*  
*Tiaturreis spectabilis* (dead?)  
*Conus arcuatus*<sup>\*</sup>  
*Conus recurvus*

<sup>1</sup>) Indicates same species found within the same depth range in the northern Gulf too.

<sup>\*</sup> Most abundant and characteristic living species.

## Scaphopoda

*Dentalium splendidum*

## Lamellibranchiata

*Nuculana laeviradius**Anadara mazatlanica*\**Anadara concinna**Anadara emarginata*\**Anodontia edentuloides*\**Chione kelletti*\**Corbula luteola**Corbula obesa*\**Periploma carpenteri*\**Cuspidaria pectinata*

## Crustacea

*Heterocarpus vicarius**Solenocarpus*, sp.*Pleuroncodes planipes**Dardanus sinistripes**Calappa saussurei**Mursia guadichaudi**Cancer porteri**Portunus iridescens**Medaeus lobipes**Stenorhynchus debilis**Ethusa ciliafrons*\*

## Polychaeta

*Protula superba*\*

## Echinoidea

*Spatangus californicus*\*

\* Most abundant and characteristic living species.

## VII. Outer Shelf, Sand Bottom, 66 to 120 Meters, Northern Gulf:

## Living only.

## Hexacorallia

*Ceratotrochus franciscana**Astrangia*, sp.

## Octocorallia

*Eugorgia*, sp.*Leptogorgia*, sp.

## Prosobranchiata

*Calyptraea conica**Calyptraea mamillaris**Crepidula onyx**Crucibulum lignarium**Polinices intemerata*\**Polinices otis**Sinum pazianum**Cymatium amictum*\**Murex recurvirostris**Nassarius insculptus gordanus*\**Fusinus dupetithouarsi**Fusinus*, sp.*Clavus* cf. *craneanus**Clathrodrillia*, sp.*Hindsiclava andromeda**Mangelia*, sp.*Turricula armilda*\**Turricula nigricans**Pleuroliria artia*\**Pleuroliria nobilis*\**Pleuroliria oxytropis**Pleuroliria oxytropis albicarinata*

## Scaphopoda

*Dentalium oerstedii*

## Opisthobranchiata

*Cyclichna*, sp.

Doridae

*Rhizorus*, sp.*Triopha*, sp.

## Lamellibranchiata

*Nucula exigua*\**Nuculana laeviradius**Amygdalum pallidulum**Plicatula inezana**Lucina excavata**Lucinoma annulata*\**Nemocardium centrifilosum*\**Nemocardium pazianum**Pitar catharius*\**Chione mariae**Macoma medioamericana*\**Corbula fragilis**Corbula luteola**Corbula obesa**Corbula ventricosa*\**Pandora* cf. *brevifrons*\**Cyathodonta dubiosa*\*

## Crustacea

*Munida tenella**Minyocerus kirki**Paguristes praedator*

\* Abundant or characteristic species.

## Crustacea (continued)

*Pylopagurus holmesi*  
*Pylopagurus longicarpus*  
*Spiropagurus occidentalis*  
*Hypoconcha lowei*  
*Calappa sausserei*  
*Iliacantha hancocki*  
*Persephona townsendi*  
*Randallia americana*  
*Randallia angelica*  
*Randallia ornata*  
*Ebalia cristata*  
*Cancer amphioctus*  
*Lophopanopeus frontalis*  
*Mesorhea belli*  
*Heterocrypta macrobrachia*  
*Collodes tenuirostris*  
*Collodes tumidus*  
*Euprognatha bifida*  
*Paradasygius depressus*  
*Podocheila lobifrons*  
*Pyromania tuberculata*  
*Sphenocarcinus agassizi*  
*Stenocionops beebei*

\* Added after Tall: I was prepared.

*Stenocionops ovata*  
*Stenorhynchus debilis*  
*Inacoides laevis*  
*Libinia mexicana*  
*Cymopolia fragilis*  
*Cymopolia zonata*  
*Clythrocerus planus*  
*Ethusa lata*  
*Chasmocarcinus latipes*  
*Speocarcinus granulimanus*

## Holothuroidea

*Parastichopus californicus*  
*Vaneyothuria zaca*

## Echinoidea

*Hesperocidaris perplexa*  
*Clypeaster europacificus*  
*Encope grandis*

## Asteroidea\*

*Astropecten californicus* Fisher (juv.)  
*Diopederma danianum* (Verrill)

## VIII. Northern Gulf Basins and Troughs, 230 to 1,500 Meters:

Living and dead.

## Octocorallia

*Acanthagorgia*, n. sp. live  
*Callogorgia flabellum* live  
*Eumuricea horrida* live

## Hexacorallia

*Ceratotrochus*, sp.  
*Coenocyathus bowersi* live  
*Desmophyllum crista-galli* live  
*Desmophyllum*, sp.  
*Balanophyllia*, sp.  
*Astrangia*, sp.  
*Dendrophyllia cortezi* live  
*Dendrophyllia*, sp.  
*Bathycyathus*, sp.  
*Porites*, sp.

## Brachiopoda

*Morrisia hornei* live  
*Terebratalia obsoleta*<sup>1</sup>  
*Terebratulina* cf. *kiiensis* live  
*Terebratulina*, sp.  
*Argyrotheca lowei*<sup>1</sup>  
*Laqueus californicus* live

## Amphineura

Genus and species unidentified live

## Prosobranchiata

*Acmaea*, sp.  
*Emarginula velascoensis*<sup>1</sup>  
*Rimula*, n. sp. A.  
*Rimula*, n. sp. B.  
*Fissurella*, sp.  
*Diodora alta*  
*Diodora aspera*  
*Calliostoma gemmulatum*  
*Calliostoma variegatum*  
*Calliostoma*, n. sp.  
*Margarites albolineatus*  
*Solariella* cf. *elegantula*  
*Solariella permabilis*  
*Solariella*, sp.  
*Turcica coffea*  
*Turbo*, sp.  
*Liotia cookeana*  
*Arene*, sp.  
*Epitonium* cf. *manzanillense*  
*Epitonium* cf. *obtusum*  
*Circostrema* cf. *dalli* (Atlantic sp.)  
*Caecum*, sp.  
*Turritella* cf. *cooperi*  
*Crepidula onyx*  
*Crucibulum scutellatum*  
*Crucibulum*, sp.  
*Torellea vallonina*

\* Abundant or characteristic species.

<sup>1</sup> Also taken on upper slope of southern Gulf.

## Prosobranchiata (continued)

- Polinices intemeratus*<sup>1</sup>  
*Polinices otis*  
*Natica chemnitzii*  
*Cypraea annettae*  
*Ficus ventricosa*  
*Cymatium adairense*  
*Cymatium amictum*  
*Pterynotis carpenteri*  
*Strombina*, sp.  
*Pyrene fuscata*  
*Boreotrophon*, n. sp.<sup>1</sup>  
*Metula amosi*  
*Nassarius cattalus*<sup>1</sup>  
*Nassarius insculptus gordanus*<sup>1</sup>  
*Nassarius*, sp.  
*Fusinus barbarensis*  
*Fusinus colpoicus*<sup>1</sup>  
*Fusinus traski* live  
*Mitra crenata*  
*Mitra marshalli*  
*Antiplanes abarbarea*  
*Hindsiclava* cf. *andromeda*  
*Pleuroliria oxytropis*  
*Cavolina longirostris*

## Scaphopoda

- Dentalium oerstedii*<sup>1</sup>  
*Dentalium pretiosum berryi* live  
*Dentalium vallicolens*<sup>1</sup>  
*Dentalium*, n. sp.  
*Dentalium* (*Laevidentalium*), sp.<sup>1</sup>  
*Cadulus perpusillus*<sup>1</sup>  
*Cadulus austinclarki* live  
*Siphonodentalium quadrifissatum* live

## Opisthobranchiata

- Cyclichna*, sp.  
*Cyclichnella*, sp.  
*Retusa*, sp.  
*Sulcaretusa*, sp.  
*Tornatina*, sp.

## Lamellibranchiata

- Solemya valvulus*<sup>1</sup> live  
*Acila castrensis*<sup>1</sup> live  
*Nuculana taphria* live  
*Nuculana hamata*  
*Yoldia martyria*  
*Arca nucleator*

- Barbatia baileyi*  
*Barbatia gradata*  
*Barbatia alternata*  
*Anadara cepoides*  
*Glycymeris corteziana*  
*Glycymeris lineata*  
*Glycymeris maculata*  
*Glycymeris multicostata*<sup>1</sup>  
*Amygdalum pallidulum*<sup>1</sup> live  
*Pododesmus cepio*  
*Pecten vogdesi*<sup>1</sup>  
*Chlamys*, n. sp.  
*Cyclopecten exquiritus*  
*Cyclopecten pernomus*  
*Cyclopecten vancouverensis*  
*Cyclopecten zaccæ*<sup>1</sup>  
*Dimya californica*  
*Crassinella varians*  
*Cardita barbarensis*<sup>1</sup>  
*Cardita megastrophia*  
*Lucina tenuisculptus*<sup>1</sup>  
*Lucinoma annulata*<sup>1</sup> live  
*Diplodonta inezensis*  
*Thyasira*, sp.  
*Chama squamuligera*  
*Pseudochama*, sp.  
*Trigoniocardia guanocastensis*  
*Nemocardium centifilosum*<sup>1</sup> live  
*Ventricolaria isocardia*  
*Tellina bodegensis*  
*Tellina carpenteri*  
*Macoma planiuscula*  
*Macoma siliqua spectri* live  
*Semele quentinensis*  
*Corbula marmorata*  
*Corbula tenuis*  
*Hiatella arctica*  
*Verticordia aequicostata*  
*Verticordia ornata*

## Crustacea

- Salmonaeus*, sp.

## Echinoidea

- Hesperocidaris perplexa* live  
*Spatangus*, sp.  
*Brisaster townsendi* live  
*Brissus*, sp.

## Asteroidea\*

- Astropecten ornatissimus* Fisher

<sup>1</sup>) Also taken on upper slope of southern and central Gulf. Unless indicated species were taken as dead Shell.

\* Added after Table I was prepared.

**Table III. Sampling Devices used to Establish Boundaries and Composition of Assemblages**

St. Number	Device	St. Number	Device
<b>I. Rocky Shores</b>		<b>IV. Northern Gulf, Nearshore Shelf, 11 to 26 meters</b>	
100	Beach collection	24	Van Veen, Orange Peel
101	Beach collection	114	Van Veen grab
103	Beach collection	172	Shell dredge
104	Beach collection	175	Shell dredge
105	Beach collection	181	Shell dredge
107	Beach collection	184	Shell dredge
108	Diving	185	Shell dredge
109	Beach collection	190	Shell dredge
115	Beach collection	191	3-meter otter trawl
118	Beach collection	194	Shell dredge
119	Diving	195	Shell dredge
11 samples 9 beach collections; 2 dives		196	Shell dredge
		208	Shell dredge
		212	3-meter otter trawl
<b>II. Beaches and Sand Flats to 10 m.</b>		14 samples 2 Van Veen (1/20 m <sup>2</sup> ) 10 Shell dredges (100 × 30 cm.) 2 3-meter otter trawls	
4	Orange peel grab	Above stations used in assessing all index groups shown in Table IV.	
5	Van Veen grab	171	Shell dredge
7	Orange peel grab	181	Shell dredge
102	Hand collection	184	Shell dredge
106	Beach collection	190	Shell dredge
111	Van Veen grab	194	Shell dredge
112	Minidredge	195	Shell dredge
113	Van Veen grab	196	Shell dredge
114	Van Veen grab	24	Van Veen grab
116	Beach collection	208	Shell dredge
117	Beach collection	9 samples 8 Shell dredges (100 × 30 cm.) 1 Van Veen (1/15 m <sup>2</sup> )	
118	Van Veen, minidredge	Above stations used in obtaining composite assemblage, figure 17.	
119	Diving	<b>IV. Southern Nearshore Shelf, 11 to 26 meters</b>	
160	Beach collection	1	Van Veen grab
162	Beach collection	5	Van Veen grab
163	Beach collection	51 a, b, c, d (4)	1/10 m <sup>2</sup> Petersen grab
165	Rock dredge	112	Minidredge
179	Beach collection	113	Van Veen grab
193	Beach collection	148	3-meter otter trawl
205	Beach collection	149	3-meter otter trawl
206	Beach collection	157	3-meter otter trawl
270	Orange peel grab	288	Orange peel grab
292	Diving	289	Orange peel grab
27 samples 3 orange peels (1/15 m <sup>2</sup> ) 5 Van Veen (1/20 m <sup>2</sup> ) 11 Beach collections 2 Minidredges (10 × 30 cm.) 2 Diving 1 Rock dredge (30 × 100 cm.)		13 samples 3 Van Veen (1/20 m <sup>2</sup> ) 4 Petersen grabs (1/10 m <sup>2</sup> ) 2 Orange peels (1/15 m <sup>2</sup> ) 3 3-meter otter trawls 1 minidredge (10 × 30 cm.)	
<b>III. Low Salinity Lagoons</b>			
292	Diving		
206	Shore collecting		
117	Shore collecting		
Overall assessment from literature and personal communications.			



Table III (continued)

St. Number	Device	St. Number	Device
V. Northern Intermediate Shelf, 27 to 65 meters		VII. Northern Outer Shelf, 66 to 126 meters	
56	Shell dredge	23	Orange peel grab
164	3-meter otter trawl	64	10-meter otter trawl
166	Rock dredge	68	Shell dredge
170	Shell dredge	69	1/10 m <sup>2</sup> Petersen grab
171	Shell dredge	70	Shell dredge
175	Shell dredge	71	Shell dredge
182	3-meter otter trawl	72	Shell dredge
185	Shell dredge	82	Rock dredge
186	Shell dredge	83	Rock dredge
188	Shell dredge	164	3-meter otter trawl
191	3-meter otter trawl	166	Rock dredge
204	Rock dredge	182	3-meter otter trawl
212	3-meter otter trawl	198	Shell dredge
13 samples 7 Shell dredges (100 × 30 cm.) 4 3-meter otter trawls 2 Rock dredges (100 × 30 cm.)		203	Rock dredge
V. Southern Intermediate Shelf, 27 to 65 meters		204	Rock dredge
2	Phleger cores	209	Shell dredge
87	12-meter otter trawl	210	Shell dredge
94	12-meter otter trawl	211	3-meter otter trawl
95	12-meter otter trawl	18 samples 1 Orange peel (1/15 m <sup>2</sup> ) 1 1/10 m <sup>2</sup> Petersen grab 7 Shell dredges (100 × 30 cm.) 1 10-meter otter trawl 3 3-meter otter trawls 5 Rock dredges (100 × 30 cm.)	
97	12-meter otter trawl	VIII. Northern Gulf Basins, 230 to 1500 meters	
98	12-meter otter trawl	18	Orange peel grab
150	3-meter otter trawl	19	Gravity corer
151	Dipnet	58	Rock dredge
153	Box dredge	59	Rock dredge
154	Box dredge	60	Gravity corer
158	3-meter otter trawl	61	Box dredge
159	3-meter otter trawl	62	Rock dredge
12 samples 5 12-meter otter trawls 3 3-meter otter trawls 2 Box dredges (100 × 30 cm.) 1 Phleger core (3 cm. diameter) 1 Dipnet		63	Box dredge
VI. Southern Outer Shelf, 66 to 126 meters		65	Deep diving dredge
6	Orange peel grab	66	Piston corer
50	Shell dredge	67	Piston corer
88	12-meter otter trawl	68	Shell dredge
89	12-meter otter trawl	72	Shell dredge
92	Shell dredge	73	Piston corer
93	Rock dredge	74	Piston corer
147	3-meter otter trawl	75	Piston corer
152	Box dredge	80	Rock dredge
8 samples 1 Orange peel (1/15 m <sup>2</sup> ) 2 Shell dredges (100 × 30 cm.) 2 12-meter otter trawls 1 3-meter otter trawl 1 Rock dredge (100 × 30 cm.) 1 Box dredge (100 × 30 cm.)		199	Rock dredge
		200	Rock dredge
		19 samples 1 Orange peel (1/15 m <sup>2</sup> ) 2 Gravity cores (4 cm. in diameter) 5 Piston cores (8 cm. in diameter) 6 Rock dredges (100 × 10 cm.) 2 Box dredges (100 × 30 cm.) 2 Shell dredges (100 × 10 cm.) 1 Deep diving dredge cutting edge 1.5 m.	

Table III (continued)

St. Number	Device	St. Number	Device
IX. Upper Slope, Southern and Central Gulf, 121 to 730 meters		XI. Abyssal Southern Basins and Outer Slope, 1800 to 4122 meters	
10	Orange peel grab	3	Mid-water trawl (bottom)
40	Rock dredge	39	1/5 m <sup>2</sup> Petersen grab
43	Box Dredge	41	Deep diving dredge
43	Box Dredge	42	Deep diving dredge
45	Box Dredge	52	Deep diving dredge
53	Box dredge	86	1/5 m <sup>2</sup> Petersen grab
54	Shell dredge	96	12-meter otter trawl
91	12-meter otter trawl	128	Deep diving dredge
99	Rock dredge	131	Deep diving dredge
156	3-meter otter trawl	134	Deep diving dredge
167	3-meter otter trawl	137	10-meter otter trawl
168	Shell dredge	139	10-meter otter trawl
187	Shell dredge	141	10-meter otter trawl
201	Shell dredge	272	5-meter otter trawl
202	Shell dredge	274	10-meter otter trawl
14 samples 1 Orange peel (1/15 m <sup>2</sup> ) 2 Rock dredges (100 × 30 cm.) 3 Box dredges (100 × 30 cm.) 5 Shell dredges (100 × 30 cm.) 1 12-meter otter trawl 2 3-meter otter trawls		275	10-meter otter trawl
X. Middle Continental Slope, 731 to 1,799 meters		276	10-meter otter trawl
39	1/5 m <sup>2</sup> Petersen grab	277	3-meter Beam trawl
40	Rock dredge	285	3-meter Beam trawl
84	Deep diving dredge	287	3-meter Beam trawl
90	12-meter otter trawl	20 samples 1 Mid-water trawl on bottom (2.5 meters) 2 1/5 m <sup>2</sup> Petersen grabs 6 Deep diving dredges (cutting edge 1.5 m.) 1 12-meter otter trawl 6 10-meter otter trawls 1 5-meter otter trawls 3 3-meter beam trawl	
127	Deep diving dredge	XII. California Borderland Basins, 1641 to 2358 meters	
135	Deep diving dredge	144	5-meter otter trawl
138	10-meter otter trawl	145	5-meter otter trawl
214	1/5 m <sup>2</sup> Petersen grab	255	5-meter otter trawl
215	Rock dredge	256	5-meter otter trawl
216	1/5 m <sup>2</sup> Petersen grab	257	5-meter otter trawl
221	1/5 m <sup>2</sup> Petersen grab	258	5-meter otter trawl
273	5-meter otter trawl	259	5-meter otter trawl
11 samples 4 1/5 m <sup>2</sup> Petersen grabs 3 Deep diving dredges (cutting edge 1.5 m.) 1 12-meter otter trawl 1 10-meter otter trawl 1 5-meter otter trawl 2 Rock dredges (100 × 30 cm.)		260	5-meter otter trawl
		271	5-meter otter trawl
		9 samples 9 5-meter otter trawls	

PLATES

PLATE I.

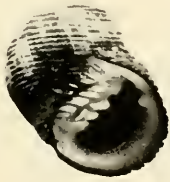
I. Intertidal and shallow rocky shores assemblage.

Fig.

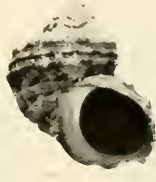
1. *Littorina aspera* Philippi, 1846. Aperture, size –  $20 \times 13$  mm.
2. *Nerita scabricosta* Lamarck, 1822. Aperture, size –  $43 \times 40$  mm.
3. *Turbo fluctuosus* Wood, 1828. Aperture, size –  $31 \times 30$  mm.
4. *Turbo saxosus* Wood, 1828. Aperture, size –  $16 \times 15$  mm.
5. *Cerithium stercusmuscarum* Valenciennes, 1833. Aperture, size –  $26 \times 11$  mm.
6. *Vernicularia pellucida* (Broderip and Sowerby, 1829). Aperture, size –  $16 \times 9$  mm.
7. *Pyrene fuscata* (Sowerby, 1832). Aperture, size –  $18 \times 11$  m.
8. *Purpura patula pansa* Gould, 1852. Aperture, size –  $37 \times 24$  mm.
9. *Jenneria pustulata* (Solander, 1786). A. Dorsal, B. Aperture, size –  $16 \times 10$  mm.
10. *Siphonaria maura* Sowerby, 1835. A. Dorsal, B. Interior and animal, size –  $7 \times 8$  mm.
11. *Arcopsis solida* Sowerby, 1833. A. Exterior, B. Interior, size –  $12 \times 7$  mm.
12. *Isognomon chemnitzianus* (Orbigny, 1853). A. Exterior, B. Interior, size –  $33 \times 23$  mm.
13. *Cardita affinis californica* Deshayes, 1854. A. Exterior, B. Interior, size –  $65 \times 28$  mm.
14. *Anomia adamas* Gray, 1850. A. Exterior, B. Interior, size –  $32 \times 27$  mm.



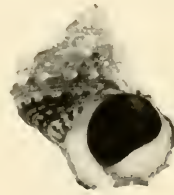
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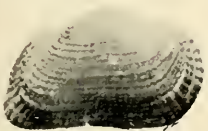
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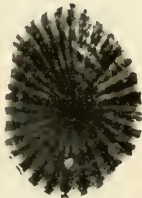
9 a



9 b



11 a



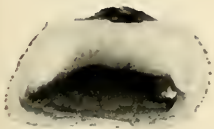
10 a



10 b



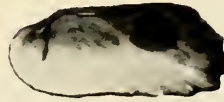
12 a



11 b



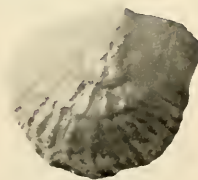
13 a



13 b



12 b



14 a



14 b



PLATE II.

II. Sand beaches and sand flats to 10 meters.

Fig.

1. *Cerithium maculosum* Kiener, 1841. Aperture, size -  $45 \times 27$  mm.
2. *Turritella leucostoma* Valenciennes, 1832. Aperture, size -  $69 \times 16$  mm.
3. *Strombus granulatus* Swainson, 1822. Aperture, size -  $81 \times 40$  mm.
4. *Oliva incrassata* (Solander, 1786). Aperture, size -  $60 \times 33$  mm.
5. *Olivella fletcheræ* Berry, 1958. Aperture, size -  $11 \times 4$  mm.
6. *Bulla gouldiana* Pilsbry, 1895. Aperture, size -  $40 \times 28$  mm.
7. *Anadara multicosata* (Sowerby, 1833). A. Exterior, B. Interior, size -  $53 \times 46$  mm.
8. *Anadara labiosa* (Sowerby, 1833). A. Exterior, B. Interior, size -  $20 \times 14$  mm.
9. *Diplodonta sericata* (Reeve, 1850). A. Exterior, B. Interior, size -  $10 \times 10$  mm.
10. *Tivela byronensis* (Gray, 1838). A. Exterior, B. Interior, size -  $39 \times 33$  mm.
11. *Megapitaria squalida* (Sowerby, 1835). A. Exterior, B. Interior, size -  $67 \times 54$  mm.
12. *Dosinia dunkeri* (Philippi, 1844). A. Exterior, B. Interior, size -  $61 \times 63$  mm.
13. *Dosinia ponderosa* (Gray, 1838). A. Exterior, B. Interior, size -  $123 \times 114$  mm.
14. *Anomalocardia subimbricata tumens* (Verrill, 1870). A. Exterior, B. Interior, size -  $29 \times 25$  mm.
15. *Pitar lupanaria* (Lesson, 1830). Exterior, size -  $26 \times 20$  mm.
16. *Heterodonax bimaculatus* (Linné, 1758). A. Exterior, B. Interior, size -  $26 \times 15$  mm.
17. *Mulinia pallida* (Broderip and Sowerby, 1829). A. Exterior, B. Interior, size -  $49 \times 36$  mm.
18. *Tellina felix* Hanley, 1844. Interior, size -  $10 \times 5$  mm.
19. *Donax carinatus* Hanley, 1843. Exterior, size -  $26 \times 15$  mm.
20. *Donax punctatostratus* Hanley, 1843. A. Exterior, B. Interior, size -  $32 \times 21$  mm.
21. *Tagelus affinis* (C. B. Adams, 1852). A. Exterior, B. Interior, size -  $48 \times 18$  mm.

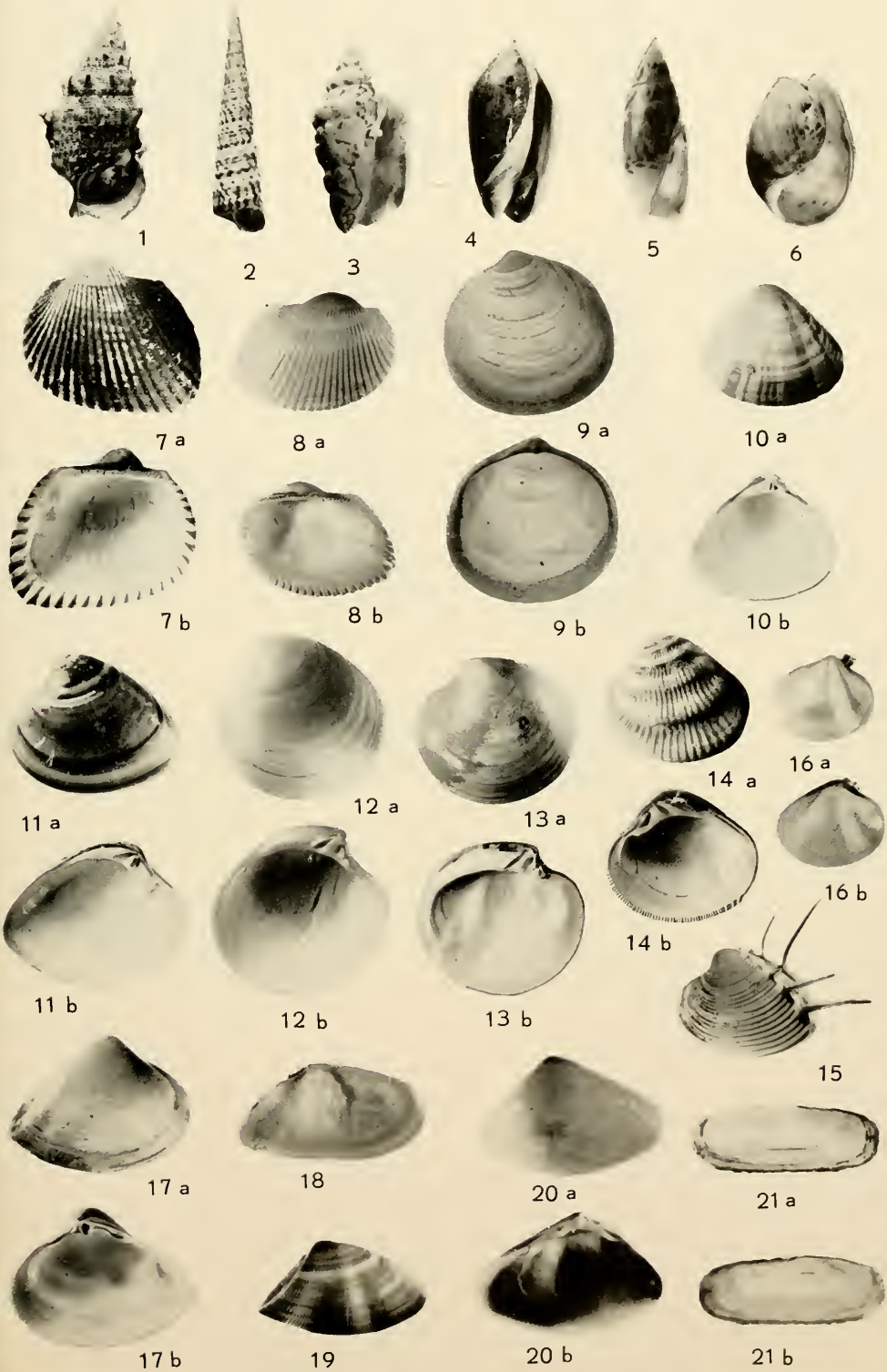


PLATE III.

III. Lagoons and mangrove swamps.

Fig.

1. *Littoridina*, sp. Aperture, size -  $3 \times 2$  mm.
2. *Cerithidea mazatlanica* Carpenter, 1856. Aperture, size -  $26 \times 11$  mm.
3. *Cerithidea montagnei* (Orbigny, 1837). Aperture, size -  $30 \times 17$  mm.
4. *Anadara tuberculosa* (Sowerby, 1833). A. Exterior, B. Interior, size -  $65 \times 45$  mm.
5. *Crassostrea corteziensis* Hertlein, 1951. A. Exterior, B. Interior, size -  $80 \times 45$  mm.
6. *Crassostrea columbiensis* Hanley, 1846. Interior, size -  $45 \times 50$  mm.
7. *Crassostrea corteziensis* Hertlein, 1951. Interior, size -  $126 \times 60$  mm (large example).
8. *Polymesoda olivacea* (Carpenter, 1855). A. Exterior, B. Interior, size -  $21 \times 18$  mm.
9. *Polymesoda mexicana* (Broderip and Sowerby, 1829). A. Exterior, B. Interior, size -  $42 \times 43$  mm.



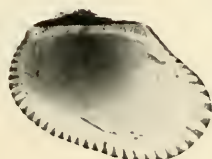
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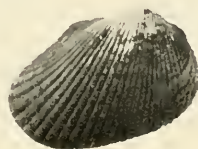
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3



4 b



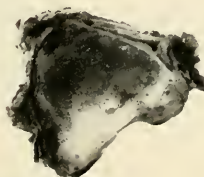
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5 a



5 b



6



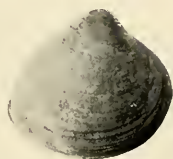
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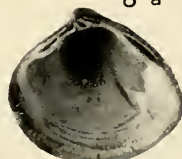
8 a



8 b



9 a



9 b

PLATE IV.

IV. Nearshore shelf, 11-26 meters.

Fig.

1. *Architectonica nobilis* Röding, 1798. Aperture, size -  $10 \times 21$  mm.
2. *Crucibulum spinosum* (Sowerby, 1824). Exterior, size  $17 \times 14$  mm.
3. *Natica broderipiana* Recluz, 1844. Aperture, size -  $24 \times 23$  mm.
4. *Polinices reclusianus* (Deshayes, 1839). Aperture, size -  $24 \times 25$  mm.
5. *Polinices otis* (Broderip and Sowerby, 1829). Aperture, size -  $10 \times 10$  mm.
6. *Sinum debile* (Gould, 1853). Aperture, size -  $8 \times 2$  mm.
7. *Hexaplex erythrostomus* (Swainson, 1831). Aperture, size -  $95 \times 71$  mm.
8. *Hexaplex brassica* (Lamarck, 1822). Aperture, size -  $79 \times 58$  mm.
9. *Strombus gracilior* Sowerby, 1825. Aperture, size -  $67 \times 47$  mm.
10. *Nassarius versicolor* (C. B. Adams, 1852). Aperture, size -  $9 \times 5$  mm.
11. *Oliya spicata* (Röding, 1798). Aperture, size -  $32 \times 17$  mm.
12. *Mitra erythrogramma* Tomlin, 1931. Aperture, size -  $17 \times 6$  mm.
13. *Hormospira maculosa* (Sowerby, 1834). Aperture, size -  $45 \times 14$  mm.
14. *Anadara obesa* (Sowerby, 1833). A. Exterior, B. Interior, size -  $22 \times 16$  mm.
15. *Anadara nux* (Sowerby, 1833). A. Exterior, B. Interior, size -  $19 \times 17$  mm.
16. *Adrana penascoensis* (Lowe, 1935). Exterior, size -  $16 \times 5$  mm.
17. *Modiolus eiseni* Strong and Hertlein, 1937. Exterior, size -  $17 \times 12$  mm.
18. *Crassatella gibbosa* Sowerby, 1832. A. Exterior, B. Interior, size -  $30 \times 18$  mm.
19. *Trigoniocardia granifera* (Broderip and Sowerby, 1829). Exterior, size -  $8 \times 7$  mm.
20. *Trachycardium panamense* (Sowerby, 1833). Exterior, size -  $18 \times 18$  mm.
21. *Chlamys tumbezensis* (Orbigny, 1846). A. Exterior, B. Interior, size -  $15 \times 14$  mm.
22. *Chlamys circularis* (Carpenter, 1864). A. Exterior, B. Interior, size -  $33 \times 30$  mm.
23. *Laevicardium elenense* (Sowerby, 1840). Exterior, size -  $13 \times 12$  mm.
24. *Mastra californica* Conrad, 1837. Exterior, size -  $33 \times 23$  mm.
25. *Pitar conceinnus* (Sowerby, 1835). A. Exterior, B. Interior, size -  $24 \times 17$  mm.
26. *Chione mariae* (Orbigny, 1846). Exterior, size -  $30 \times 20$  mm.
27. *Pandora claviculata* Carpenter, 1856. A. Exterior, B. Interior, size -  $30 \times 12$  mm (Broken).
28. *Tellina arenica* Hertlein and Strong, 1949. Exterior, size -  $13 \times 8$  mm.
29. *Donax gracilis* Hanley, 1845. A. Exterior, B. Interior, size -  $18 \times 7$  mm.
30. *Lyonsia gouldii* Dall, 1915. Exterior, size -  $13 \times 6$  mm.





PLATE V.

V. Intermediate shelf, 27 to 65 meters.

Fig.

1. *Calliostoma bonita* Strong, Hanna, and Hertlein, 1933. Aperture, size -  $20 \times 21$  mm.
2. *Astele rema* (Strong, Hanna, and Hertlein, 1933). Aperture, size -  $9 \times 12$  mm.
3. *Solariella triplostephanus* Dall, 1910. Aperture, size -  $6 \times 7$  mm.
4. *Architectonica placentalis* (Hinds, 1844). Aperture, size -  $8 \times 19$  mm.
5. *Polinices uber* (Valenciennes, 1832). Aperture, size -  $16 \times 12$  mm.
6. *Cassis centiquadrata* (Valenciennes, 1832). Aperture, size -  $42 \times 32$  mm.
7. *Distorsio decussatus* (Valenciennes, 1832). Aperture, size -  $47 \times 25$  mm.
8. *Bursa californica sonora* Berry, 1960. Aperture, size -  $51 \times 36$  mm.
9. *Bursa nana* (Broderip and Sowerby, 1829). Aperture, size -  $50 \times 30$  mm.
10. *Murex recurvirostris* Broderip, 1833. Aperture, size -  $43 \times 23$  mm.
11. *Eupleura muriciformis* (Broderip, 1833). Aperture, size -  $26 \times 16$  mm.
12. *Cantharus*, n. sp. Aperture, size -  $37 \times 24$  mm.
13. *Fusinus dupetitthouarsi* (Kiener, 1846). Aperture, size -  $79 \times 25$  mm.
14. *Mitra hindsii* Reeve, 1844. Aperture, size -  $24 \times 8$  mm.
15. *Harpa crenata* Swainson, 1822. Aperture, size -  $34 \times 21$  mm.
16. *Clavus roseolus* (Hertlein and Strong, 1955). Aperture, size -  $17 \times 7$  mm.
17. *Pleuroliria picta* (Reeve, 1843). Aperture, size -  $36 \times 11$  mm.
18. *Anodontia edentuloides* (Verrill, 1870). A. Exterior, B. Interior, size -  $40 \times 37$  mm.
19. *Trachycardium belcheri* (Broderip and Sowerby, 1829). A. Exterior, B. Interior, size -  $29 \times 30$  mm.
20. *Eucrassatella gibbosa* forma *rudis* Sowerby, 1832. A. Exterior, B. Interior, size -  $45 \times 28$  mm.
21. *Tellina pristiphora* Dall, 1900. A. Exterior, B. Interior, size -  $38 \times 28$  mm.
22. *Semele paziana* Hertlein and Strong, 1949. A. Exterior, B. Interior, size -  $27 \times 21$  mm.
23. *Nemocardium pazianum* (Dall, 1916). Exterior, size -  $11 \times 10$  mm.

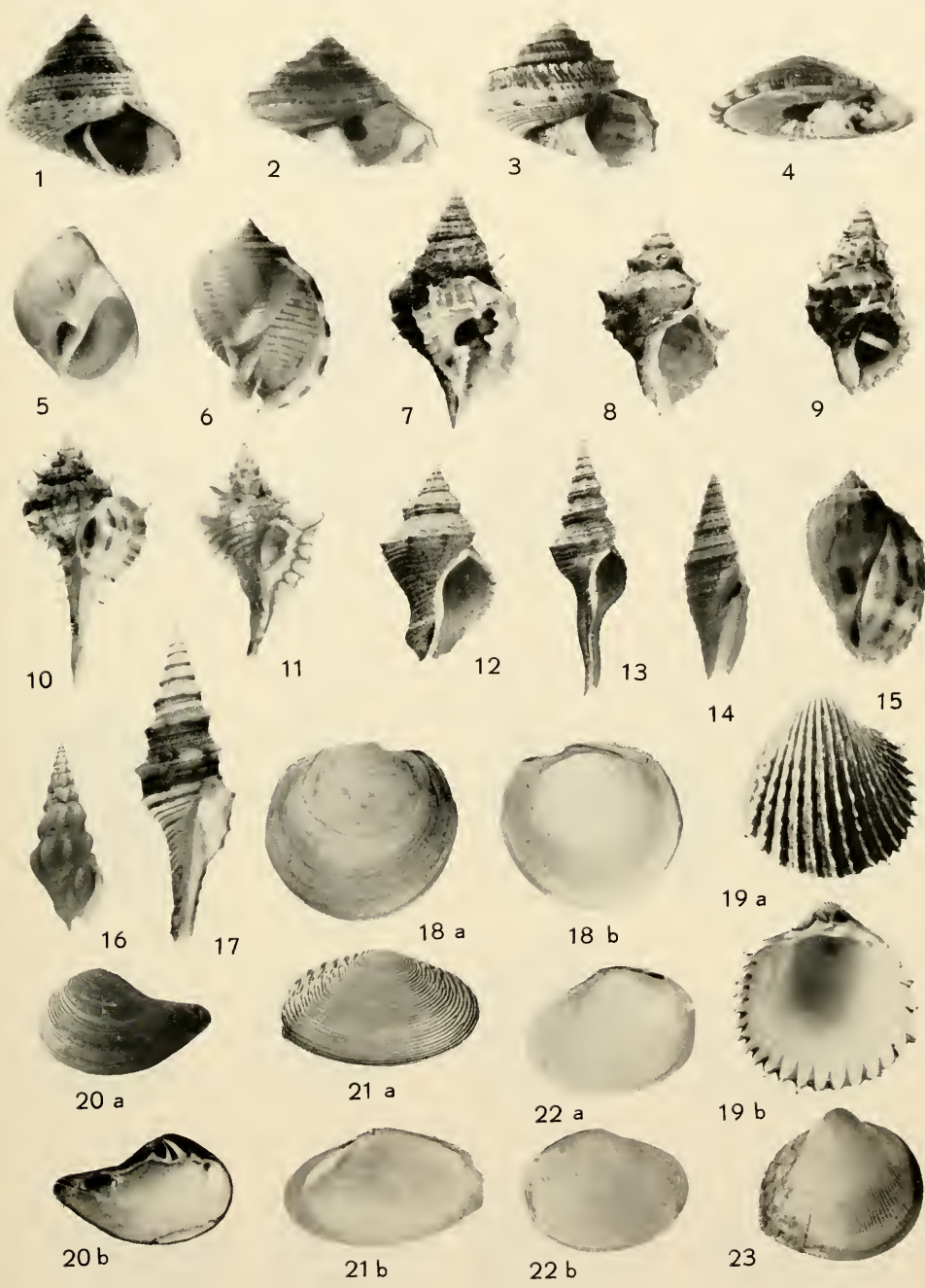


PLATE VI.

VI. Outer shelf, southern gulf, clay bottom, 66-120 meters.

Fig.

1. *Crucibulum*, n. sp. A. Exterior, B. Interior, size -  $31 \times 27$  mm.
2. *Nassarius catallus* Dall, 1908. Aperture, size -  $17 \times 10$  mm.
3. *Conus arcuatus* Broderip and Sowerby, 1829. Aperture, size -  $40 \times 20$  mm.
4. *Anadara mazatlanica* (Hertlein and Strong, 1943). A. Exterior, B. Interior, size -  $42 \times 27$  mm.
5. *Chione kelletii* (Hinds, 1845). A. Exterior, B. Interior, size -  $53 \times 43$  mm.
6. *Pitar mexicanus* Hertlein and Strong, 1948. A. Exterior, B. Interior, size -  $50 \times 40$  mm.
7. *Periploma carpenteri* Dall, 1896. A. Exterior, B. Interior, size -  $30 \times 42$  mm.

VII. Outer shelf, northern gulf, sand bottom, 66-120 meters.

8. *Polinices intemeratus* (Philippi, 1853). Aperture, size -  $9 \times 9$  mm.
9. *Strombus granulatus* Swainson, 1822. (Pliocene?). Aperture, size -  $69 \times 43$  mm.
10. *Cymatium anictum* (Reeve, 1844). Aperture, size -  $34 \times 18$  mm.
11. *Pleuroliria nobilis* (young) (Hinds, 1843). Aperture, size -  $32 \times 17$  mm.
12. *Pleuroliria oxytropis* (Sowerby, 1834). Aperture, size -  $19 \times 6$  mm.
13. *Glycymeris tessellata* (deep form) (Sowerby, 1833). Exterior, size -  $25 \times 25$  mm.
14. *Lucinoma annulata* (Reeve, 1850). A. Exterior, B. Interior, size -  $43 \times 38$  mm.
15. *Nemocardium centifilosum* (Carpenter, 1864). A. Exterior, B. Interior, size -  $10 \times 9.5$  mm.
16. *Macoma lamproleuca* (Pilsbry and Lowe, 1932). A. Exterior, B. Interior, size -  $36 \times 21$  mm.
17. *Corbula ventricosa* Adams and Reeve, 1850. Exterior (whole), size -  $11 \times 7$  mm.



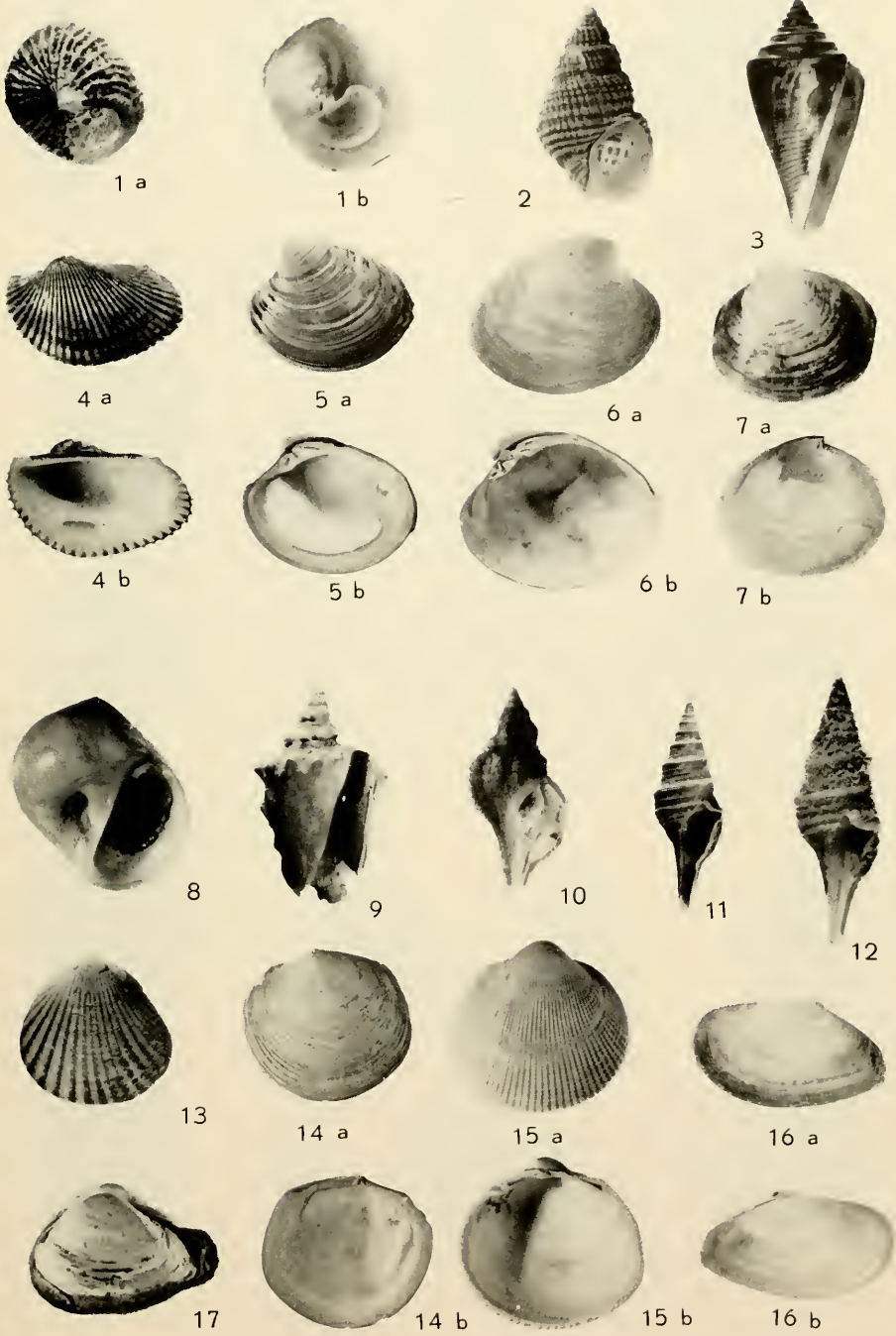




PLATE VII.

VIII. Deep northern basins and troughs, 230-1,500 meters.

Fig.

1. *Turritella*, sp. Aperture, size -  $37 \times 10$  mm.
2. *Boreotrophon*, n. sp. Aperture, size -  $40 \times 19$  mm.
3. *Fusinus traski* Dall, 1915. Aperture, size -  $43 \times 15$  mm.
4. *Acila castrensis* Hinds, 1843. Exterior, size -  $11 \times 10$  mm.
5. *Nuculana taphria* (Dall, 1897). Exterior, size -  $13 \times 8$  mm.
6. *Nuculana hamata* Carpenter, 1864. A. Exterior, B. Interior, size -  $11 \times 6$  mm.
7. *Glycymeris cortezianus* (Dall, 1901). A. Exterior, B. Interior, size -  $19 \times 8$  mm.
8. *Cardita barbarensis* (Stearns, 1890). A. Exterior, B. Interior, size -  $17 \times 15$  mm.
9. *Lucina tenuisculpta* (Carpenter, 1864). A. Exterior, B. Interior, size -  $8 \times 7.5$  mm.
10. *Hiatella arctica* (Linne, 1767). A. Exterior, B. Interior, size -  $11 \times 6$  mm.

IX. Upper slope, central and southern gulf, 121-730 meters.

11. *Puncturella expansa* Dall, 1896. A. Exterior, B. Interior (animal), size -  $23 \times 20$  mm.
12. *Solariella permabilis* Carpenter, 1864. Aperture, size -  $7 \times 9$  mm.
13. *Nassarius insculptus gordanus* Hertlein and Strong, 1951. Aperture, size -  $22 \times 12$  mm.
14. *Nassarius miser* (Dall, 1908). Aperture, size -  $12 \times 7$  mm.
15. *Clathurella thalassoma* (Dall, 1908). Aperture, size -  $22 \times 8$  mm.
16. *Nucula cardara* Dall, 1917. Exterior, size -  $10 \times 7$  mm.
17. *Cyclopecten zacae* (Hertlein, 1935). Exterior, size -  $8 \times 7$  mm.

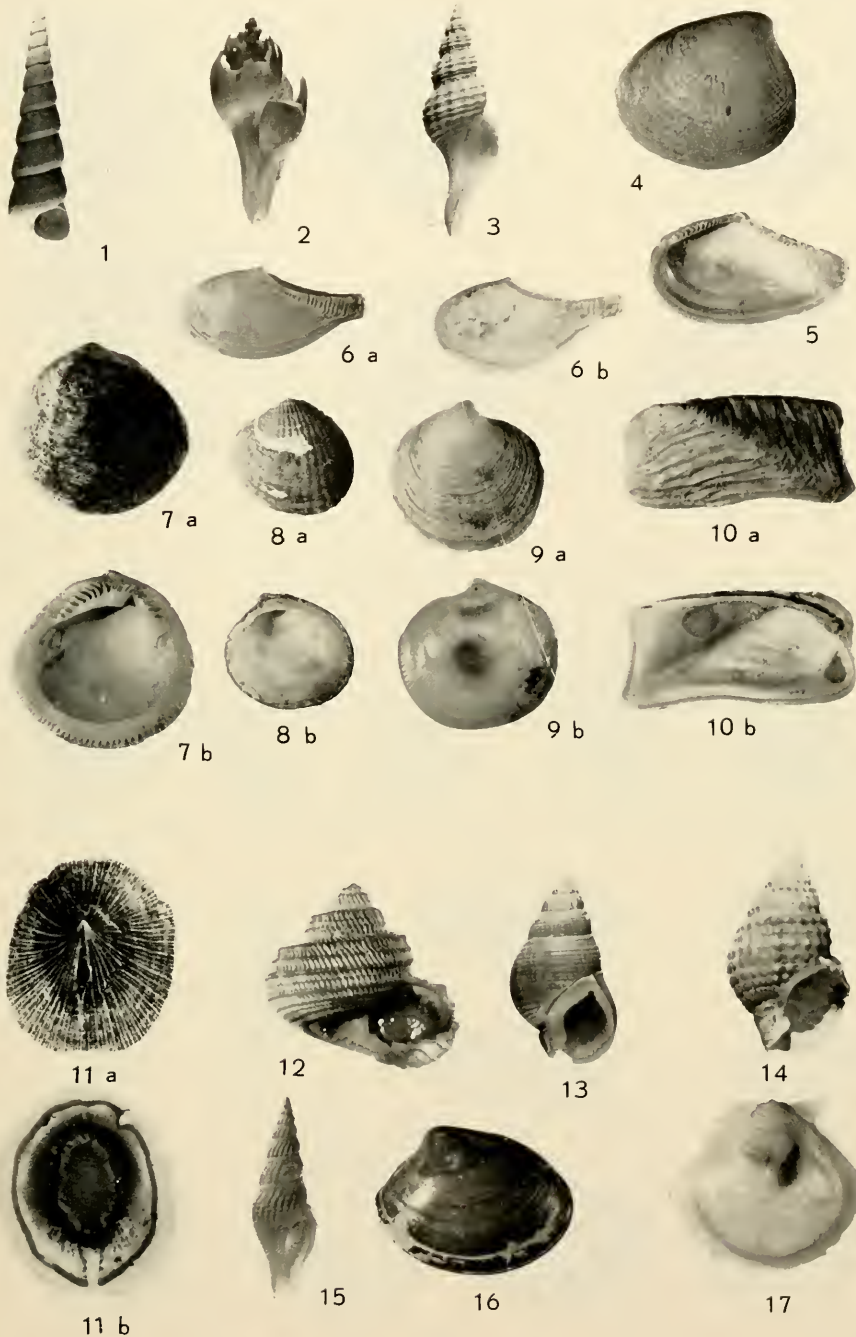


PLATE VIII.

X. Middle slope, 731 to 1,799 meters.

Fig.

1. *Coeculina diomedea* Dall, 1908 (?). Exterior, size -  $9 \times 6$  mm.
2. *Turricula bairdii* Dall, 1889. Aperture, size -  $44 \times 41$  mm.
3. *Solariella nuda* Dall, 1896. Aperture, size -  $10 \times 13$  mm.
4. *Solemya agassizi* Dall, 1908. A. Exterior, B. Interior, size -  $42 \times 18$  mm.
5. *Vesicomya lepta* Dall, 1896. A. Exterior, B. Interior, size -  $45 \times 33$  mm.

XII. California borderland basins, 1,641 to 2,358 meters.

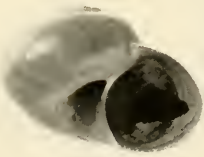
6. *Colus halidonus* Dall, 1919. Aperture, size -  $34 \times 20$  mm.
7. *Colus* cf. *halli* Dall, 1873. Aperture, size -  $34 \times 20$  mm.
8. *Colus trophius* Dall, 1919. Aperture, size -  $29 \times 16$  mm.
9. *Ancistrolepis magnus* Dall, 1894. Aperture, size -  $60 \times 46$  mm.
10. *Buccinum diplosetum* Dall, 1907. Aperture, size -  $16 \times 11$  mm.
11. *Chrysodomus liratus* Martyn, 1784. Aperture, size -  $67 \times 37$  mm.
12. *Antiplanes vinosa* Dall, 1874. Aperture, size -  $27 \times 13$  mm.
13. *Solemya* cf. *johnsoni* Dall, 1891. A. Exterior, B. Interior, size -  $65 \times 30$  mm.
14. *Malletia faba* Dall, 1897. A. Exterior, B. Interior, size -  $18 \times 11$  mm.
15. *Cyclopecten randolphi tillamookensis* (Arnold, 1906). Exterior, size -  $23 \times 23$  mm.
16. *Chlamys latiaurata monotimeris* (Conrad, 1837). Exterior, size -  $23 \times 23$  mm.
17. *Vesicomya stearnsi* Dall, 1895. A. Exterior, B. Interior, size -  $45 \times 33$  mm.



1



2



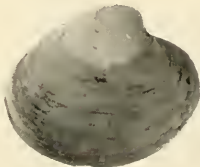
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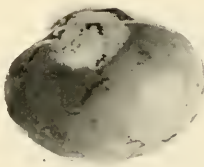
4 a



4 b



5 a



5 b



6



7



8



9



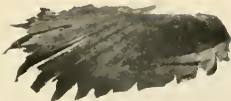
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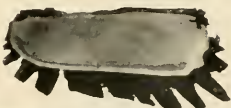
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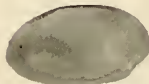
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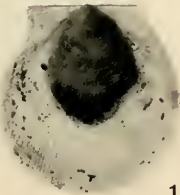
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14 a



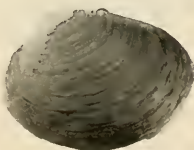
14 b



15



16



17 a



17 b

PLATE IX.

XI. Abyssal southern borderland basins and lower slope,  
1,800 to 4,122 meters.

Fig.

1. Chitinous gastropod (?). A. Aperture, B. Back, size -  $50 \times 35$  mm.
2. *Solariella ceratophora* Dall, 1896. Aperture, size -  $21 \times 19$  mm.
3. *Solariella equatorialis* Dall, 1908. Aperture, size -  $23 \times 20$  mm.
4. *Fusinus rufocandatus* Dall, 1896. Aperture, size -  $40 \times 11$  mm.
5. *Tractolira sparta* Dall, 1896. Aperture, size -  $19 \times 9$  mm.
6. *Pleuromella clarinda* Dall, 1908. Aperture and animal, size -  $67 \times 29$  mm.
7. *Steiraxis anilaca* Dall, 1896. Aperture, size -  $52 \times 21$  mm.
8. *Turris (Gemmula)* sp. (see Dall, 1889). Aperture, size -  $42 \times 29$  mm.
9. *Solemya agassizi* Dall, 1908. A. Exterior, B. Interior, size -  $42 \times 18$  mm.
10. *Nucula panamina* Dall, 1908. A. Exterior, B. Interior, size -  $15 \times 10$  mm.
11. *Nuculana agapea* (Dall, 1908). A. Exterior, B. Interior, size -  $21 \times 12$  mm.
12. *Tindaria compressa* Dall, 1908. A. Exterior, B. Interior, size -  $10 \times 8$  mm.
13. *Limopsis compressus* Dall, 1908. A. Exterior, B. Interior, size -  $29 \times 20$  mm.
14. *Arca corpulenta pompholynx* Dall, 1908. A. Exterior, B. Interior, size -  $25 \times 29$  mm.
15. *Arca* cf. *nucleator* Dall, 1908. A. Exterior, B. Interior, size -  $14 \times 15$  mm.
16. *Abra profundorum* E. A. Smith, 1885. Exterior (Broken, whole), size -  $20 \times 13$  mm.
17. *Cuspidaria panamensis* Dall, 1908. Exterior, size -  $42 \times 25$  mm.
18. *Myonera garretti* Dall, 1908. Exterior, size -  $21 \times 15$  mm.
19. *Poromya perla* Dall, 1908. Exterior (whole), size -  $18 \times 17$  mm.



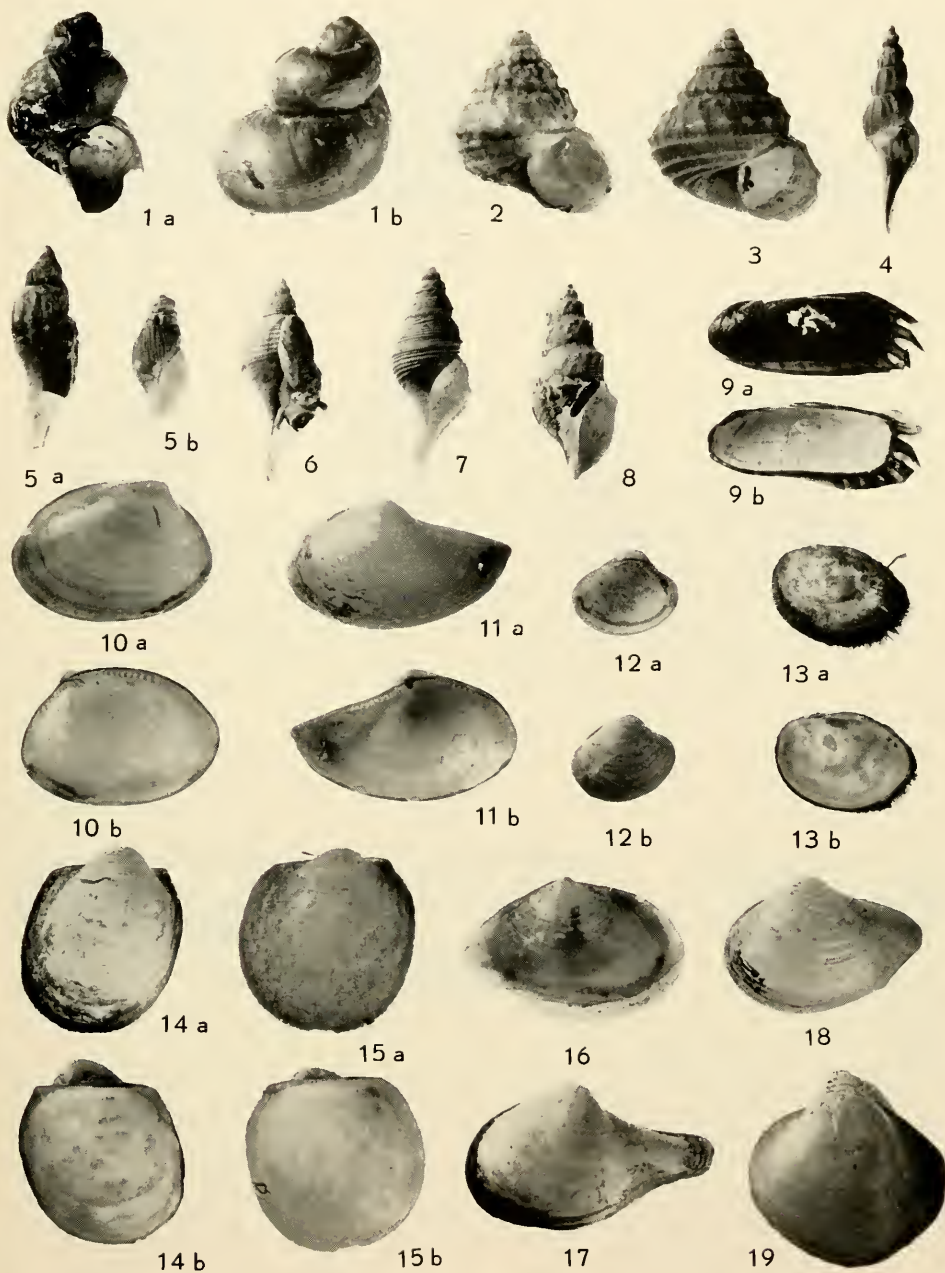


PLATE X.

Some bathyal and abyssal mollusks illustrated by artist Poul Winther  
of Copenhagen, Denmark.

Fig.

1. *Emarginula velascoensis* Shasky, 1961. Upper slope.  
A. Side view, B. Top, C. Interior with animal.
2. Chitonous gastropod (?). Abyssal southern borderland. Aperture (see Plate 1X).
3. *Steiraxis aulaca* Dall, 1896. Abyssal southern borderland. Aperture (see Plate 1X).
4. *Fusinus rufocaudatus* Dall, 1896. Abyssal southern borderland. (see Plate 1X).
5. *Turris (Gemmula)*, sp. Abyssal southern borderland, Aperture (see Plate 1X).
6. *Solemya agassizi* Dall, 1908. Abyssal southern borderland. A. Whole live specimen, with undescribed hydroid attached to one end, B. Interior (see Plate 1X).
7. *Solemya valvulus* Carpenter, 1864. Upper slope. Whole live specimen.

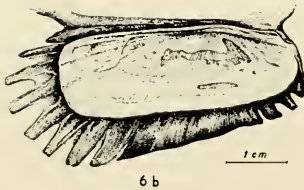
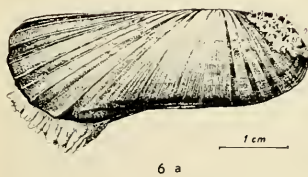
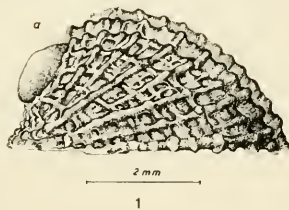
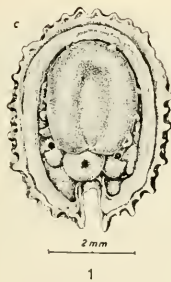


PLATE XI.

Abyssal holothurian, probably in the family Psychropotidae, photographed on the bottom in 3550 meters at 28° 56' N. Lat., 117° 30' W. Long., Guadalupe Basin near Biology Station 276, off Punta Eugenia, Baja California. Courtesy DALE F. KRAUSE.





PLATE XII.

Photograph of bottom at a depth of 1935 meters at  $31^{\circ}19' N.$  Lat.,  $117^{\circ}28' W.$  Long. off Cabo Colnett, Baja California, a few miles from Biology Station 137. Appearing in area of about 2 square meters are three ophiuroids, a 6 inch long holothurian, two large chitonous tube-forming polychaetes, and a possible Antipitharian. Most of these were taken in the nearby trawl. Courtesy DALE F. KRAUSE.



PLATE XIII.

Photograph from same area as PLATE XII., off Cabo Colnett. Shown here in less than 2 square meters are one Hexactinellid sponge, two ophiuroids, one fish and 4 polychaetes.

Note tracks of armoured polychaetes. Courtesy DALE F. KRAUSE.



PLATE XIV.

Same station as PLATE XIII. Area less than one square meter. Note polychaete extending out of tube. Munid crab (possibly *Munidopsis bairdii*), apparently clinging to glass sponge, and ophiuroid in left-hand corner. Courtesy DALE F. KRAUSE.





PLATE XV.

- A. Sea bottom near same station 137 in Animal Basin off Cape Colnett, 1935 meters. Area about 3 square meters. Note 4 large ophiuroids, 3 tubed-polychaetes, and numerous large burrows. Courtesy DALE F. KRAUSE.
- B. Enlargement of polychaete in PLATE XIV. Note signs of intense bottom activity, consisting of tracks, holes, and general disturbance. Courtesy of DALE F. KRAUSE.



