ZOOGEOGRAPHY AND ECOLOGY OF MACRO-INVERTEBRATES OF GULF OF CALIFORNIA AND CONTINENTAL SLOPE OF WESTERN MEXICO[1]

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ABSTRACT

Based on a reconnaissance study of the zoogeography and ecology of benthic invertebrates in the Gulf of California, 11 faunal assemblages have been established which characterize various environments—(I) intertidal rocky shores; (II) intertidal beaches and sand flats to 10 m; (III) low-salinity lagoons and mangrove mud flats; (IV) nearshore shelf, sand bottom, 11–26 m; (V) intermediate shelf, clayey sand and sandy clay bottom, 27–65 m; (VI) outer shelf, clay bottom, southern Gulf, 66–120 m; (VII) outer shelf, sand bottom, northern Gulf, 66–120 m; (VIII) northern Gulf basins and troughs, 230–1,500 m; (IX) upper slope, central and southern Gulf, 121–730 m; (X) middle slope, 731–1,799 m; (XI) abyssal southern borderland basins and lower slope, 1,800–4,122 m.

Compared with benthic communities elsewhere in the world, the diversity of shallow-water species in the Gulf of California is striking. No single species is dominant. The distribution of shell remains with depth provides indications for former low stands of sea level. Shells of shallow-water species at 110–115 m were dated by radiocarbon method at 17,000 to 19,000 years B.P. Shells belonging to the California shelf province are found in abundance in deposits of the northern Gulf basins and in deep water in the southern end of the Gulf. The occurrence of these cold-water species implies that during the Pleistocene, migration southward of more than 700 miles was possible.

Comparisons between the macro-invertebrate assemblages of the Gulf of California and those of the Gulf of Mexico and other parts of the world demonstrate that great similarities, generally at the subgeneric level, exist in similar environments throughout the subtropical and tropical regions of the world.

INTRODUCTION

Previous studies of the ecology and environmental distribution of macro-invertebrates by the author (Parker, 1956, 1959, 1960; Parker and Curray, 1956) were concerned with lagoons, bays, deltas, and, in part, with the continental shelf. In contrast, the investigation of the Gulf of California primarily deals with the continental shelf between 18 and 64 m, and with the continental slope and adjacent basins to a depth of more than 4,000 m. The present study, based on approximately 270 stations, is a reconnaissance intended to provide the basis for more detailed investigations in the future. It is the purpose of this paper to delineate the faunal assemblages of the Gulf of California, define in general terms their environments, and examine similarities and differences between the Gulf of California and other tropical and subtropical marine environments.

Sample stations are shown in Figures 1 (Gulf of

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Numerous staff members of the Scripps Institution of Oceanography have contributed material to this study. The assistance of F.P. Shepard, Tj.H. van Andel, and J.R. Curray has been especially valuable. R.W. Rowland assisted in the processing of the samples and in field work. Jerry Cook, Gail Cook, and Linda Lightbowen, summer students in a National Science Foundation program, helped in the compilation of the data. The statistical analysis used in the paper was programmed for the C.D.C. 1604 computer by E. Ferguson, Mrs. Anna Devore, R. Mitchell, and Mrs. Eileen Mitchell of the Computer Facility of the University of California in San Diego. C.L. Hubbs, R. Rosenblatt, R.L. Fisher, and G.I. Roden, all of Scripps Institution of Oceanography, supplied information and counsel.

A considerable portion of the biological work was carried out by the author at the Zoological Museum of the University of Copenhagen. The author is grateful for the permission to use its facilities and collections, and is especially indebted to H. Lemche, J. Knudsen, and N. Bjarnov for their criticism and assistance. Valuable ideas and information were also obtained from G. Thorson, W.K. Ockelmann and A. Møller-Christiensen of the University of Copenhagen Marine Biological Laboratory in Helsingør, Denmark. A large number of specialists in many institutions assisted in the identification of the specimens collected. To them, the author acknowledges his debt collectively. Most of the illustrations were prepared by N. Bjarnov; J. Freitas, of Denmark; and J.R. Moriarty, of Scripps Institution of Oceanography; the drawings of Plate 10 were executed by P. Winther.

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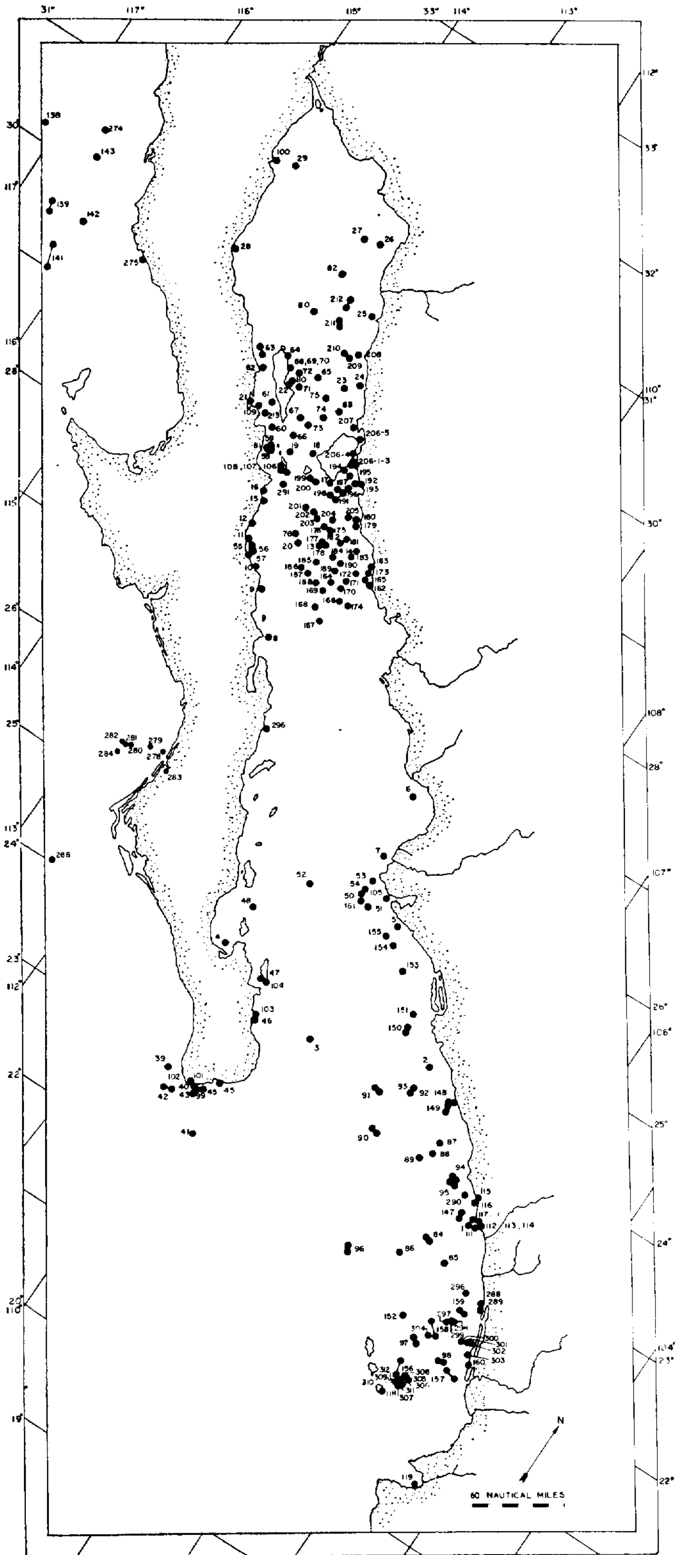


FIG. 1.—Station locations of biological samples, Gulf of California and west coast of Baja California.

California) and 2 (continental slope of western Mexico and California). Samples at the majority of the shallow-water stations were taken with a small shell dredge towed for 5 to 10 minutes, or with otter trawls; at all the deeper stations, with large beam and otter trawls or with a high-speed, deep-diving dredge (Isaacs and Kidd, 1953). A series of quantitative samples was obtained with Petersen and Van Veen grab samplers.

A fairly large set of physical and chemical data for the Gulf of California exists in the literature. In addition, numerous measurements were made in connection with the present program of Gulf of California studies. Sediment analyses are available for nearly all biological stations, and sediment maps are presented in papers by van Andel and by Curray and Moore (both, this volume).

The principal factors considered in explaining the distribution of invertebrates in the Gulf of California are depth, sediment composition, bottom-water temperature, salinity, turbulence, upwelling and oxygen content, and various biological processes.

METHODS OF COLLECTION AND DATA PROCESSING

Collections of biological material were made on the following expeditions—*Tuna Oceanographic Cruise II*, November 1958; *Vermilion Sea Expedition*, March-June 1959; *Southern Borderland Cruise III*, February 1960; *Orca Cruise, Gulf of California*, March–April 1960; *Holt Expedition*, December 1960; *Baja Slope Expedition*, May 1961; *Gulf of California Cruise*, November 1961—all under the sponsorship of the Scripps Institution of Oceanography (Figs. 1, 2). In all programs, biological sampling was part of a larger undertaking, so that sampling patterns were, in some instances, incidental. Few quantitative and standing-crop samples could be taken. After thorough sorting, all material that could not be identified by the author was sent to specialists. Sets of the mollusk material are stored at the Scripps Institution of Oceanography and at the Zoological Museum in Copenhagen; most of the other material was retained by the specialists who identified it. A complete list of these is included in Parker (1964).

DATA PROCESSING

Following methods partly developed by Tj.H. van Andel and J.R. Curray for geological data, all information obtained on the approximately 270 stations and 1,150 identified species has been recorded on I.B.M. cards. The system is discussed in detail in a comprehensive paper on the macro-invertebrate studies of the Gulf of California (Parker, 1964), which contains all data. By inspection, the ranges of various environmental parameters (depth, oxygen, sediment types, geographic locality) were subdivided into classes. A computer was used to list all species occurring in each of the environmental categories so established.

In another analysis, species were grouped on the basis of affinity calculated for all possible pairs of species. The index used was the geometric mean of the proportion of co-occurrences of each pair of species, minus a term that corrects for sample size (modified after Fager, 1957). Two sets of data, one for 136 species occurring in more than 8 stations each, and another 114 species with only 5 to 7 station occurrences, were used. For the first set, pairs of species were judged to show affinity if the index had a value of 0.495 or over; a cutoff value of 0.295 was used for a rerun of the first set and for the second set. A total of 55 groups with more than 5 affiliated species was formed from the first set of species; 22 groups with more than 3 affiliated species were formed from the second set. For each group, all stations that had large numbers of associated species were examined as to location and common environmental factors. Most of the significant species-groups produced station groupings with distinct geographic location and a well-defined range of environmental parameters. Details of the analysis are given in Parker (1964), and a program description can be obtained from the author. A similar analysis is feasible for ancient sediments if adequate paleontological data are available, and a direct comparison of the results with modern assemblages established in the same manner can be carried out rigorously.

Several other methods were used to determine the faunal assemblages of the Gulf of California. About 350 areal distribution maps of common species were prepared and compared with the distribution of ecological factors. Graphs of the depth ranges of living and dead specimens of the 1,150 species identified in the area were used to determine the depth concentration of each (Parker, 1964), and were checked against known

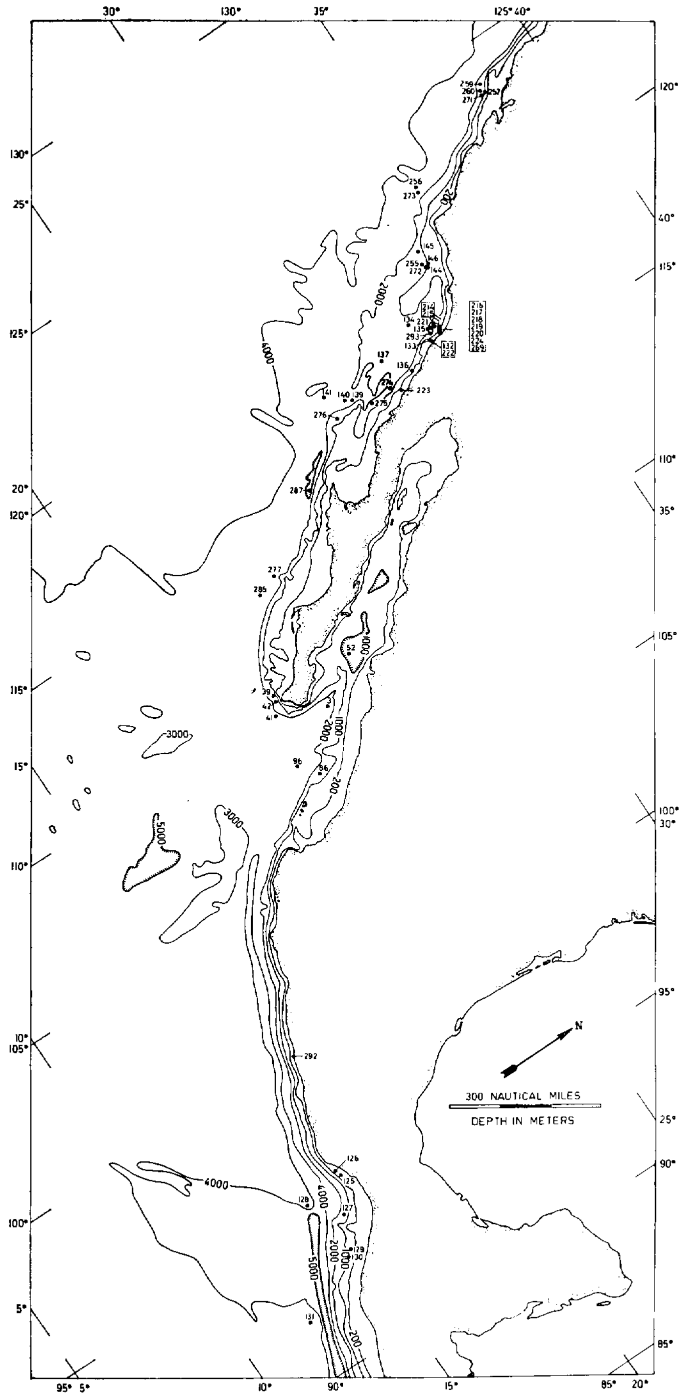


FIG. 2.—Station locations of biological samples, continental slope from San Francisco, California, to Guatemala.

ranges in the literature (Keen, 1958; Olsson, 1961; and various papers in the *Albatross Expedition* Reports). Complete taxonomic data have been listed by Parker (1964).

DESCRIPTION OF THE REGION INVESTIGATED

Most of the samples were collected in the Gulf of California and the adjacent southern area extending to Banderas Bay and the Tres Marías Islands (Fig. 3). The geology and morphology of this region have been discussed by Allison (this volume); Rusnak, Fisher, and Shepard (this volume); Anderson (1950); and Byrne and Emery (1960). Much of the Gulf, in particular along the western side, is bordered by high-cliff coasts with an abundance of rocky shores and numerous pocket beaches. The eastern side, on the other hand, is bordered by broad sandy beaches and mud flats in the area of the Colorado Delta, along the Costa de Hermosillo north of Guaymas, and south from the Yaqui River. Coastal lagoons are rare over most of the Gulf coastal region, which receives little rainfall, but they become important south of Mazatlán, where the rainfall increases to more than 50 inches near Puerto Vallarta. Information concerning these lagoons was obtained from J.R. Curray and F.B Phleger (oral communication), and from Keen (1958). A number of semi-enclosed bays in open contact with Gulf water occur along the west side, and a few tidal lagoons, some with hypersaline conditions, are found north of Guaymas. A few large lagoons occur on the Fuerte River delta, but little is known about their fauna. The continental shelf was sampled in detail in only two areas, the Costa de Hermosillo north of Guaymas, and the Costa de Nayarit south of Mazatlán. The shelf in this area is broad and gently sloping, and faunal assemblages are found that parallel those of the Gulf of Mexico. The western shelf is very narrow and absent locally. Little level bottom is present, and the rocky bottom is mainly inhabited by epifaunal species. The northern Gulf, north of Angel de Guarda and Tiburón Islands, contains a large, gently sloping shelf, very similar to the shelf of the Gulf of Mexico.

The largest part of the central and southern Gulf is occupied by deep basins, ranging from 1,000 to 3,600 m in depth, and bordered by relatively steep slopes. The basin floors are relatively flat, but the area available for level-bottom communities is small compared to the total area of the Gulf (Fig. 4).

The sediments of the Gulf of California (Figs. 5, 6) are discussed in detail by van Andel (this volume).

The northern Gulf, from the shoreline to depths exceeding 400 meters, is predominantly sandy. The only exceptions are the deep basin between Angel de la Guarda Island and the Peninsula, and its northern extension, a zone directly off the Colorado and Concepción River deltas, and some deeper deposits just east of Angel de la Guarda. In the central and southern Gulf, the sediments predominantly consist of silty clay, except for the shelf on the western side and the inner portions of the eastern shelf. The deeper basins and adjacent slopes north of the Fuerte River are covered with diatomaceous sediments. The eastern shelf generally shows a gradation from sands on the inner and middle portions to clayey silts on the outer margin and upper slope. Studies by Curray (oral communication; also *see* Fig. 6) show that, in detail, the pattern is complex and the deposits are commonly patchy, resulting in patchiness of the faunal assemblages.

OCEANOGRAPHIC CONDITIONS

Roden (this volume; also *see* Roden, 1958; Roden and Groves, 1959) has presented a summary of the physical oceanography of the Gulf of California. In addition, a substantial volume of information is available in the files of Scripps Institution of Oceanography. The following discussion is based on material from both sources.

Oxygen concentration data for bottom waters have been compiled for a depth range from about 40 to 3,000 m (Fig. 7). The northern Gulf is characterized by a normal decrease of oxygen content with increasing depth. South of Tiburón Island, a pronounced oxygen minimum is present at intermediate depth. Between approximately 100–200 and 1,200 m, the oxygen values are below 0.5 ml/L. Below 1,200 m, the values rise again to 1 ml/L in the southern basins and even higher at the entrance to the Gulf. An exception to this pattern is the basin off Guaymas, which has oxygen values of less than 0.5 ml/L at the bottom,

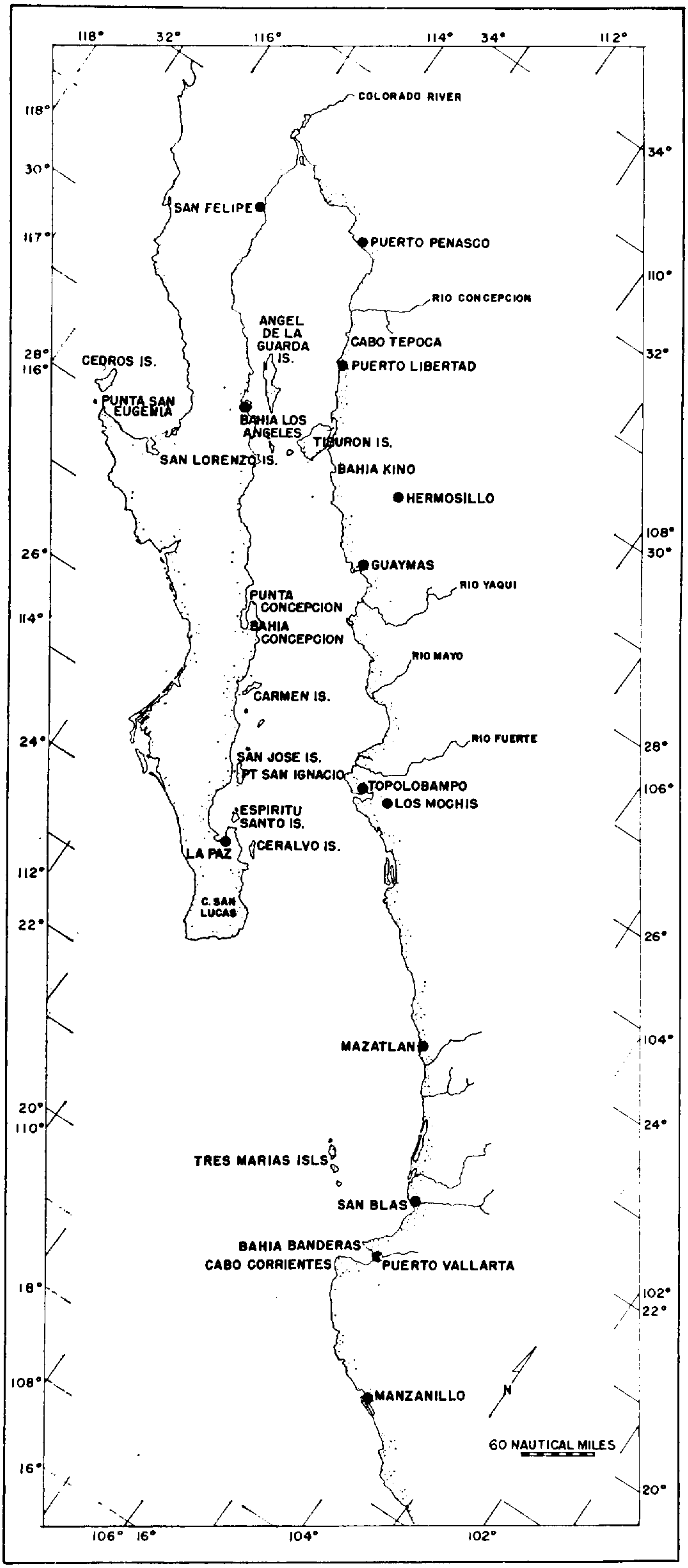


FIG. 3.—Place names of the Gulf of California region.

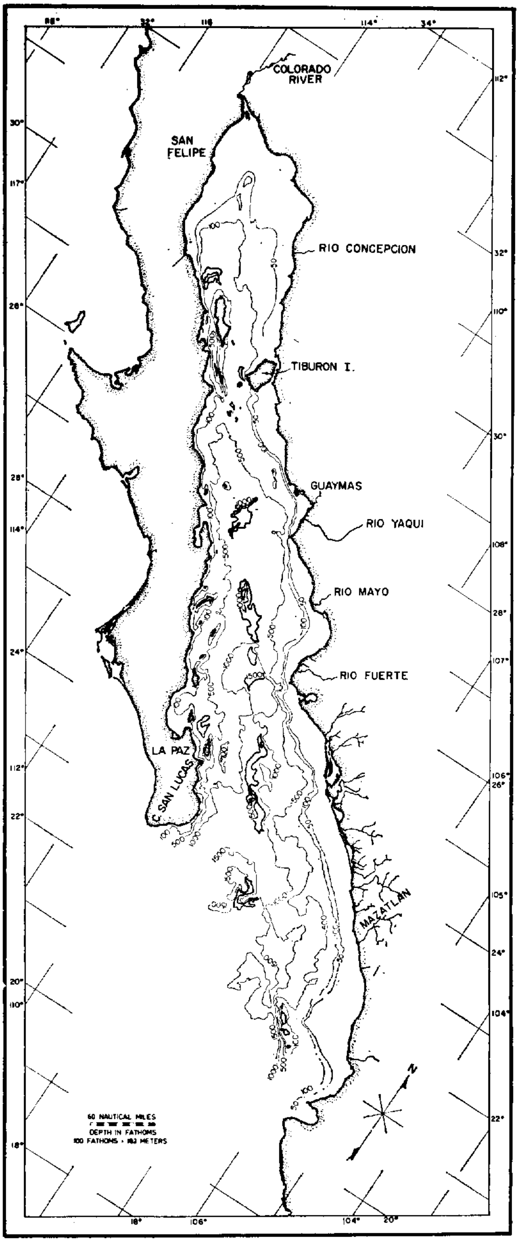


FIG. 4.—Bathymetry of the Gulf of California. Depth in fathoms. Simplified after Rusnak, Fisher, and Shepard (this volume).

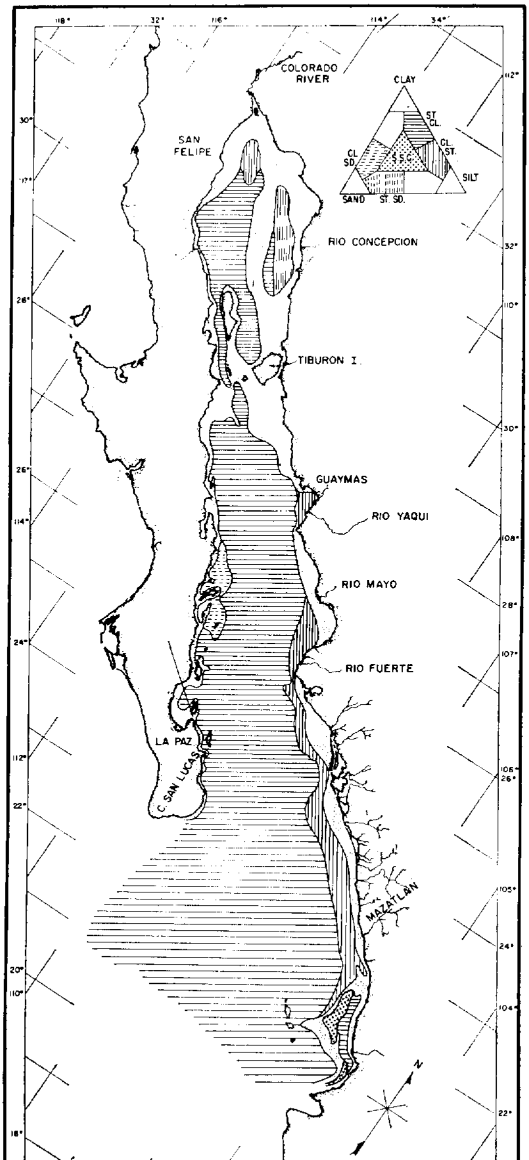


FIG. 5.—Sediments of the Gulf of California, based on data from van Andel (this volume, Fig. 21) and J.R. Curray (personal communication). Classification according to Shepard (1954).

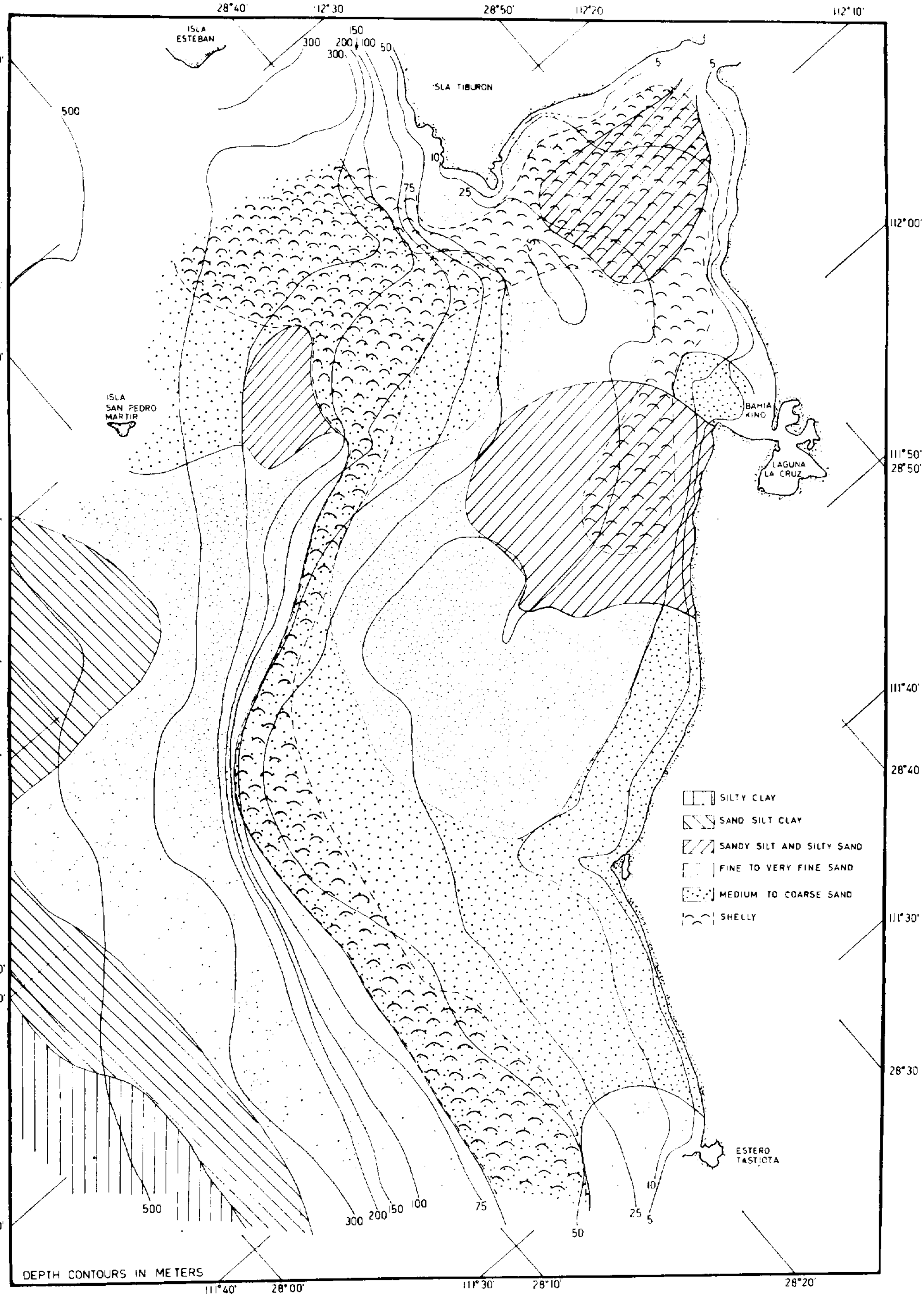


FIG. 6.—Sediment distribution in the Costa de Hermosillo region, southeast of Tiburón Island. Depth and sediment contours after J.R. Curray (personal communication). Shell zone added by this author.

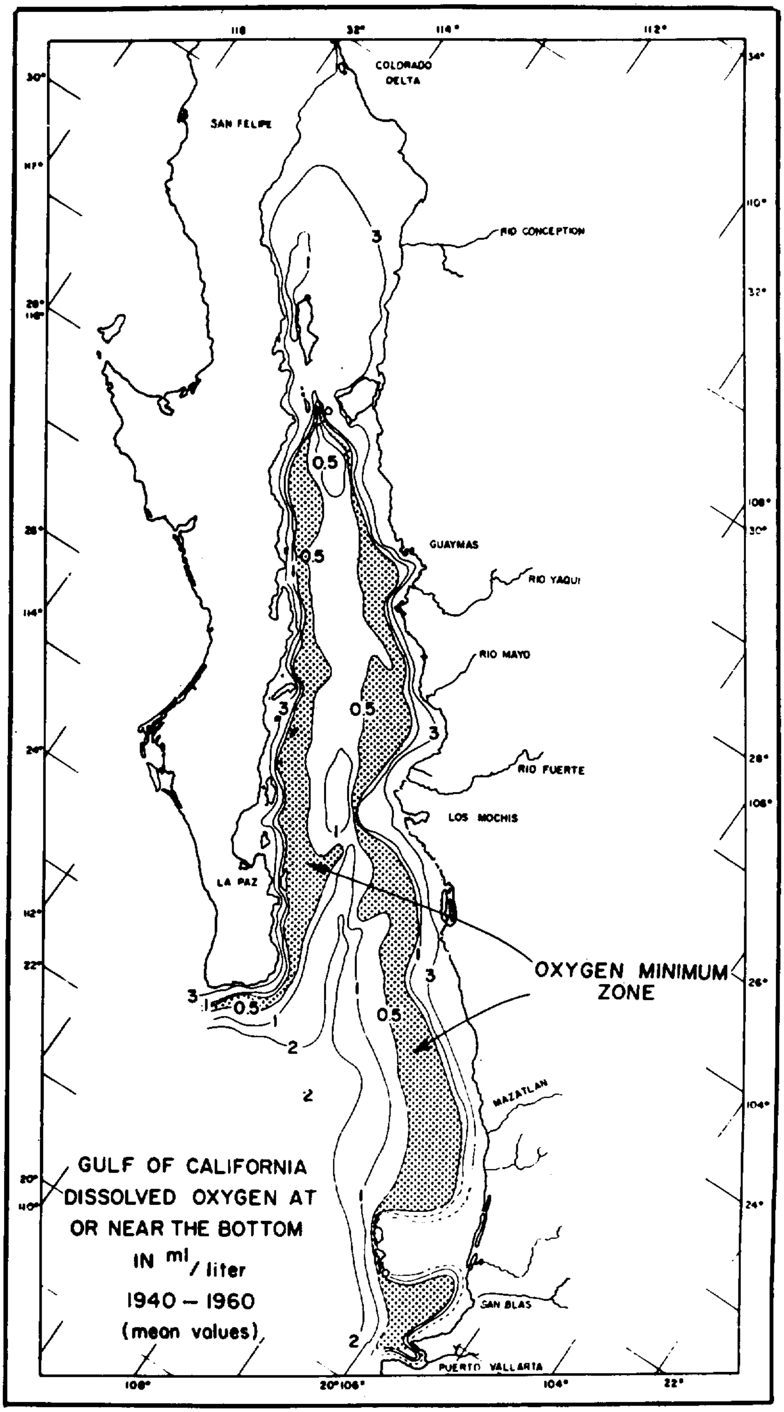


FIG. 7.—Dissolved oxygen in bottom waters of the Gulf of California, based on published (Roden, 1958; Roden and Groves, 1959) and unpublished data, taken in various seasons over a 20-year period.

and shows little disturbance of its sediments by burrowing organisms. The apparent lack of benthonic life may be attributed to the oxygen deficiency. Similar conditions on a seasonal basis have been described by Emery and Hülsemann (1962) for the Santa Barbara Basin in the California borderland. The areas of lowest oxygen concentration on the slopes coincide with zones of maximum upwelling and abundant plankton blooms (Fig. 8).

In the channel between the Peninsula and the San Lorenzo and Angel de la Guarda Islands, waters are well oxygenated over the entire column, notwithstanding the great depth (1,000–1,500 m). The high, uniform oxygen values of between 1 and 3 ml/L in this area result from mixing by tidal currents, and give rise to abundant animal life.

The faunas at the southern end of the Gulf also reflect the presence of abundant oxygen in deep water. Trawls taken in this region were very rich and comparable to slope samples elsewhere along the coast of Central America, in striking contrast to deep stations in the central Gulf.

On the continental shelf, oxygen values are normally high, except in some areas where depletion by prolific organic productivity locally may occur close to shore. This is especially true north of Mazatlán, where the oxygen minimum occurs close to the land, despite the appreciable width of the shelf. This condition seems to influence the faunal assemblage, which has an abnormal character in depths between 65 and 120 m. However, the somewhat different sediments of this area may contribute to the change in faunas.

The *temperature of the water near the bottom* (Fig. 9) decreases systematically from a mean of 14°C in shelf depths to 2°C in the deepest portions of the Gulf. Between Tiburón Island and Puerto Vallarta, the edge of the continental shelf is fairly well marked by bottom temperatures between 14° and 10°. In the central Gulf, the basin floors have temperatures of 4°; farther south the minimum temperature is 2°, similar to the bottom-water temperature of the equatorial Pacific.

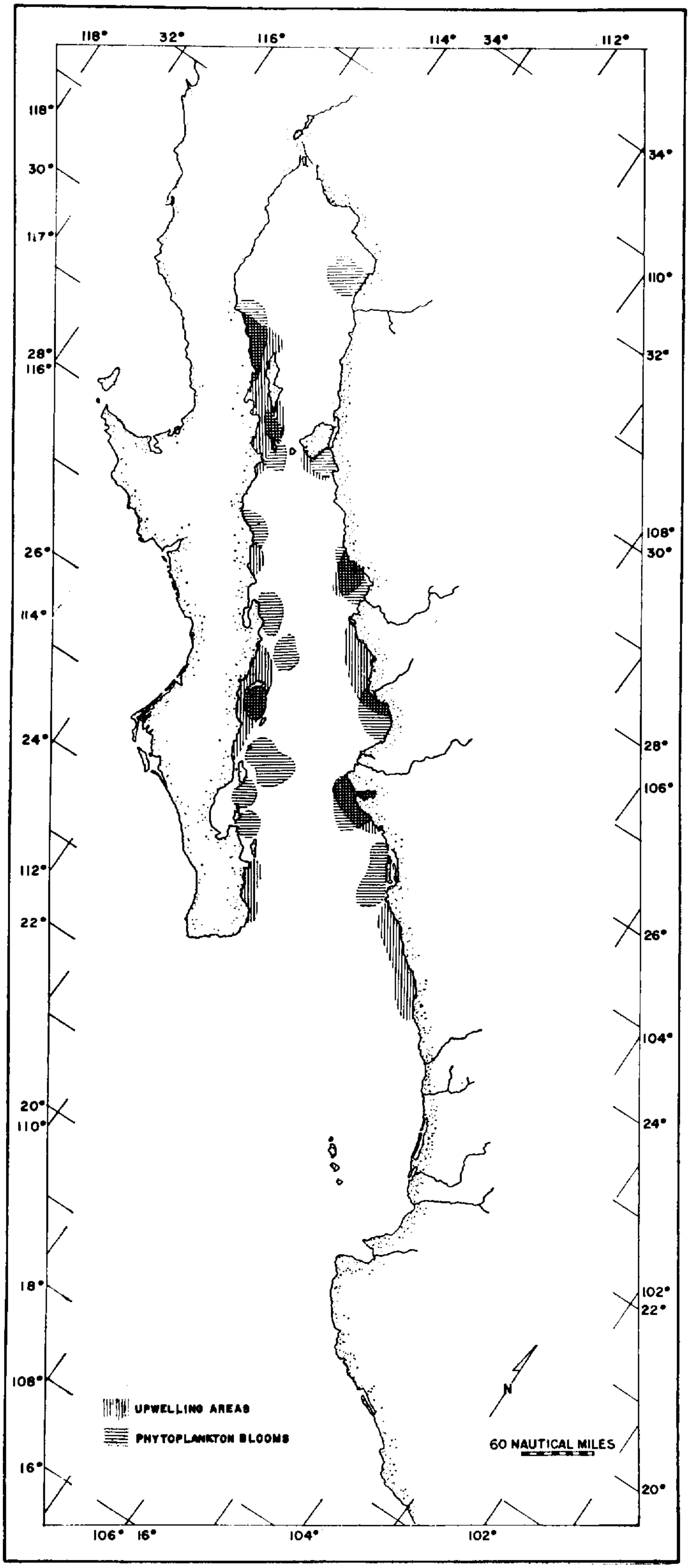
Between Angel de la Guarda and the Peninsula, and east of the island, temperatures are nearly uniform from surface to bottom as a result of tidal mixing. Roden and Groves (1959) have shown that in April the surface temperature is about 15°, while the bottom value is 12°. During the warmest month, August, surface waters may be as high as 28°; at 200 m, the temperature is still 15°, and at 1,000 m it is 12°. These high values found at such great depths have a marked effect on the composition of the fauna of the slopes and floors of the depressions. Vertical stratification, which is normal elsewhere in the Gulf, is lacking, and many species generally found in 150 to 200 m occur here at the bottom in depths of 1,500 m.

The water temperatures of the nearshore shelf are subject to a pronounced seasonal variation, which is most extreme in the northern Gulf. In the vicinity of San Felipe, the annual range of water temperature is from 16° in January to more than 31° in August. This variation possibly excludes many species; the Tiburón region is, in fact, the northern end of the geographic range for many invertebrates (Fig. 10). The summer temperatures are high enough for many Panamic or tropical forms, but the winter minima probably are limiting for many species with a small temperature tolerance.

Between Guaymas and Tiburón, the annual range of shallow-water temperature is 13.8°, which still is limiting to many tropical forms. At Mazatlán, however, temperatures range from only 20° to 30°. This area is the northern limit for a few southern species and the southern boundary for many northern forms. The geographic ranges of 253 common living species show that many geographic breaks in species distribution correspond well with temperature changes and other physical barriers (Fig. 10).

The temperature distribution along the western side of the Gulf is less well known. At Los Angeles Bay on the Peninsula, west of Angel de la Guarda Island, the range is about 15°, whereas between Los Angeles Bay and the southern end of the Peninsula the temperature ranges from 19° to 29°. Records at La Paz, which is sheltered from the open Gulf, are approximately the same as at Mazatlán, with a range of 9.3°. The narrowest temperature range is reported from Cape San Lucas (8.5°). Cape San Lucas temperatures are comparable to oceanic equatorial Pacific temperatures, which may explain why a number of Indo-Pacific invertebrates and fish are found only in

Fig. 8.—Areas of upwelling and plankton blooms in the Gulf of California. After Byrne and Emery (1960) and Roden and Groves (1959).



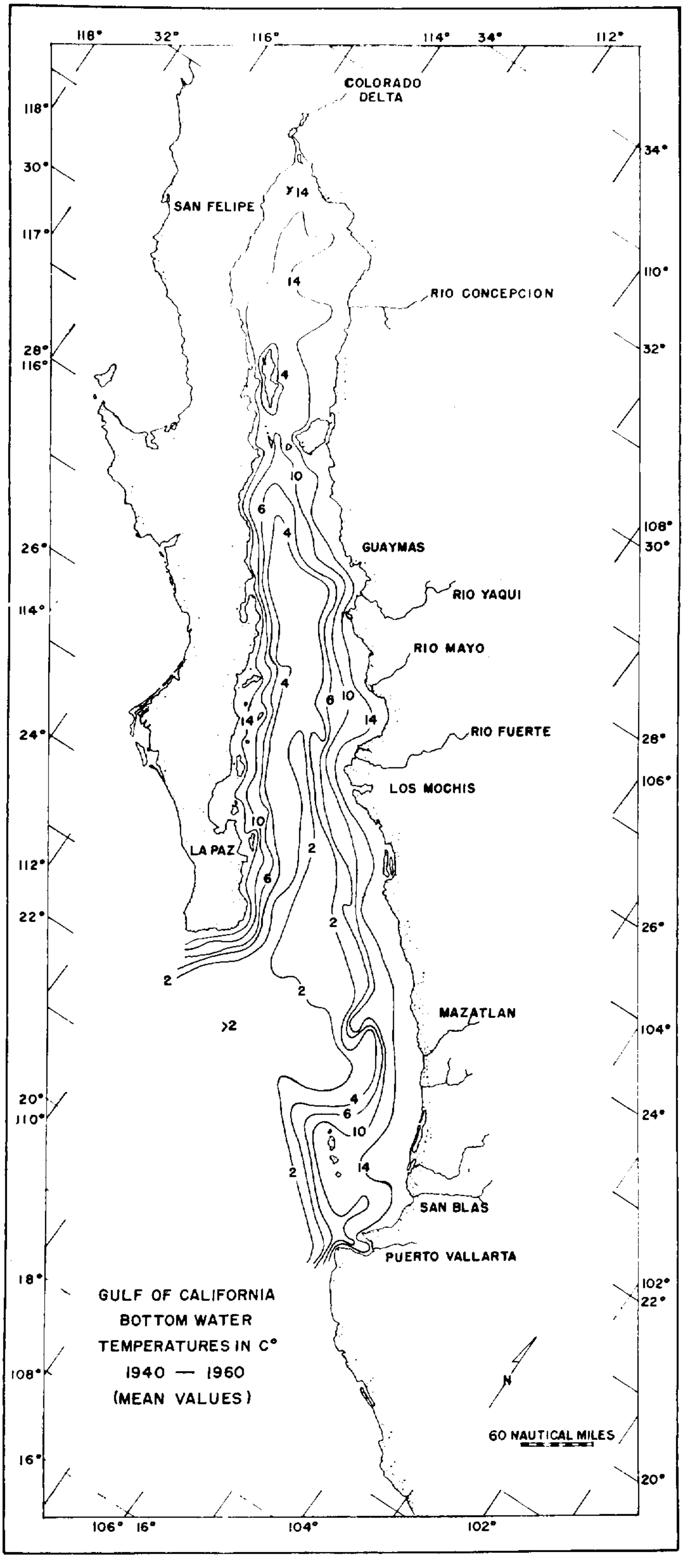


FIG. 9.—Bottom-water isotherms of the Gulf of California, based on published (Roden, 1958; Roden and Groves, 1959) and unpublished data, taken in various seasons during a 20-year period.

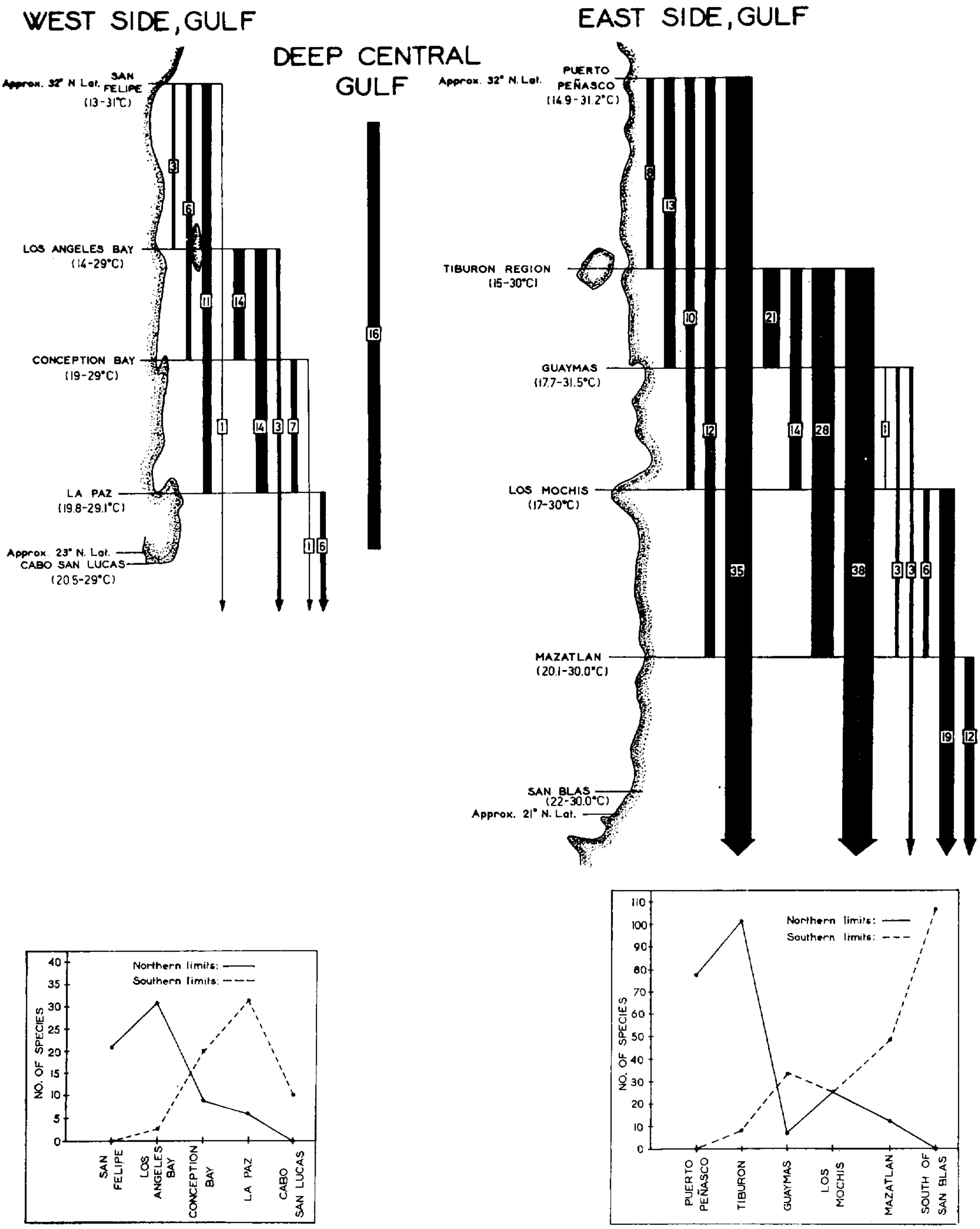


FIG. 10.—Zoogeographic boundaries in the Gulf of California, based on ranges of common invertebrates. Thickness of bars is related to number of species. Small graphs represent geographic variation of number of species with principal northern and southern distribution in dependence of geographic position.

this locality (Walker, 1960; Rosenblatt, 1959; Keen, 1958). In general, the faunal breaks along the western side of the Gulf also can be correlated with various temperature regimes.

Salinity differences in the open Gulf from north to south and from surface to bottom are small (Roden, this volume; Roden and Groves, 1959) and relatively unimportant in the distribution of benthic animals. The range from north to south is about 1°/₀₀, and from the surface to 1,800 meters it is approximately 1.4°/₀₀. The seasonal variation is equally small.

Certain inshore regions of the Gulf of California, however, are characterized by salinity changes large enough to affect animal distribution. Such areas are the lagoons and bays of the east coast between Tiburón Island and San Blas. North of the Yaqui River, the lagoons seldom receive much fresh water runoff, and long-period hypersaline conditions prevail (Nichols, 1962). Few benthic animals can live permanently in these lagoons, but observations on Indian middens indicate that brackish-water and lagoonal species have been present at some time in the past. South of the Fuerte River and as far as Mazatlán, the lagoons receive more fresh water, and seasonal populations of shrimp and permanent populations of oysters are known to exist there. South of Mazatlán, the numerous large lagoons are frequently almost fresh, although higher salinities may occur in the summer. A permanent population of shrimp, *Corbula*, oysters, and *Anadara* clams which are used as food, occur there. Rainfall and river discharge are sufficient permanently to maintain a low-salinity regime which renders these lagoons similar to those of the Texas-Louisiana coast (Parker, 1959).

Circulation in the Gulf of California is complex and not completely understood (Roden, 1958; this volume). In the winter months, strong, steady, northerly winds produce a surface current which drives surface water out to the Pacific. This water is replaced by inflow of Pacific water at moderate depths. At the same time, the high-salinity water of the northern Gulf is cooled and fills the deeper basins, moving southward along the coast of the Peninsula. Together with the high tidal currents existing in the narrow channels between islands, this water movement causes complete mixing in the basin between Angel de la Guarda and the mainland. In the summer, coastal surface currents move northwestward along the eastern side of the Gulf with average velocities of between 5 and 20 cm/sec.

The surface currents probably have little affect on the adult benthic populations. They are important, however, in the transport of the larval stages of many benthic animals. The termination of northward currents near Tiburón Island may account for the northern limit of most Panamic species with planktonic larvae in this area. The fact that many mollusk and crustacean species occurring on the eastern side of the Gulf are not found on the western side, and vice-versa, also may be due to the fact that the currents on both sides flow in opposite directions.

DESCRIPTION OF MACRO-INVERTEBRATE ASSEMBLAGES AND ENVIRONMENTS

The present sample coverage is inadequate to establish all faunal assemblages that may exist in the Gulf of California, but probably it is sufficient to discuss the most common and important groups. The number of ecological niches is very great for such a relatively small region, particularly along the rocky, dissected coast of the Peninsula. With the exception of fine-grained carbonate environments, nearly all possible environments that have occurred during the Tertiary history of the Americas are found in the Gulf of California, although reef environments are small and insignificant (Squires, 1959). Polychaetes, ophiuroids, asteroids, anthozoans, sponges, and bryozoans are not included in the following discussion, although some of them are very characteristic of certain environments.

I. THE INTERTIDAL ROCKY SHORES ASSEMBLAGES

The fauna of the intertidal rocky shores is widespread along the Gulf of California (Fig. 11) and the coast of Central America. Although the literature on this fauna is extensive (*see* review by Doty, 1957), few papers deal with this assemblage in the Gulf of California (Steinbeck and Ricketts, 1941; Keen, 1958; McLean, 1961; Dushane, 1962). A selection of the most important species is given in the Appendix (Table I); a more complete

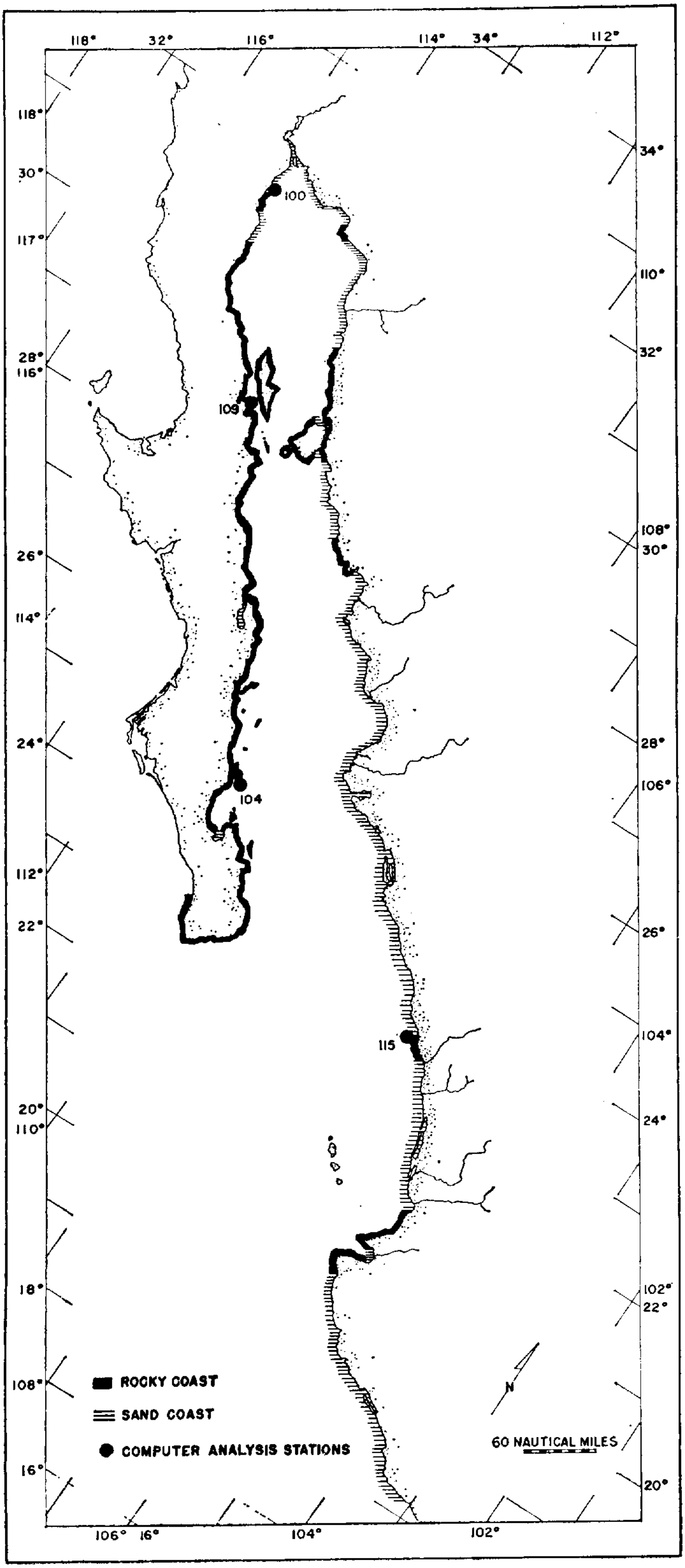


FIG. 11.—Distribution of sandy and rocky areas along the coasts of the Gulf of California. Numbers indicate stations highly correlated by contingency matrix.

list can be found in Parker (1964). Most of the species occur only in one or a few stations; the following appear to be highly correlated in this environment.

Gastropods
Nerita scabricosta Lamarck, 1822
Purpura patula pansa Gould, 1852
Turbo fluctuosus Wood, 1828
Pyrene fuscata (Sowerby, 1832)
Lamellibranchs
Barbatia reeveana (d'Orbigny, 1846)
Isognomon chemnitziana (d'Orbigny, 1853)
Ostrea conchophila Carpenter, 1856
Anomia adamas Gray, 1830
Cardita affinis californica Deshayes, 1854

Inspection of the total number of stations assigned to this group shows that these species represent only a minor portion of the assemblage. A total of 53 living species has been identified in this environment; another 18 species, known to live in it, were taken as dead shell. A few of the typical mollusks are shown on Plate 1. Much more extensive lists of species than are found in the present study are reported by the authors mentioned above, but the same predominant species are found by both.

II. Intertidal Sand Beach and Sand Flats to 10 Meters

The faunal assemblages found in this environment resemble those of the sand beaches and flats of the Gulf of Mexico (Parker, 1956, 1960). In the Gulf of California, this environment is almost as widespread as that of the intertidal rocky shores. One-third to one-half of all known mollusk species from the Gulf of California have been found in this environment, but it is difficult to ascertain from the literature which species were found alive. The species list of the present paper is mainly based on the author's own collections.

Relatively few species are found in more than a single station, and only a few are closely correlated statistically.

Cardita megastropha (Gray, 1825)
Tivela byronensis (Gray, 1838)
Heterodonax bimaculatus (Linné, 1758)

All species had between three and five station occurrences in common and were taken alive. Other common invertebrates from this environment are listed in the Appendix (Table I). Most species range from the head of the Gulf to the Gulf of Panama, but a few are restricted to the southern Gulf of California.

Many other invertebrates are reported in the literature as abundant on sand beaches. Dushane lists 112 living species for sand and sand-mud bottoms near Puertocitos (1962). McLean (1961) found two living sand dollars, *Encope grandis* L. Agassiz and *E. californica* Verrill, and the following list of living mollusks on sand flats near Los Angeles Bay.

Prosobranchs
Calliostoma eximium (Reeve)
Neritina luteofasciata Miller*
Balcis cf. *rutila* (Carpenter)
Cerithium sculptum Sowerby
Cerithidea albonodosa Gould and Carpenter*
C. mazatlanica Carpenter
Natica chemnitzii Pfeiffer
Polinices bifasciatus (Gray)
P. uber (Valenciennes)
P. reclusianus (Deshayes)
Strombus gracilior (Sowerby)
S. granulatus Swainson*
Hexaplex erythrostomus (Swainson)

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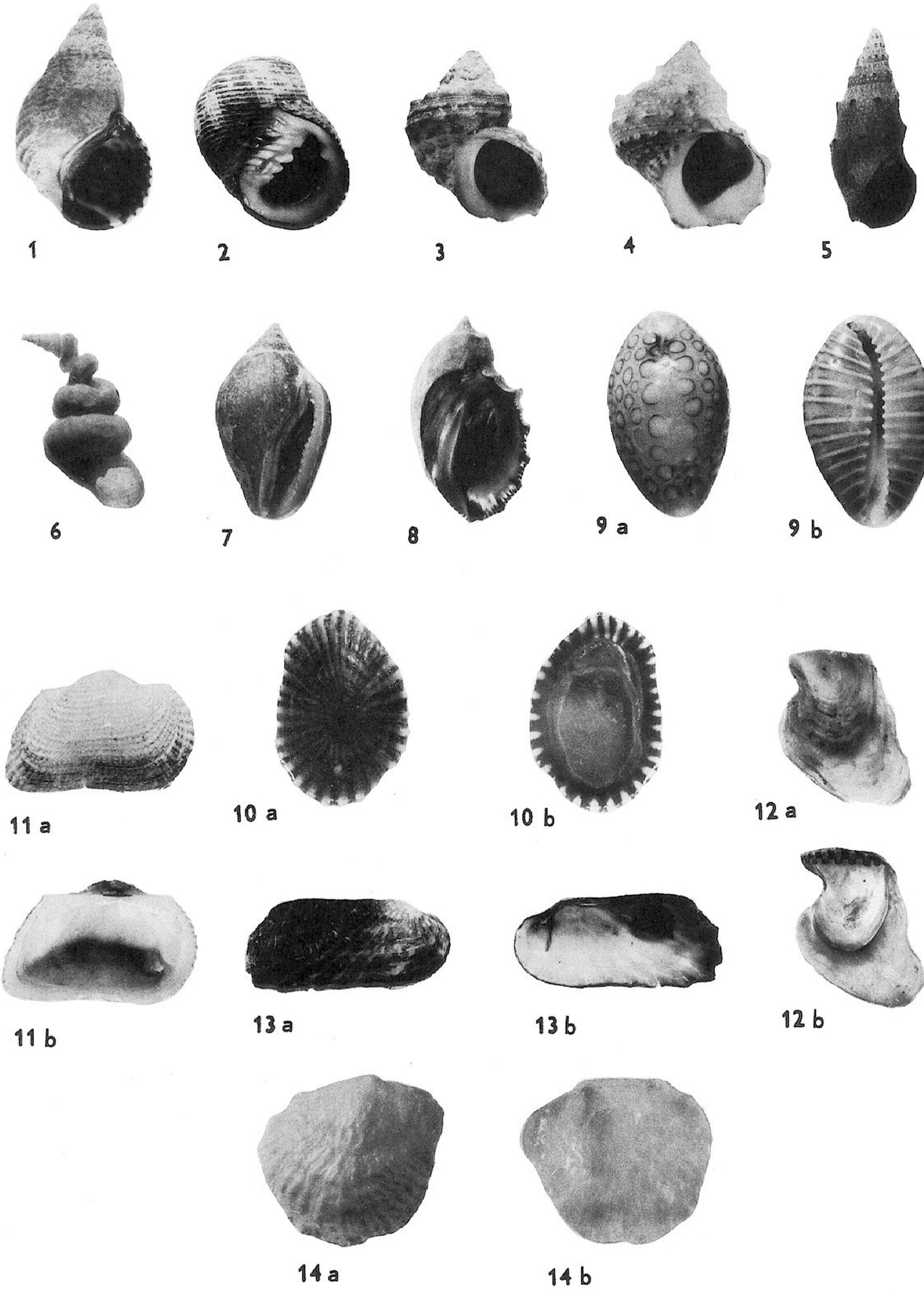
Explanation of Plate 1

Intertidal Rocky Shores Assemblage

Figs. 1.—*Littorina aspersa* Philippi, 1846. Aperture; size 20×13 mm.
2.—*Nerita scabricosta* Lamarck, 1822. Aperture; size 43×40 mm.
3.—*Turbo fluctuosus* Wood, 1828. Aperture; size 31×30 mm.
4.—*Turbo saxosus* Wood, 1828. Aperture; size 16×15 mm.
5.—*Cerithium stercusmuscarum* Valenciennes, 1833. Aperture; size 26×11mm.
6.—*Vermicularia pellucida* (Broderip and Sowerby, 1829). Aperture; size 16×9 mm.
7.—*Pyrene fuscata* (Sowerby, 1832). Aperture; size 18×11 mm.
8.—*Purpura patula pansa* Gould, 1852. Aperture; size 37×24 mm.
9.—*Jenneria pustulata* (Solander, 1786). *a.* dorsal; *b.* aperture; size 16×10 mm.
10.—*Siphonaria maura* Sowerby, 1835. *a.* dorsal; *b.* interior and animal; size 7×8 mm.
11.—*Arcopsis solida* Sowerby 1833. *a.* exterior; *b.* interior; size 12×7 mm.
12.—*Isognomon chemnitzianus* (d'Orbigny, 1853). *a.* exterior; *b.* interior; size 33×23 mm.
13.—*Cardita affinis californica* Deshayes, 1854. *a.* exterior; *b.* interior; size 65×28 mm.
14.—*Anomia adamas* Gray, 1850. *a.* exterior; *b.* interior; size 32×27 mm.

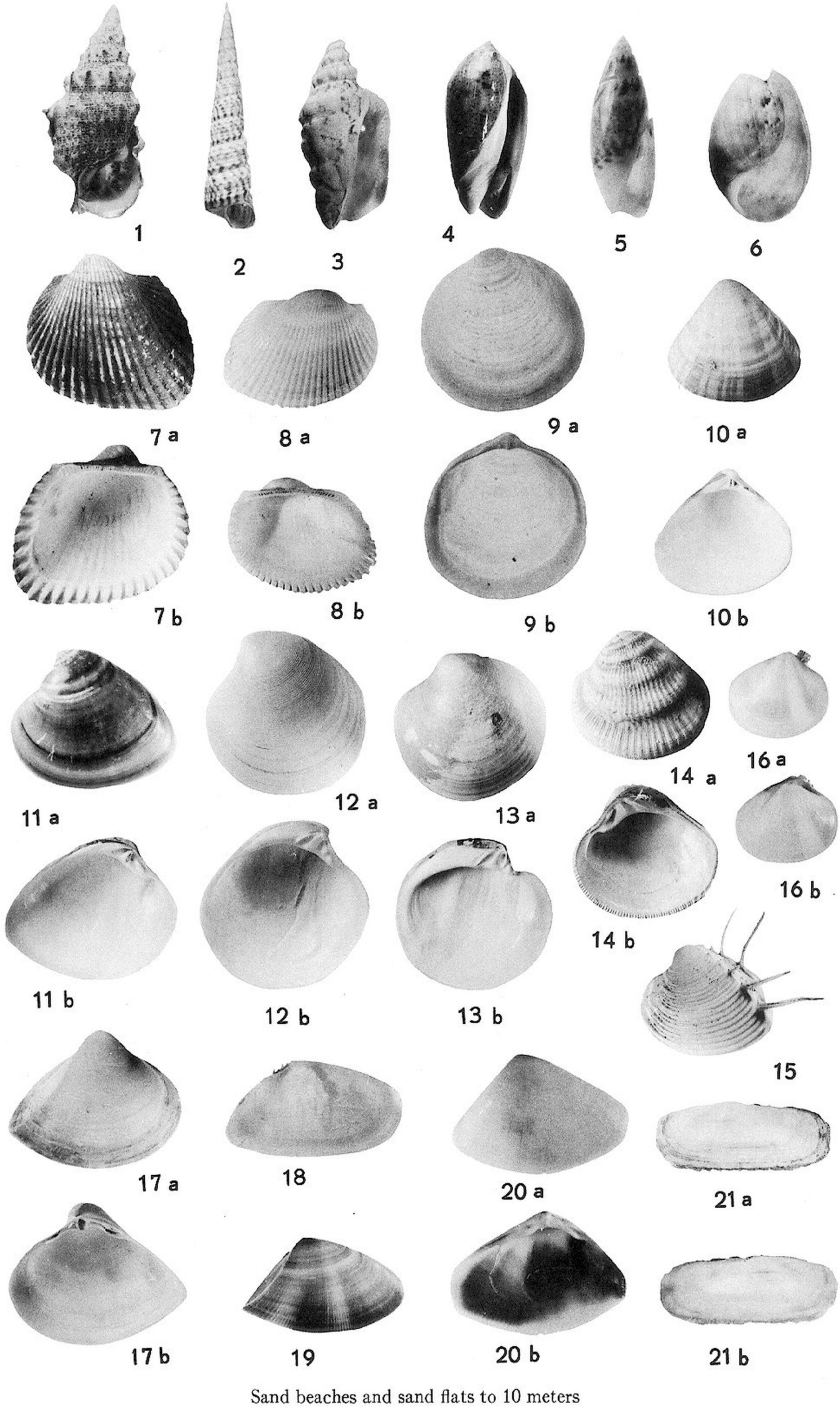


Intertidal rocky shores assemblage

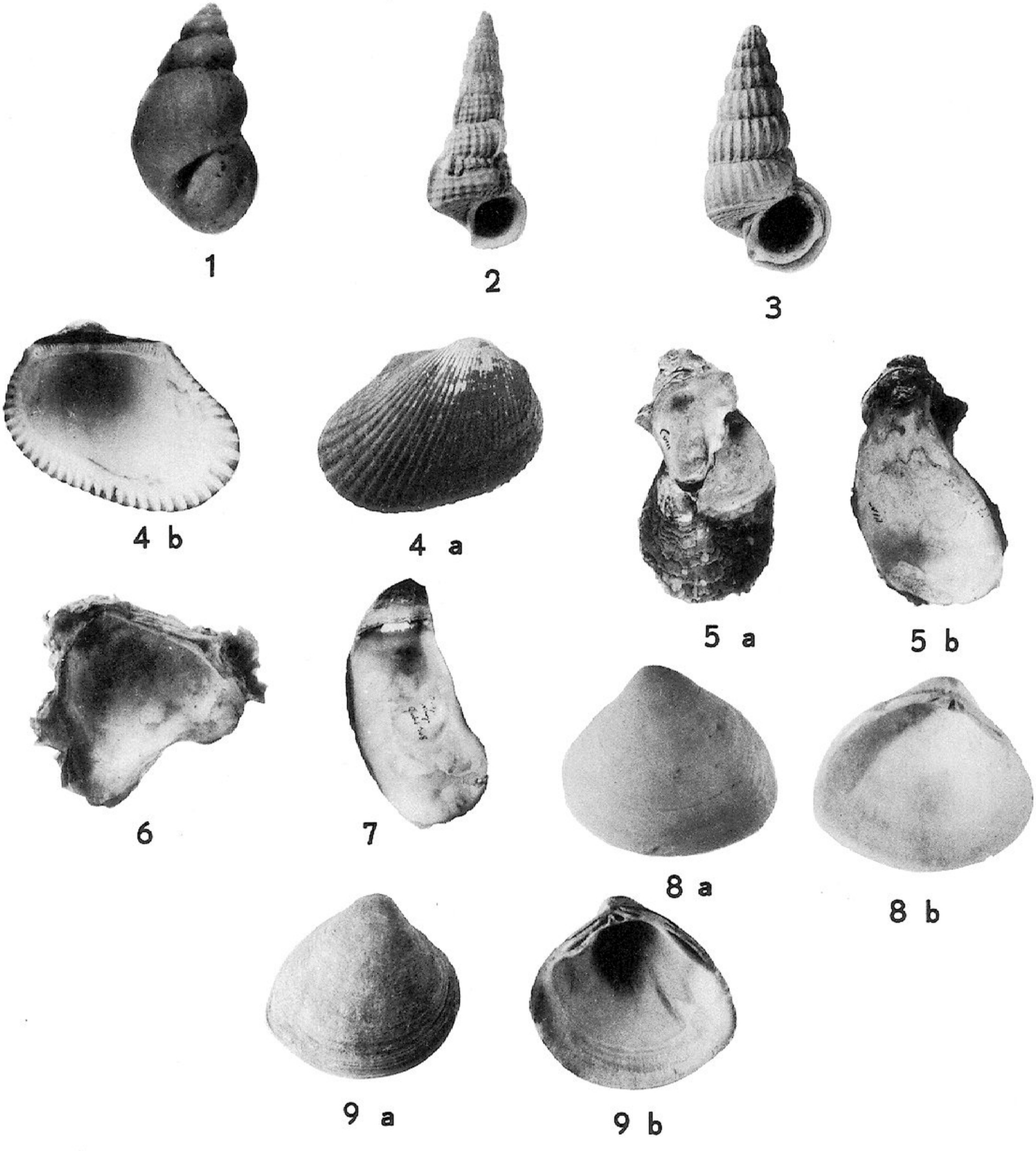
Explanation of Plate 2

SAND BEACHES AND SAND FLATS TO 10 METERS

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



Sand beaches and sand flats to 10 meters

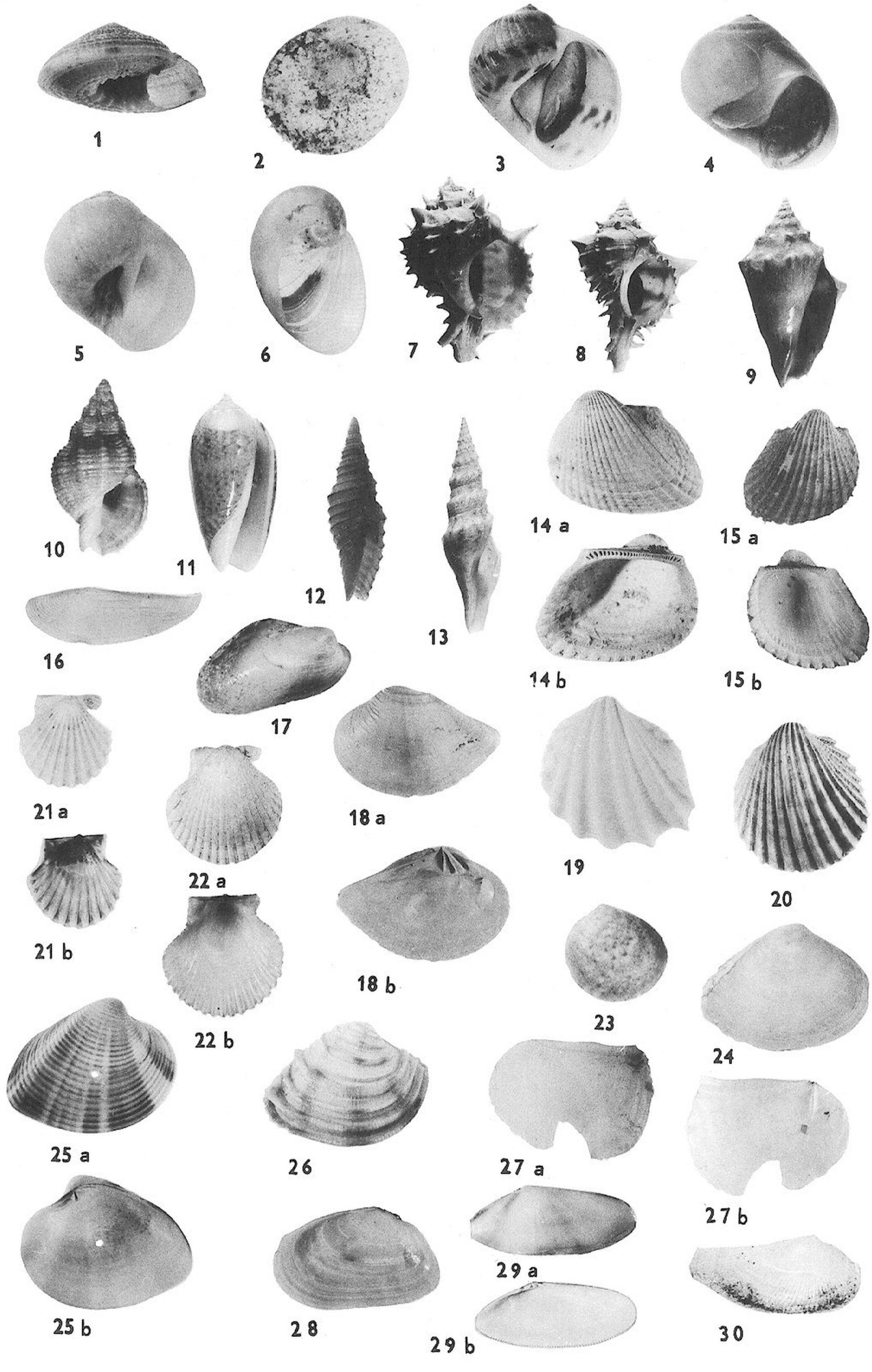


Lagoons and mangrove swamps

Explanation of Plate 3

LAGOONS AND MANGROVE MUD FLATS

Figs. 1.—*Littoridina* sp. Aperture; size 3×2 mm.
2.—*Cerithidea mazatlanica* Carpenter, 1856. Aperture; size 26×11 mm.
3.—*Cerithidea montagnei* (d'Orbigny, 1837). Aperture; size 30×17 mm.
4.—*Anadara tuberculosa* (Sowerby, 1833). *a*. exterior; *b*. interior; size 65×45 mm.
5.—*Crassostrea corteziensis* Hertlein, 1951. *a*. exterior; *b*. interior; size 80×45 mm.
6.—*Crassostrea columbiensis* Hanley, 1846. Interior; size 45×50 mm.
7.—*Crassostrea corteziensis* Hertlein, 1951. Interior; size 126×60 mm (large specimen).
8.—*Polymesoda olivacea* (Carpenter, 1855). *a*. exterior; *b*. interior; size 21×18 mm.
9.—*Polymesoda mexicana* (Broderip and Sowerby, 1829). *a*. exterior; *b*. interior; size 42×43 mm.



Nearshore shelf, 11 to 26 meters

Explanation of Plate 4

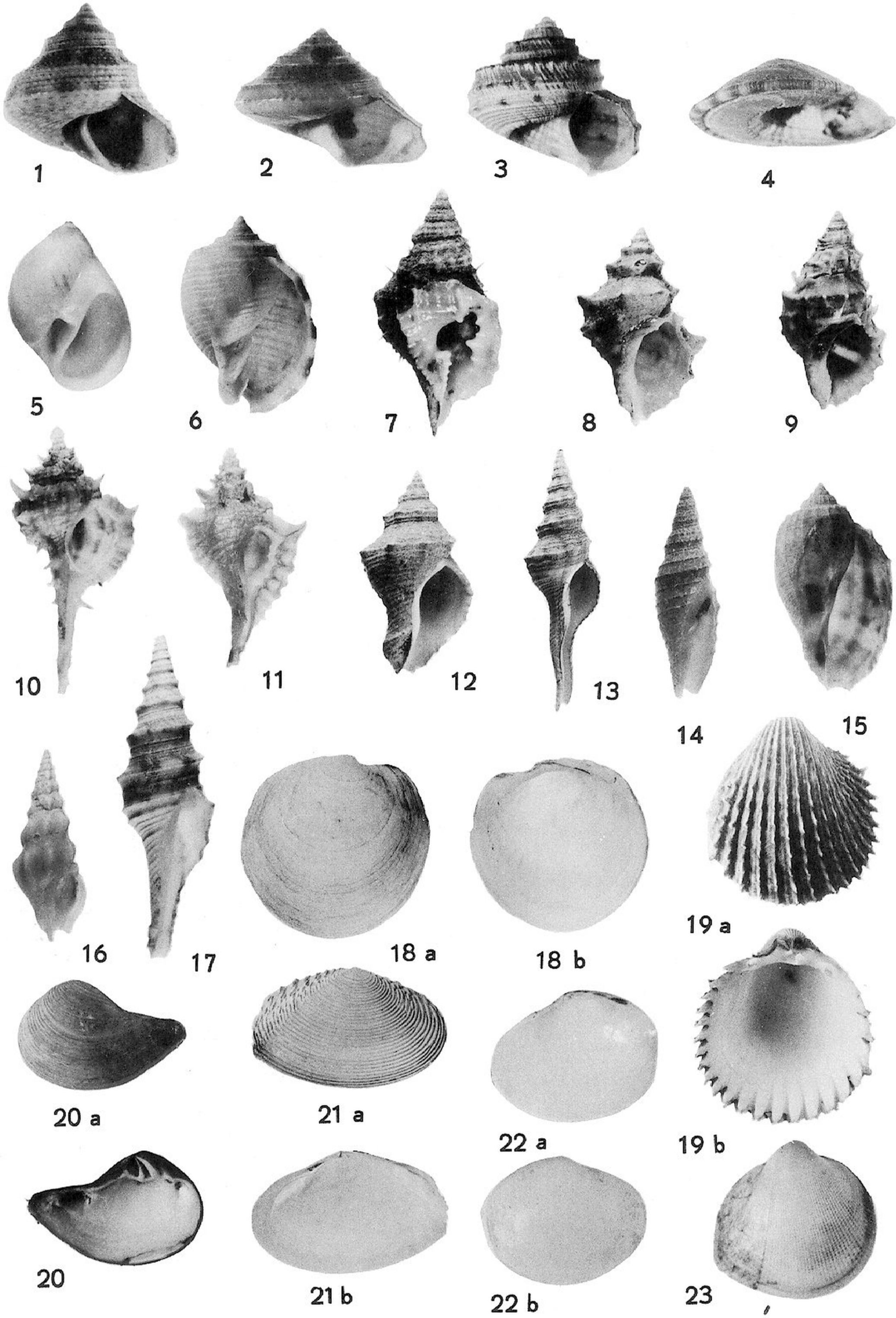
NEARSHORE SHELF, 11 TO 26 METERS

FIGS. 1.—*Architectonica nobilis* Röding, 1798. Aperture; size 10×21 mm.
2.—*Crucibulum spinosum* (Sowerby, 1824). Exterior; size 17×14 mm.
3.—*Natica broderipiana* Recluz, 1844. Aperture; size 24×23 mm.
4.—*Polinices reclusianus* (Deshayes, 1839). Aperture; size 24×25 mm.
5.—*Polinices otis* (Broderip and Sowerby, 1829). Aperture; size 10×10 mm.
6.—*Sinum debile* (Gould, 1853). Aperture; size 8×2 mm.
7.—*Hexaplex erythrostomus* (Swainson, 1831). Aperture; size 95×71 mm.
8.—*Hexaplex brassica* (Lamarck, 1822). Aperture; size 79×58 mm.
9.—*Strombus gracilior* Sowerby, 1825. Aperture; size 67×47 mm.
10.—*Nassarius versicolor* (C.B. Adams, 1852). Aperture; size 9×5 mm.
11.—*Oliva spicata* (Röding, 1798). Aperture; size 32×17 mm.
12.—*Mitra erythrogramma* Tomlin, 1931. Aperture; size 17×6 mm.
13.—*Hormospira maculosa* (Sowerby, 1834). Aperture; size 45×14 mm.
14.—*Anadara obesa* (Sowerby, 1833). *a.* exterior; *b.* interior; size 22×16 mm.
15.—*Anadara nux* (Sowerby, 1833). *a.* exterior; *b.* interior; size 19×17 mm.
16.—*Adrana penascoensis* (Lowe, 1935). Exterior; size 16×5 mm.
17.—*Lioberus salvadoricus* (Hertlein and Strong, 1946). Exterior; size 17×12 mm.
18.—*Crassatella gibbosa* Sowerby, 1832. *a.* exterior; *b.* interior; size 30×18 mm.
19.—*Trigoniocardia granifera* (Broderip and Sowerby, 1829). Exterior; size 8×7 mm.
20.—*Trachycardium panamense* (Sowerby, 1833). Exterior; size 18×18 mm.
21.—*Chlamys tumbezensis* (d'Orbigny, 1846). *a.* exterior; *b.* interior; size 15×14 mm.
22.—*Chlamys circularis* (Carpenter, 1864). *a.* exterior; *b.* interior; size 33×30 mm.
23.—*Laevicardium elenense* (Sowerby, 1840). Exterior; size 13×12 mm.
24.—*Mactra californica* Conrad, 1837. Exterior; size 33×23 mm.
25.—*Pitar concinnus* (Sowerby, 1835). *a.* exterior; *b.* interior; size 24×17 mm.
26.—*Chione mariae* (d'Orbigny, 1846). Exterior; size 30×20 mm.
27.—*Pandora claviculata* Carpenter, 1856. *a.* exterior; *b.* interior; size 30×12 mm.
28.—*Tellina arenica* Hertlein and Strong, 1949. Exterior; size 13×8 mm.
29.—*Donax gracilis* Hanley, 1845. *a.* exterior; *b.* interior; size 18×7 mm.
30.—*Lyonsia gouldii* Dall, 1915. Exterior; size 13×6 mm.

Explanation of Plate 5

INTERMEDIATE SHELF, 27 TO 65 METERS

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



Intermediate shelf, 27 to 65 meters

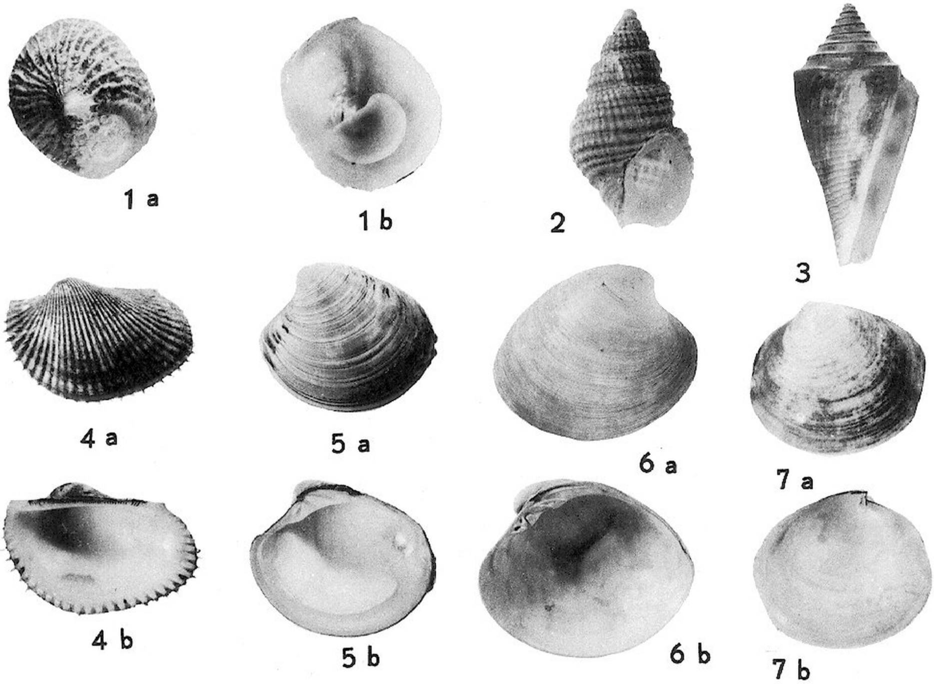
Explanation of Plate 6

OUTER SHELF, SOUTHERN GULF, CLAY BOTTOM, 66 TO 120 METERS

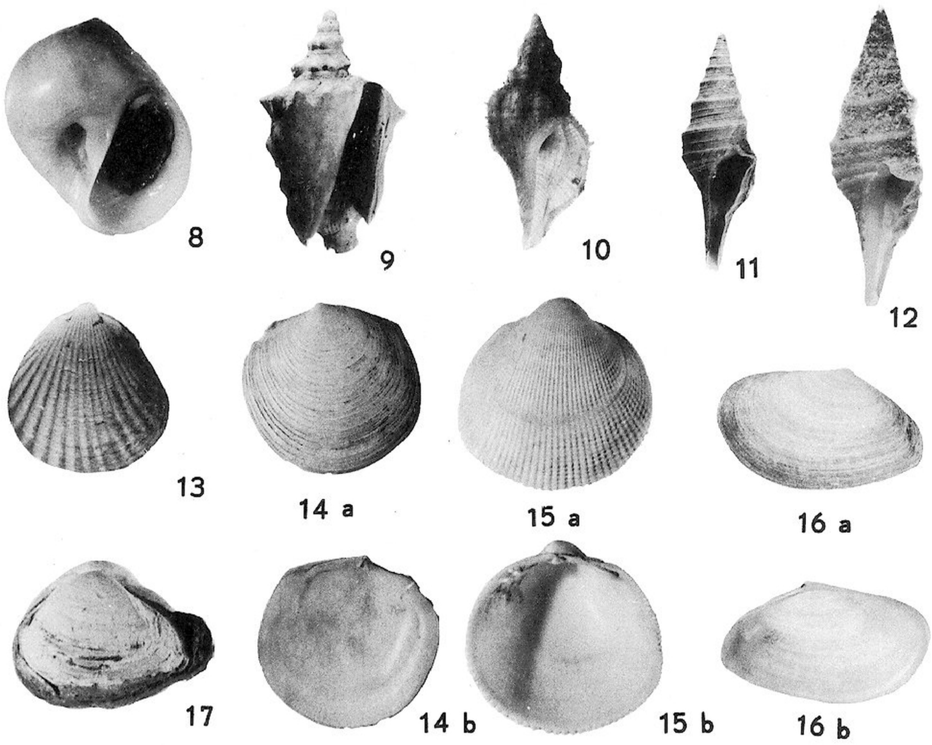
Figs. 1.—*Crucibulum* n. sp. *a.* exterior; *b.* interior; size 31×27 mm.
2.—*Nassarius catallus* Dall, 1908. Aperture; size 17×10 mm.
3.—*Conus arcuatus* Broderip and Sowerby, 1829. Aperture; size 40×20 mm.
4.—*Anadara mazatlanica* (Hertlein and Strong, 1943). *a.* exterior; *b.* interior; size 42×27 mm.
5.—*Chione kellettii* (Hinds, 1845). *a.* exterior; *b.* interior; size 53×43 mm.
6.—*Pitar mexicanus* Hertlein and Strong, 1948. *a.* exterior; *b.* interior; size 50×40 mm.
7.—*Periploma carpenteri* Dall, 1896. *a.* exterior; *b.* interior; size 30×42 mm.

OUTER SHELF, NORTHERN GULF, SAND BOTTOM, 66 TO 120 METERS

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



Outer shelf, southern Gulf, clay bottom, 66 to 120 meters



Outer shelf, northern Gulf, sand bottom, 66 to 120 meters

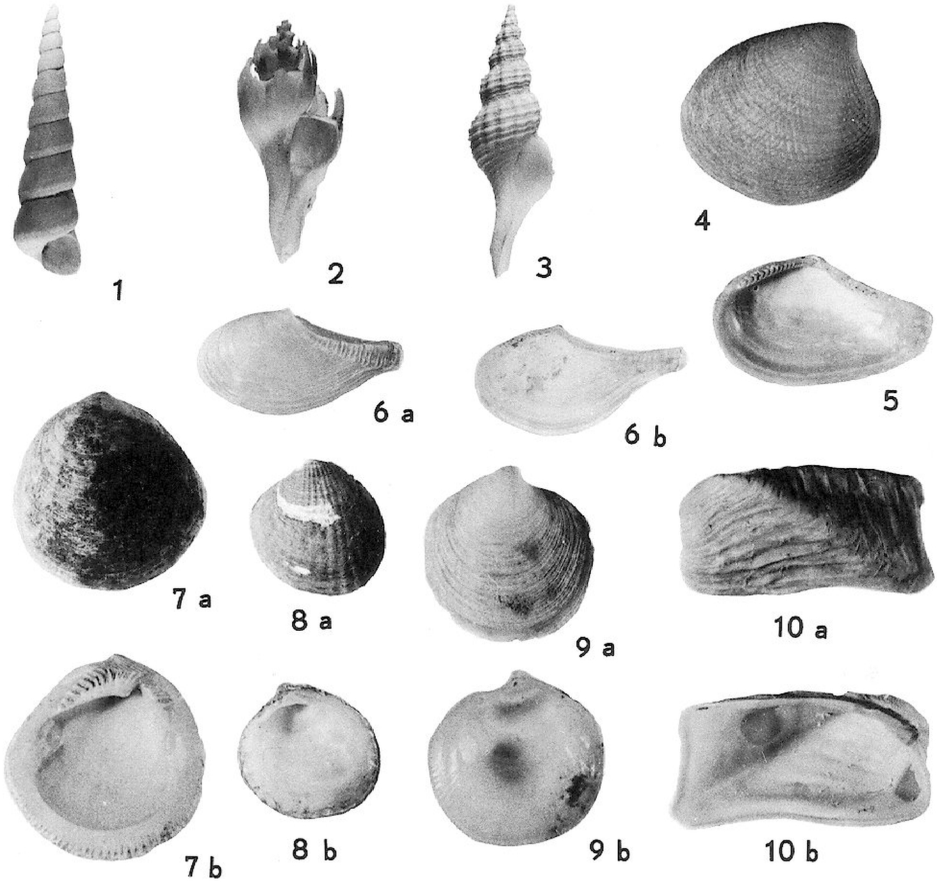
Explanation of Plate 7

DEEP NORTHERN BASINS AND TROUGHS, 230 TO 1,500 METERS

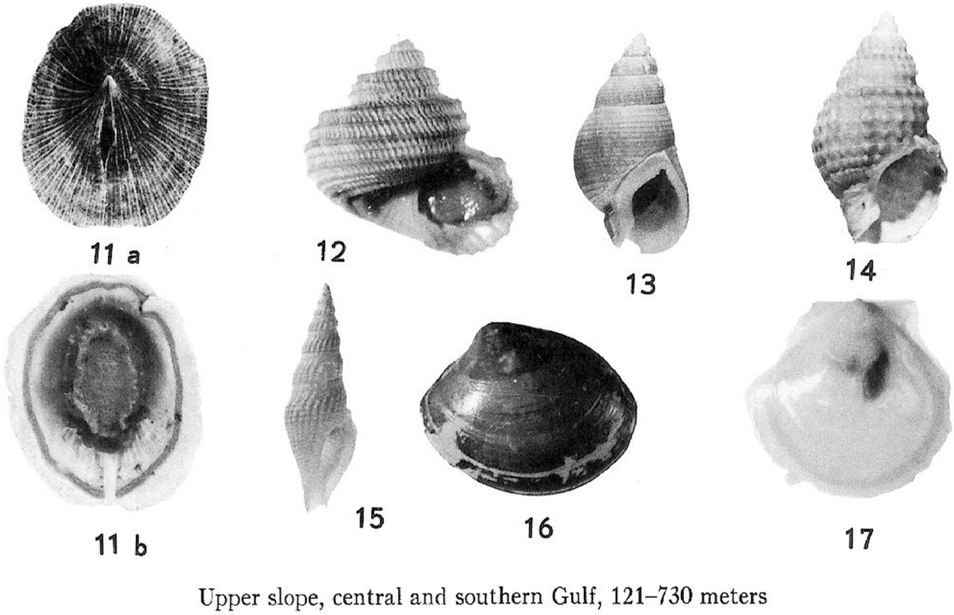
Figs. 1.—*Turritella* sp. Aperture; size 37×10 mm.
2.—*Boreotrophon* n. sp. Aperture; size 40×19 mm.
3.—*Fusinus traski* Dall, 1915. Aperture; size 43×15 mm.
4.—*Acila castrensis* Hinds, 1843. Exterior; size 11×10 mm.
5.—*Nuculana taphria* (Dall, 1897). Exterior; size 13×8 mm.
6.—*Nuculana hamata* Carpenter, 1864. *a.* exterior; *b.* interior; size 11×6 mm.
7.—*Glycymeris corteziana* Dall, 1901. *a.* exterior; *b.* interior; size 19×8 mm.
8.—*Cardita barbarensis* (Stearns, 1890). *a.* exterior; *b.* interior; size 17×15 mm.
9.—*Lucina tenuisculpta* (Carpenter, 1864). *a.* exterior; *b.* interior; size 8.7×5 mm.
10.—*Hiatella arctica* (Linné, 1767). *a.* exterior; *b.* interior; size 11×6 mm.

UPPER SLOPE, CENTRAL AND SOUTHERN GULF, 121 TO 730 METERS

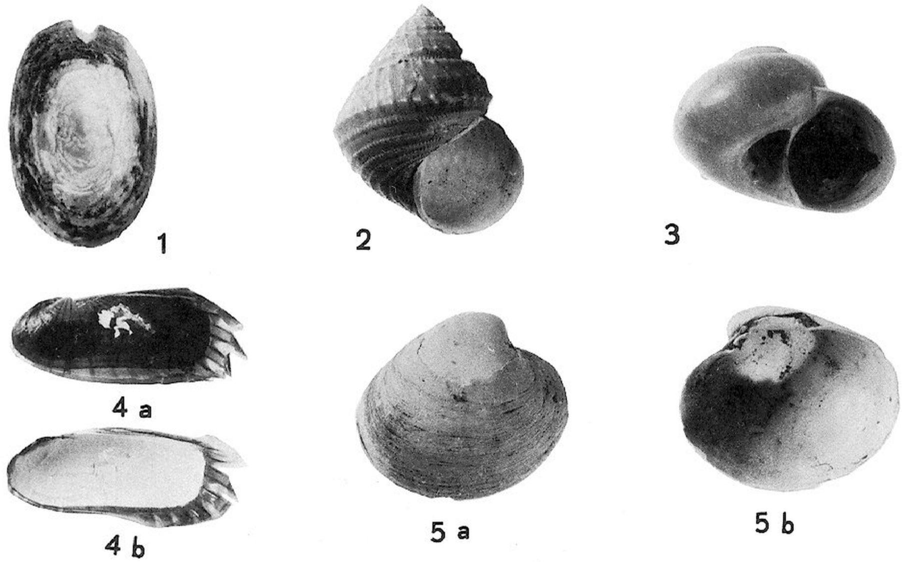
11.—*Puncturella expansa* Dall, 1896. *a.* exterior; *b.* interior (animal); size 23×20 mm.
12.—*Solariella permabilis* Carpenter, 1864. Aperture; size 7×9 mm.
13.—*Nassarius insculptus gordanus* Hertlein and Strong, 1951. Aperture; size 22×12 mm.
14.—*Nassarius miser* (Dall, 1908). Aperture; size 12×7 mm.
15.—*Clathurella thalassoma* (Dall, 1908). Aperture; size 22×8 mm.
16.—*Nucula cardara* Dall, 1917. Exterior; size 10×7 mm.
17.—*Cyclopecten zacae* (Hertlein, 1935). Exterior; size 8×7 mm.



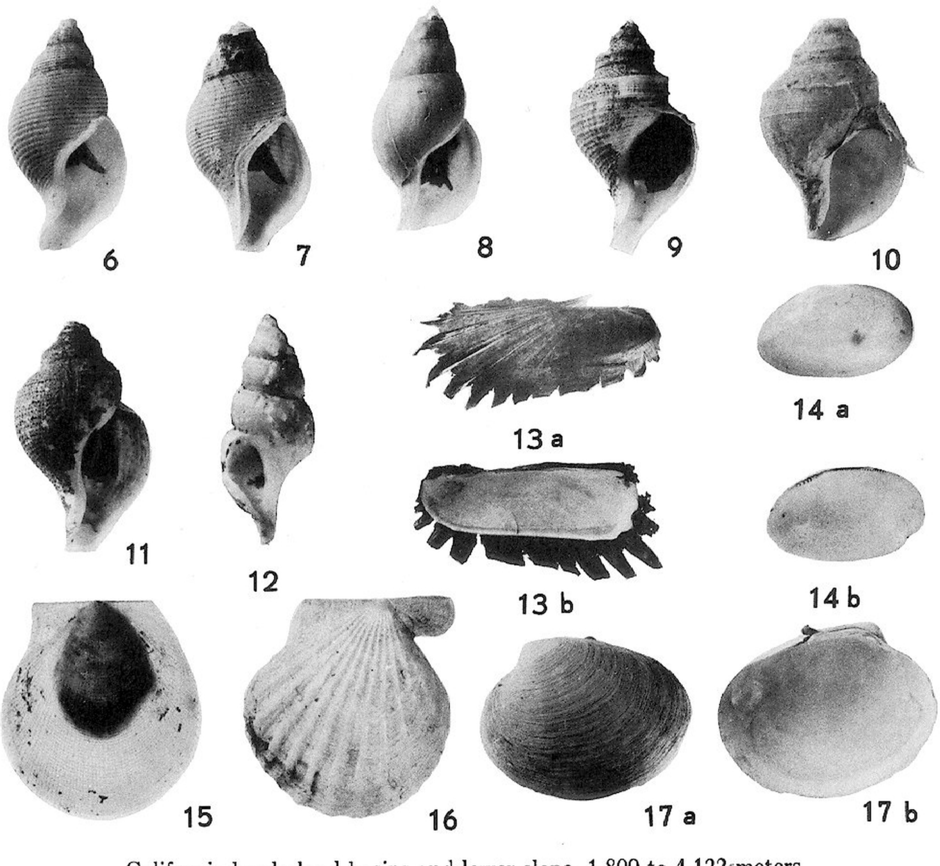
Deep northern basins and troughs, 230 to 1,500 meters



Upper slope, central and southern Gulf, 121–730 meters



Middle slope, 731 to 1,799 meters

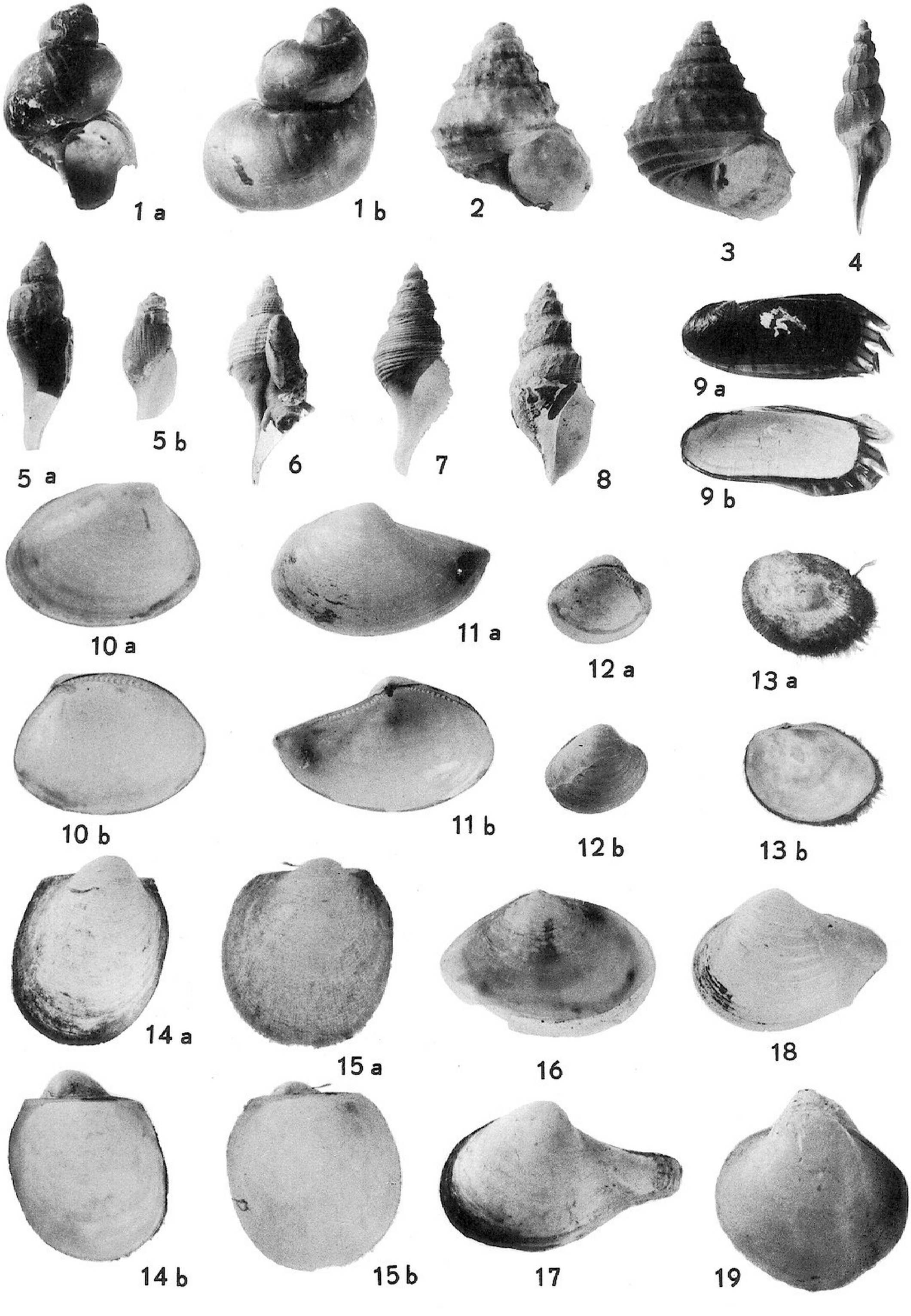


California borderland basins and lower slope, 1,800 to 4,122 meters

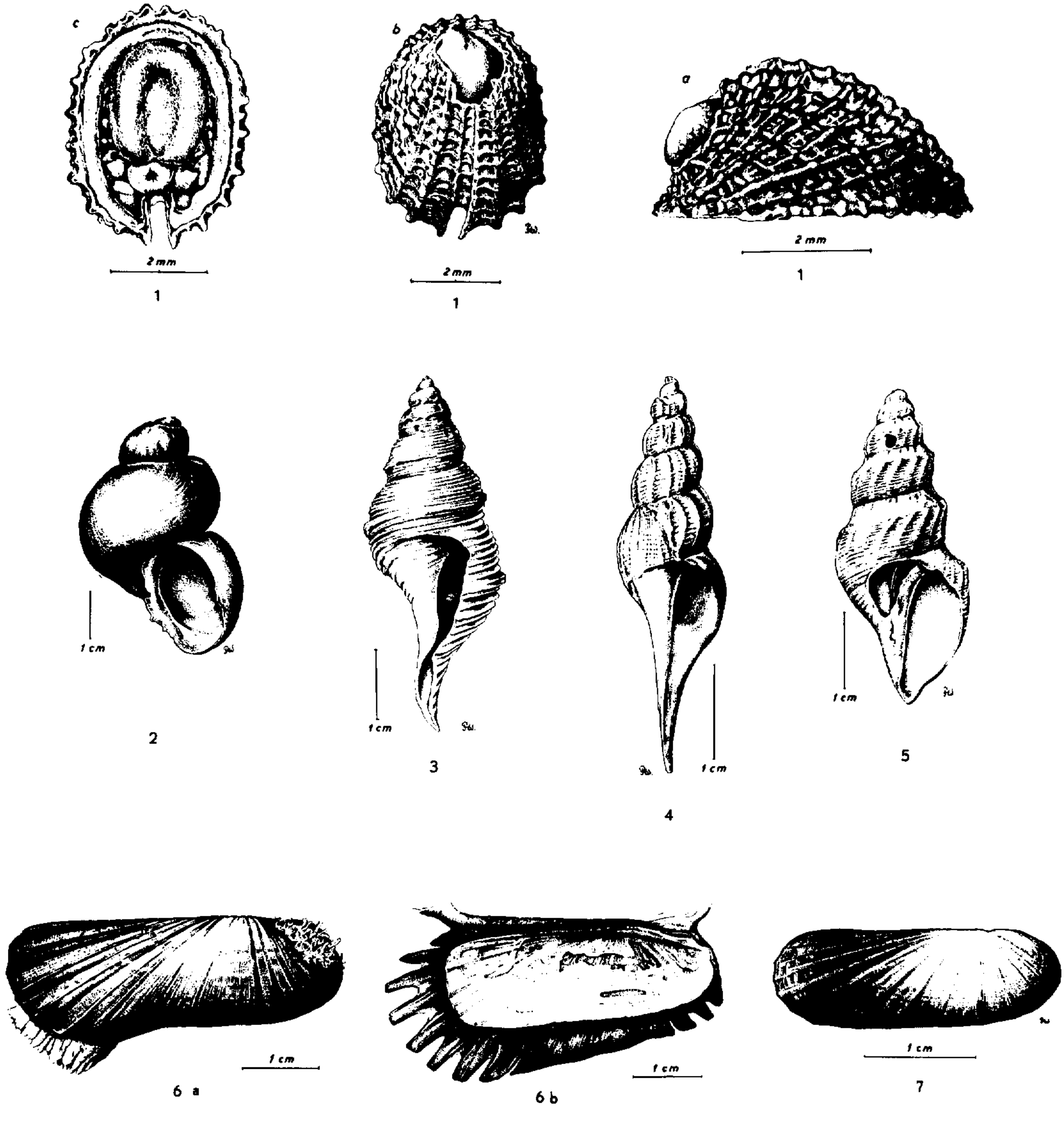
Explanation of Plate 9

ABYSSAL SOUTHERN BORDERLAND BASINS AND LOWER SLOPE, 1,800 TO 4,122 METERS

Figs. 1.—Chitinous gastropod? *a.* aperture; *b.* back; size 50×35 mm.
2.—*Solariella ceratophora* Dall, 1896. Aperture; size 21×19 mm.
3.—*Solariella equatorialis* Dall, 1908. Aperture; size 23×20 mm.
4.—*Fusinus rufocaudatus* Dall, 1896. Aperture; size 40×11 mm.
5.—*Tractolira sparta* Dall, 1896. Aperture; size 19×9 mm.
6.—*Pleurotomella clarinda* Dall, 1908. Aperture and animal; size 67×29 mm.
7.—*Steiraxis aulaca* Dall, 1896. Aperture; size 52×21 mm.
8.—*Turris* (*Gemmula*) sp. (see Dall, 1889). Aperture; size 42×29 mm.
9.—*Solemya agassizi* Dall, 1908. *a.* exterior; *b.* interior; size 42×18 mm.
10.—*Nucula panamina* Dall, 1908. *a.* exterior; *b.* interior; size 15×10 mm.
11.—*Nuculana agapea* (Dall, 1908). *a.* exterior; *b.* interior; size 21×12 mm.
12.—*Tindaria compressa* Dall, 1908. *a.* exterior; *b.* interior; size 10×8 mm.
13.—*Limopsis compressus* Dall, 1908. *a.* exterior; *b.* interior; size 29×20 mm.
14.—*Arca corpulenta pompholynx* Dall, 1908. *a.* exterior; *b.* interior; size 25×29 mm.
15.—*Arca* cf. *nucleator* Dall, 1908. *a.* exterior; *b.* interior; size 14×15 mm.
16.—*Abra profundorum* E.A. Smith, 1885. Exterior (broken, whole); size 20×13 mm.
17.—*Cuspidaria panamensis* Dall, 1908. Exterior; size 42×25 mm.
18.—*Myonera garretti* Dall, 1908. Exterior; size 21×15 mm.
19.—*Poromya perla* Dall, 1908. Exterior (whole); size 18×17 mm.



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



Some bathyal and abyssal mollusks

EXPLANATION OF PLATE 10

SOME BATHYAL AND ABYSSAL MOLLUSKS

Drawings by Poul Winther

FIGS. 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 9).

3.—*Steiraxis aulaca* Dall, 1896. Abyssal southern borderland. Aperture (Plate 9).

4.—*Fusinus rufocaudatus* Dall, 1896. Abyssal southern borderland (see Plate 9).

5.—*Turris* (*Gemmula*) sp. Abyssal southern borderland. Aperture (see Plate 9).

6.—*Solemya agassizi* Dall, 1908. Abyssal southern borderland. a. whole live specimen with undescribed hydroid attached. b. interior (see Plate 9).

7.—*Solemya valvulus* Carpenter, 1864. Upper slope. Whole live specimen.

Nassarius iodes (Dall)
N. moestus (Hinds)
N. tiarula (Kiener)*
Oliva spicata (Röding)*
Olivella dama (Wood)
Cancellaria cassidiformis (Sowerby)
Conus ximines Gray
Terebra variegata Gray

TECTIBRANCHS
Bulla gouldiana Pilsbry*
Haminoea angelinsis Baker and Hanna
H. strongi Baker and Hanna

PULMONATES
Melampus olivaceus Carpenter

LAMELLIBRANCHS
Anadara multicostata (Sowerby)
A. cepoides (Reeve)
Glycymeris gigantea (Reeve)
G. maculata (Broderip)
G. multicostata (Sowerby)
Atrina tuberculosa (Sowerby)
Trachycardium consors (Sowerby)
T. panamense (Sowerby)
Trigoniocardia granulifera (Broderip and Sowerby)
Laevicardium elenense (Sowerby)
Pitar newcombianus (Gabb)
Megapitaria squalida (Sowerby)
Dosinia ponderosa (Gray)
Protothaca grata (Say)
Heterodonax bimaculatus (Linne)*
Lyonsia gouldii Dall
Pinna rugosa Sowerby

* Species also taken alive on sand beach and flat area during present study.

Many of these species also were collected by the present author, but they were not found to be living. Many others were found alive at greater depth, where they form an important part of other living assemblages. Typical species are illustrated on Plate 2.

III. LOW-SALINITY LAGOON AND MANGROVE MUD FLATS

Only small collections were made in this environment by the author and various other members of Scripps' expeditions. The discussion is confined to the mollusks, but several species of shrimp and crabs occur in large numbers in the lagoons between Mazatlán and Panamá. The lagoon inlets south of Mazatlán generally are restricted and commonly are entirely closed. For this reason, salinities are rarely high enough to support a wholly marine fauna, and few strictly marine species are able to survive in the lagoons. A list of the typical mollusks found in this environment, selected from Keen (1958), is presented below. Species marked with an asterisk also have been taken in the present investigation. A few of the low-salinity species are shown on Plate 3.

PROSOBRANCHS
Neritina luteofasciata Miller, 1879
N. latissima Broderip, 1833
Cerithidea mazatlanica Carpenter, 1856*
C. montagnei (d'Orbigny, 1837)*
Ellobium stagnalis (d'Orbigny, 1835)
Littoridina, sp.*

TECTIBRANCHS
Bulla gouldiana Pilsbry, 1895*

PULMONATES
Melampus olivaceus Carpenter, 1856*

LAMELLIBRANCHS
Anadara tuberculosa (Sowerby, 1833)*
Mytella falcata (d'Orbigny, 1846)
Ostrea columbiensis Hanley, 1846
O. corteziensis Hertlein, 1951*
Polymesoda mexicana (Broderip and Sowerby, 1829)*
Polymesoda (7 other species)
Cyrenoides panamensis Pilsbry and Zetek, 1931
Mytilopsis adamsi Morrison, 1946
Rangia mendica (Gould, 1851)
Corbula inflata (C.B. Adams, 1852)

* Species also taken alive in low-salinity lagoons during present study.

IV. NEARSHORE SAND AND SAND-MUD ASSEMBLAGE, 11–26 METERS

This is by far the most prolific assemblage in species and numbers of individuals in the Gulf of California, because conditions in this environment are optimal for most marine species. Salinities are constant at normal oceanic values, and the temperature has a much smaller annual range than in the inshore environments. The water is relatively quiet near the bottom, and sediments are silty sands, clayey sands, and sand-silt-clay, containing relatively large quantities of organic matter. This permits a large population of deposit-feeding and burrowing animals. Under these optimal conditions, a total of 258 species of identified invertebrates were taken at 17 stations—an average per station significantly higher than in any other environment in the Gulf of California.

The separation between northern and southern Gulf is very distinct in this assemblage. The association matrix shows two assemblages, both on sand bottom and in depths from 11 to 26 m; one is in the Tiburón region and the other is south of Mazatlán. Ecological differences between the two regions are the higher water-temperature extremes and higher primary productivity of the Tiburón area. The greater annual range (16°C) in the Tiburón area as compared with Mazatlán (10°C) probably is the main limiting factor.

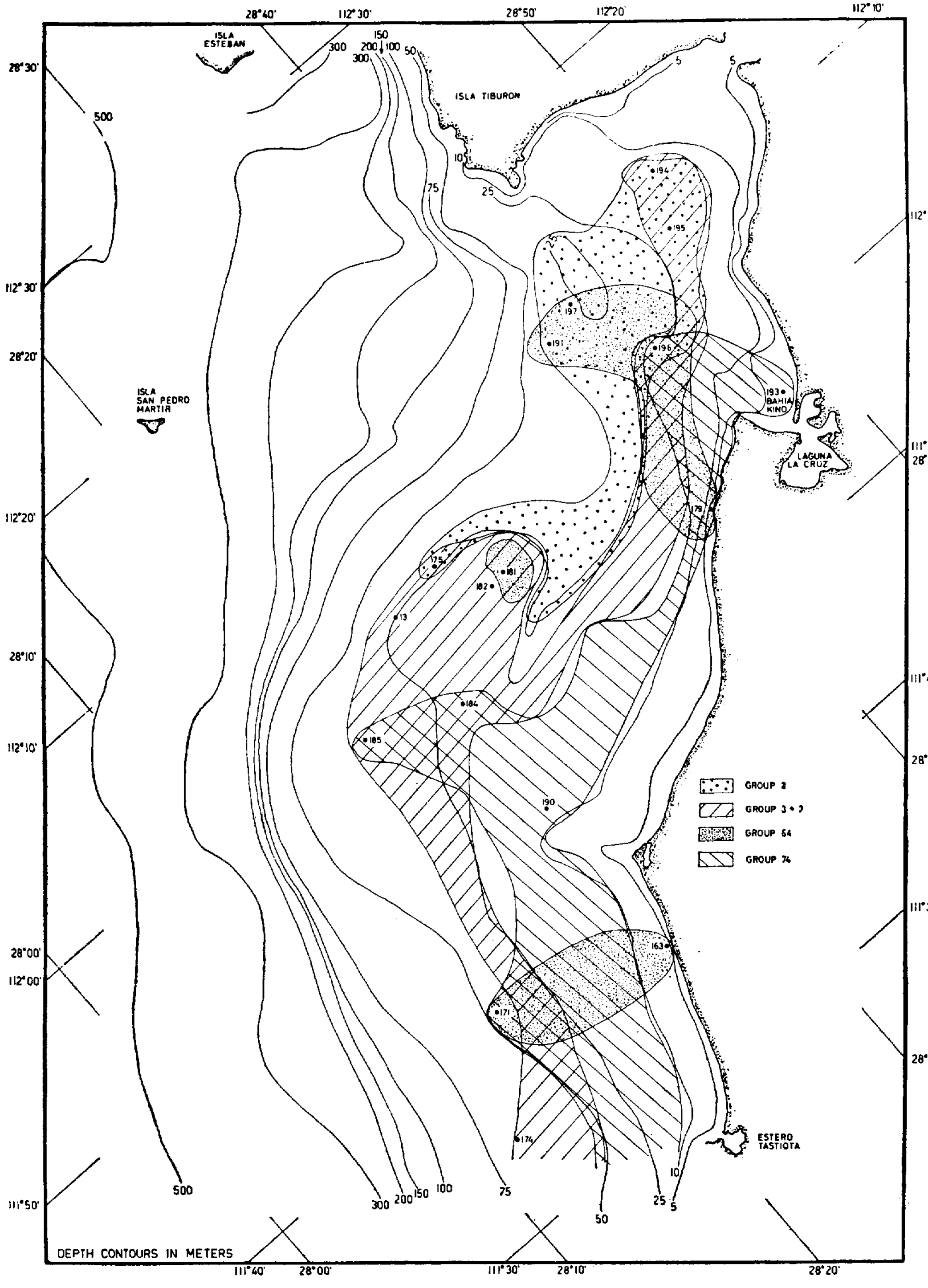


FIG. 12.—Areal distribution of index groups of assemblages in the northern nearshore shelf environment of the Costa de Hermosillo. Species and station composition of each index group are listed in the Appendix, Table II.

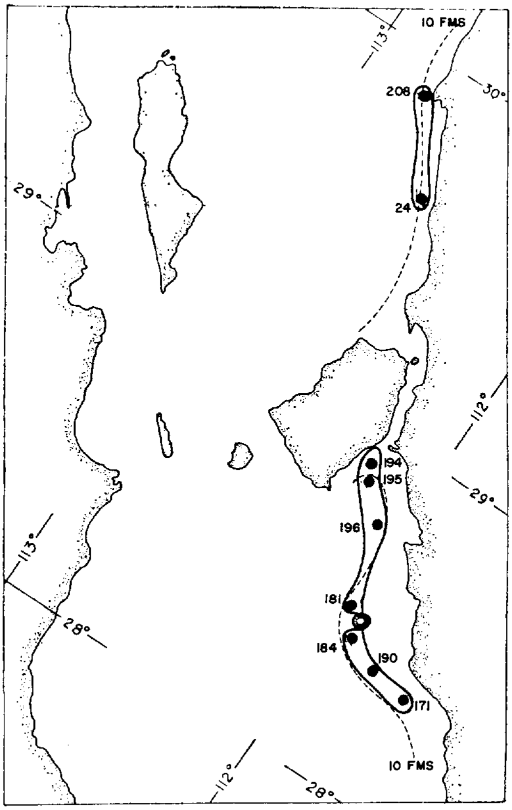


FIG. 13.—Areal distribution of stations characteristic for the nearshore shelf environment in the northeastern Gulf of California. These stations have the largest number of common occurrences of species belonging to all index groups.

Many invertebrate species are common to both regions. The Tiburón area between 4 and 30 m shows a very complex pattern of invertebrate assemblages. Five different associations, each occupying different areas but with considerable overlap, can be recognized (Fig. 12). Table II of the Appendix lists the species for each association and the environmental factors. Only stations with living faunas were used in establishing the faunal groups.

In order to describe the general faunal characteristics of the shallow-water environment of the Tiburón region, all species which were most frequently found together alive were listed, and all stations in which this group had the greatest abundance were selected (Fig. 13). The index species for this supergroup are given in Table III, with the percentage of occurrence in nine typical stations and the percentage of occurrence over the entire Gulf. For example, *Laevicardium elatum* was found living or dead in eight of the nine samples, but five of the seven living occurrences in the Gulf as a whole are in the Tiburón area. These two percentages were averaged to form an index of "uniqueness" for this species in this environment. The species in Table III are listed in order of decreasing importance; the last four were found only dead. Although they are statistically important components of the assemblage, they may be subfossil.

The 21 species of mollusks of Table III are only part of the important invertebrates in the nearshore sand environment. Others are listed in Table I in the Appendix. Many species taken in the 9 stations typical of this environment also occur in other environments and in similar depths in the southern Gulf. The fact that 3 species of corals, 14 crustaceans, 7 echinoids, 1 ophiuroid, 1 asteroid, 35 pelecypods, 3 scaphopods, and 54 species of gastropods so far have been identified from the 9 type stations demonstrates the diversity of life in this small area.

Although some of the important species are ubiquitous throughout the Gulf in this environment, a large number disappear south of the Fuerte River and are replaced by closely related types of the same genus or subgenus. Consequently, a separate station group with a well-defined assemblage can be recognized south of the Fuerte River (Fig. 14). A few of the more abundant invertebrates that are restricted to the southern area are listed below. A complete list can be found in Parker (1964); a few characteristic types are illustrated on Plate 4.

HEXACORALS
- *Astrangia conferta* Verrill

GASTROPODS
- *Architectonica placentalis* Hinds, 1944
- *Natica chemnitzii* Pfeiffer, 1840
- *N. othello* Dall, 1908
- *Sinum debile* (Gould, 1853)
- *S. sanctijohannis* (Pilsbry and Lowe, 1932)
- *Distorsio decussatus* (Valenciennes, 1832)
- *Bursa nana* (Broderip and Sowerby, 1829)
- *Typhis cummingii* Broderip, 1833
- *Cominella subrostrata* (Wood, 1828)
- *Olivella anazora* (Duclos, 1835)
- *Cancellaria exopleura* Dall, 1908

LAMELLIBRANCHS
- *Anadara nux* (Sowerby, 1832)
- *Chlamys tumbezenzis* (d'Orbigny, 1846)
- *Pitar frizzeli* (Hertlein and Strong, 1948)

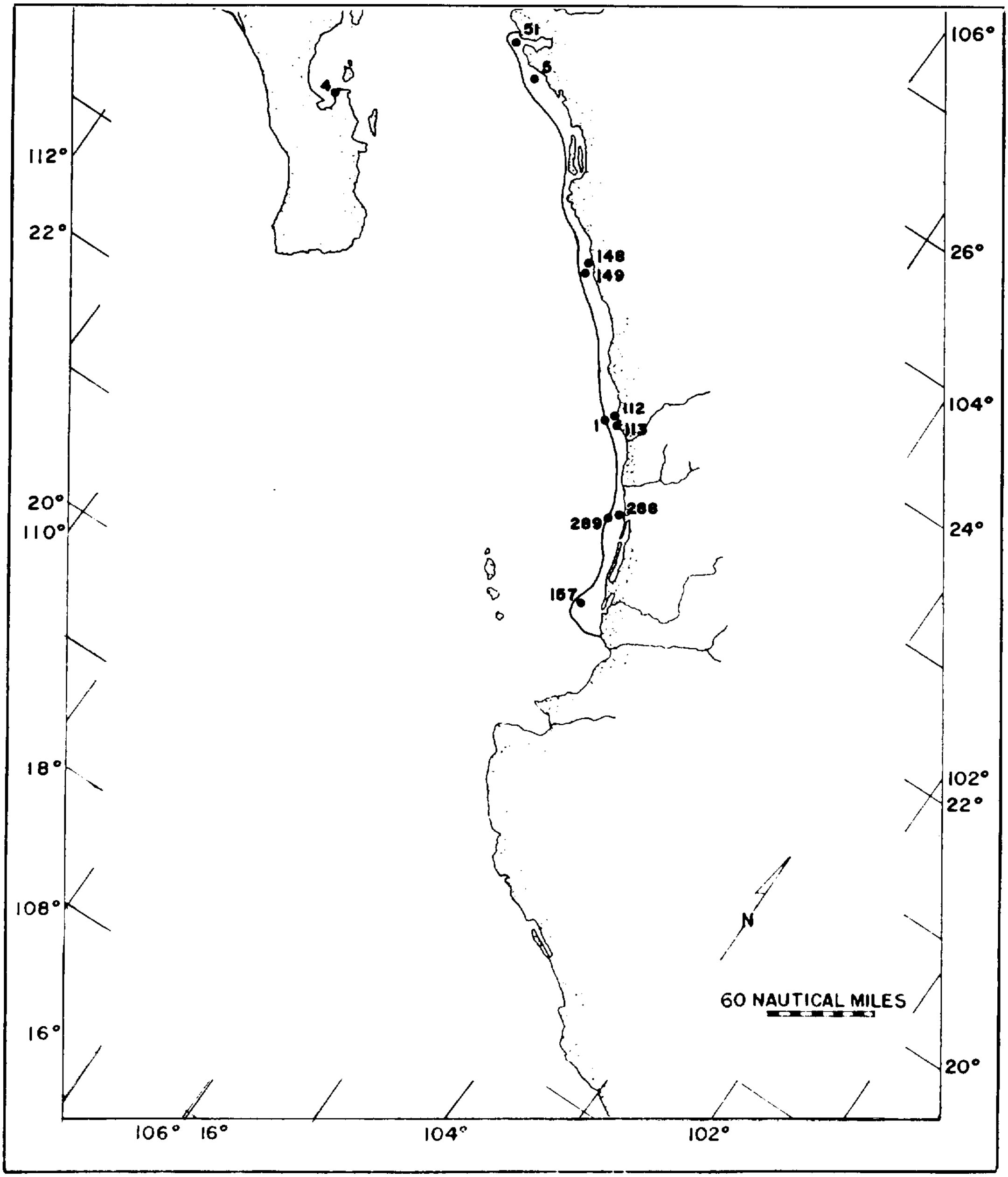


FIG. 14.—Location of stations characteristic for the nearshore shelf assemblage in the southern Gulf of California.

Mulinia bradleyi Dall, 1894
Tellina cognata C.B. Adams, 1854
Abra palmeri Dall, 1915
CRUSTACEANS
Euceramus panatelus Glassell
Pagurus smithi (Benedict)
ASTEROIDS
Astropecten californicus Fisher
OPHIUROIDS
Amphiura seminuda Lütken and Mortensen?

V. INTERMEDIATE SHELF, 27 TO 65 METERS

This environment also is very distinct and is second only to the nearshore shelf in the diversity and number of organisms. Differences occur between the northern and southern Gulf, both in the richness of the fauna and in the species compositions. The contingency matrix indicates a close association between a group of animals at 6 stations in the Tiburón region, ranging in depth from 66 to 74 m, and between those of 4 others from 25 to 74 m (Fig. 15). Few mollusks were taken alive in these stations, but a large number of dead specimens, representing many species, was collected. The crustaceans appear to be the best indicators for this assemblage. A list of species, proving to be closely associated by the contingency matrix, is given below, including both living and dead species. Most of the pelecypods are more abundant as dead shells.

Species	*Degree of Association*
GASTROPODS	
Polinices uber (Valenciennes, 1837)	11
Fusinus dupetitthouarsi (Kiener, 1846)	12
Natica grayi Philippi, 1852	15
LAMELLIBRANCHS	
Nemocardium pazianum (Dall, 1916)	6
Chione mariae (d'Orbigny, 1846)	8
Diplodonta subquadrata (Carpenter, 1846)	9
Macoma siliqua (C.B. Adams, 1852)	13
Cyclopecten pernomus (Hertlein, 1935)	14
Solecurtus guaymasensis (Lowe, 1935)	16
Plicatula inezana Durham, 1950	18
CRUSTACEANS	
Euprognatha bifida Rathbun	1
Mesorhea belli (A. Milne-Edwards)	2
Randallia americana (Rathbun)	3
Collodes tenuirostris Rathbun	4
Pagurus gladius (Benedict)	5
Cancer amphioetus Rathbun	7
Paradasygius depressus (Bell)	10
Cymopolia zonata Crane	14

Most of the characteristic living species of this assemblage are listed in Table I of the Appendix (also *see* Parker, 1964). All stations in the northern portion of this environment were taken on

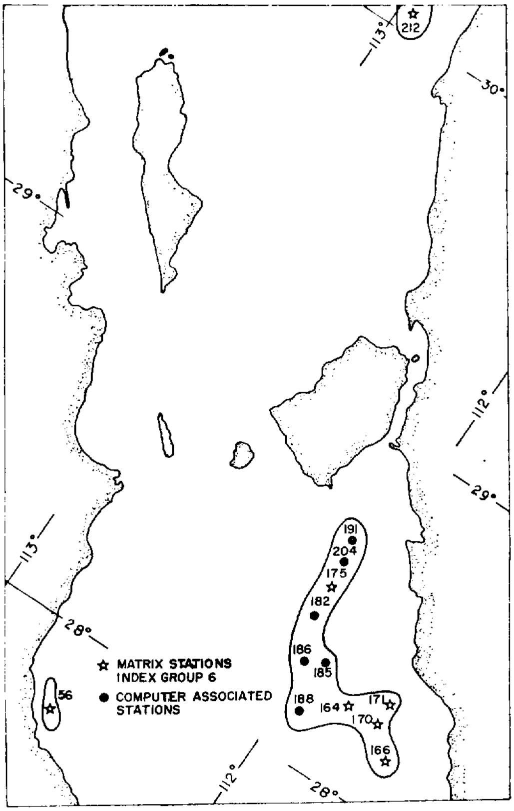


FIG. 15.—Location of stations highly correlated with the intermediate shelf assemblage of the northern Gulf of California. These stations are characterized primarily by *Euprognatha bifida* (index group 6).

sand bottom in well-oxygenated water with a temperature range from 13° to approximately 20° C.

A distinct assemblage exists in this environment in the southern portion of the Gulf. Species occurring at seven closely related stations are listed in Table IV of the Appendix and are shown in Figure 16. Selected species are illustrated on Plate 5. All stations occur on silty clay and range in depth from 36 to 75 m. As in the northern shelf region, crustaceans outnumber all other important components. Several other stations, although they contain the animals listed in Table IV, have a more heterogeneous composition and form a peripheral group. Of the 128 live species of invertebrates in 11 southern stations, 40 species occur both on sand and on silty clay. Sixteen of

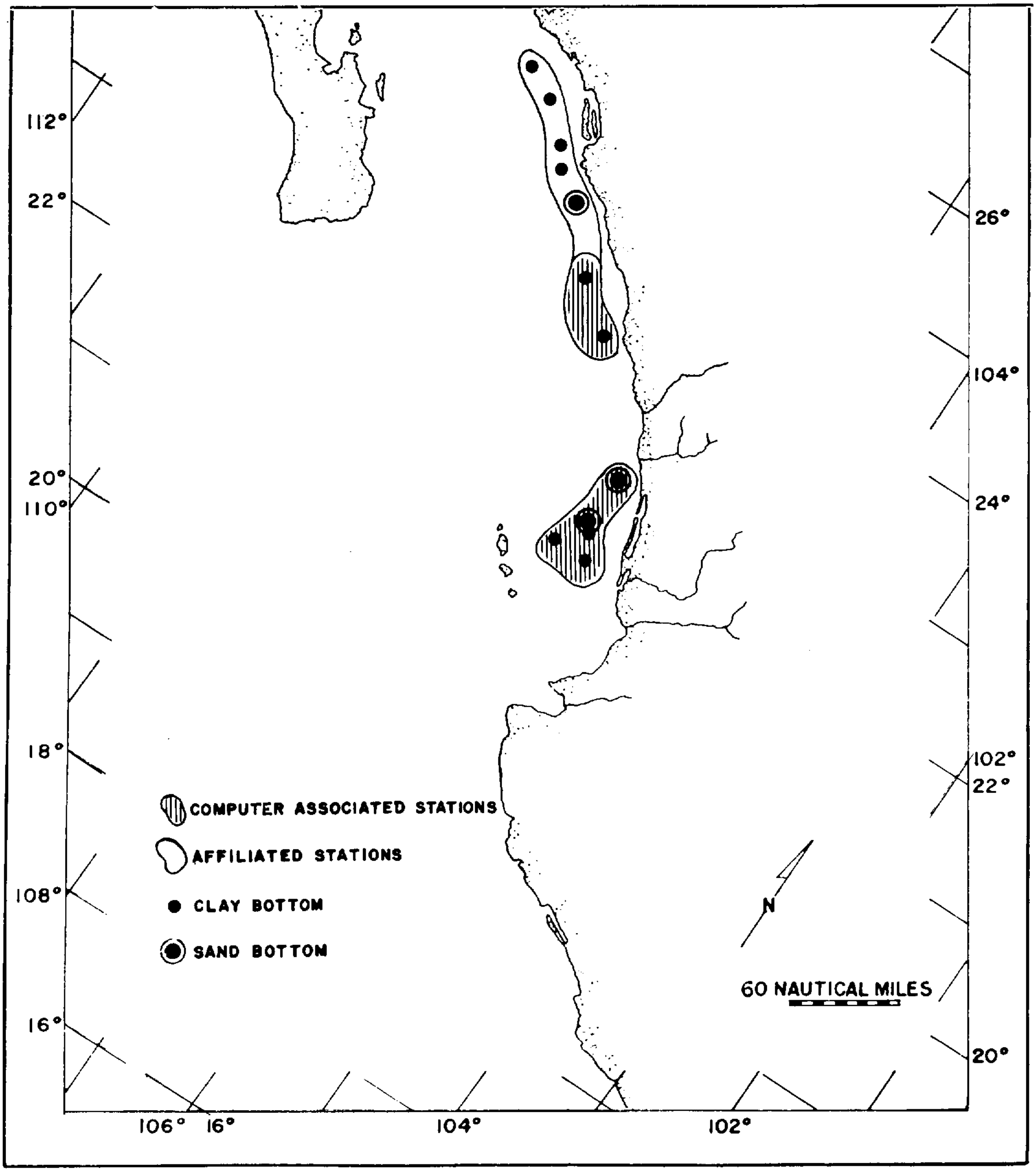


FIG. 16. Location of characteristic and related stations of the intermediate shelf assemblage on sand and clay in the southern Gulf of California.

these also occur on both sediment types in the northern area. In the southern area, only 28 species are restricted to silty clay, 3 of which occur on sand in the north. On the other hand, 57 species in 2 stations were found only on sand, of which only 8 also were taken in the north.

VI. OUTER SHELF, 66 TO 120 METERS, CLAY BOTTOM, SOUTHERN GULF

A distinct faunal region can be recognized on the outer shelf from the Fuerte River to just south of Mazatlán. Six stations are closely associated on the basis of five common species, sufficient in number to characterize the environment (Fig. 17). All six stations were taken on silty clay. The five common species are—

POLYCHAETA
Protula superba
GASTROPODS
Crucibulum n. sp. (allied to *C. striatum* of the Atlantic)
Conus arcuatus Broderip and Sowerby, 1829
LAMELLIBRANCHS
Anadara mazatlanica (Hertlein and Strong, 1943)
Chione kelletti (Hinds, 1845)

Most of the important species are listed in Table I of the Appendix and are illustrated on Plate 6. A complete list can be found in Parker (1964). Two other outer-shelf stations in the southern Gulf were taken on sandy bottom, but only two of the species from these stations also were found on clay bottom, both epifaunal in nature.

VII. OUTER SHELF, 66 TO 120 METERS, SAND BOTTOM, NORTHERN GULF

All faunas collected between Tiburón Island and the Colorado Delta in the northern Gulf, in depths between 66 and 120 m, occur on sand bottoms. They are completely different from the assemblage occurring at the same depths on clay bottom in the southern Gulf. The substrate of these stations (Fig. 17) probably is the relict littoral transgressive sand deposited by the post-Pleistocene rise in sea level (van Andel, this volume), a conclusion borne out by the abundance of dead shell belonging to nearshore assemblages in each sample. A total of 91 living invertebrate species was found at 18 stations, but the number of dead species was many times greater. The composition of the 18 stations is heterogeneous and no statistically significant assemblage can be established. Only two species occur at enough stations to be considered diagnostic—the echinoid *Clypeaster europacificus* H.L. Clark, 1914, and the pelecypod *Lucinoma annulata* (Reeve, 1850). The latter also is common in the deeper waters of the northern Gulf and on the outer shelf off California. The most interesting aspect of the assemblage is the large number of living gastropods and crustaceans. Most of these belong to species which occur also on inshore sand bottom to depths of less than 20 m. Apparently, the nature of the bottom is more important than depth or temperature in limiting the distribution of more motile invertebrates in the northern Gulf of California. Most of the important invertebrates from this environment are listed in Table I of the Appendix and in Parker (1964); some common mollusks are illustrated on Plate 6.

VIII. NORTHERN GULF BASINS, 230 TO 1,500 METERS

Owing to the peculiar temperature conditions in this deep portion of the northern Gulf, this environment may well be unique in the world today. Virtually uniform conditions of temperature, salinity, and oxygen exist throughout the water column, and the bottom consists of a complex pattern of gravels, sand, and mud. There is almost no vertical stratification of faunas on the slopes.

Only 34 living species were taken on 16 stations (Fig. 18). Those unique to the northern basins are (number of stations in parentheses)—

OCTOCORALS
Acanthogorgia n. sp. (2)
Callogorgia flabellum (Ehrenberg) (1)
Eumuricea horrida (Mobius) (1)
Eumuricea n. sp. (1)
HEXACORALS
Balanophyllia sp. (2)
Caenocyathus bowersi Vaughn (1)
Desmophyllum crista-galli Milne-Edwards and Haime (3)
Dendrophyllia cortezi Durham and Barnard (1)
BRACHIOPODS
Laqueus californianus (1)
Morrisia horneii (2)
Terebratulina kiiensis (1)
GASTROPODS
Fusinus traski Dall, 1915 (1)
SCAPHOPODS
Dentalium pretiosum berryi Smith and Gordon, 1958 (1)
Cadulus austinclarki Emerson (1)

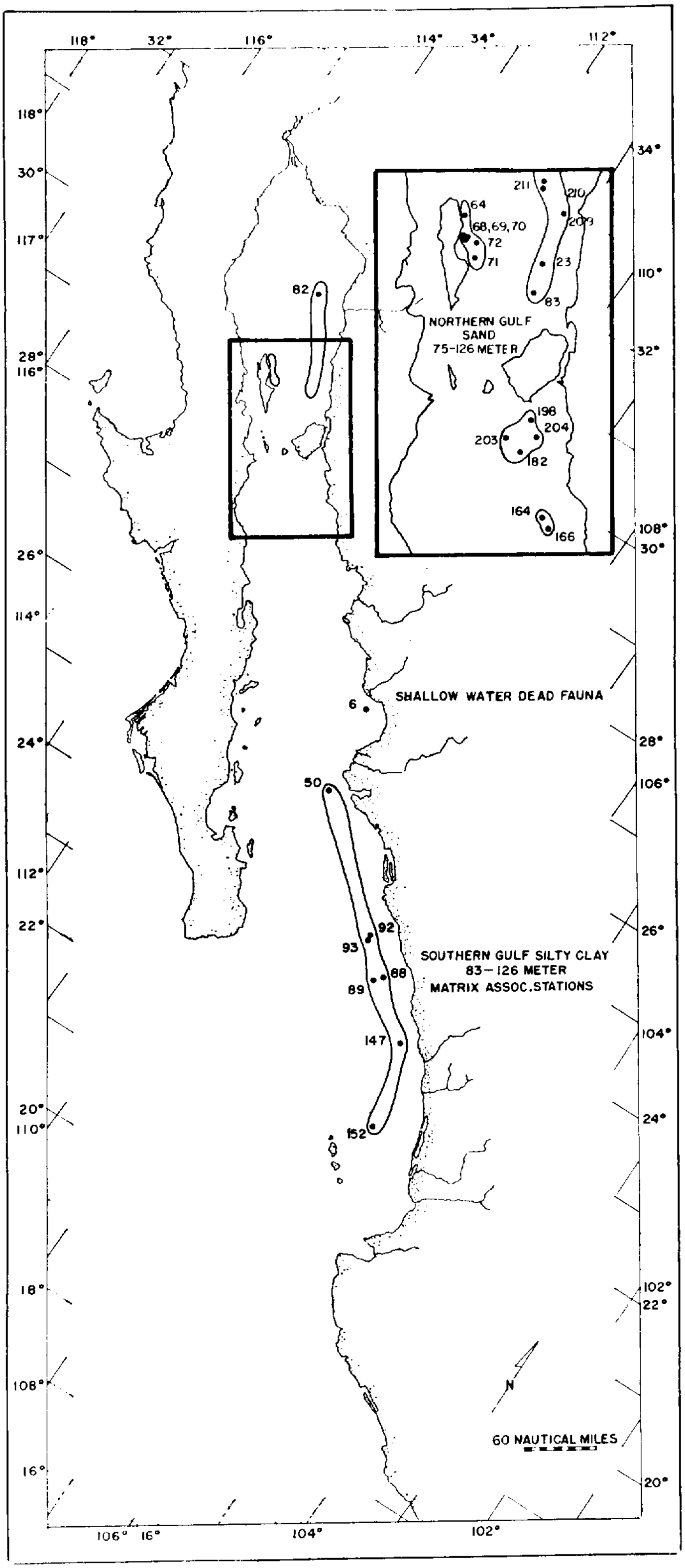


FIG. 17.—Location of characteristic stations of the outer shelf environment on sand bottom (northern Gulf) and clay bottom (southern Gulf).

Siphonodentalium quadrifisatum (Pilsbry and Sharp, 1898) (1)
LAMELLIBRANCHS
Macoma siliqua spectri Hertlein and Strong, 1949 (2)
Nuculana taphria (Dall, 1897) (1)
CRUSTACEANS
Salmoneus sp. (1)
ECHINOIDS
Brissaster townsendi (A. Agassiz) (1)
Hesperocidaris perplexa (H.L. Clark) (1)
ASTEROIDS
Astropecten californicus Fisher

Another 14 species are common both to this area and to the same depth zone in the southern and central Gulf (Appendix, Table I). A complete species list is given by Parker (1964); a few typical species are illustrated on Plate 7.

The dead shells collected from the northern Gulf basins can be divided into two groups. The first group consists of a large number of local shallow-water rock-bottom and shallow-water sand species, which either have been transported into deeper water by slumps or turbidity currents, or actually may live there as a result of high bottom-water temperatures. Some of these species are listed below (station occurrences in parentheses).

GASTROPODS
Acmaea sp. (2)
Fissurella sp. (1)
Diodora alta (C.B. Adams, 1852) (1)
D. aspera Escholtz (1)
Turbo sp. (1)
Crucibulum scuttelatum (Wood, 1828) (1)
Crepidula onyx Sowerby, 1824 (1)
Natica chemnitzi Pfeiffer, 1840 (1)
Polinices otis (Broderip and Sowerby, 1829) (2)
Cypraea annettae Dall, 1909 (1)
Ficus ventricosa (Sowerby, 1825) (1)
Olivella sp. (1)
Pyrene fuscata (Sowerby, 1832) (2)
Mitra crenata Broderip, 1836 (1)
Hindsiclava andromeda (Dall, 1919) (1)
Pleuroliria oxytropis (Sowerby, 1834) (1)
SCAPHOPODS
Dentalium oerstedii Mörch, 1861 (2)
D. vallicolens Raymond, 1901 (2)
Cadulus perpusillus Sowerby, 1832 (4)
LAMELLIBRANCHS
Barbatia alternata Sowerby, 1833 (1)
B. baileyi Bartsch, 1931 (1)
B. gradata (Broderip and Sowerby, 1839) (1)
Anadara cepoides (Reeve, 1834) (2)
Glycymeris multicostata (Sowerby, 1833) (1)
Pecten vogdesi Arnold, 1906 (1)
Cyclopecten pernomus (Hertlein, 1935) (1)
Pododesmus cepio (Gray, 1850) (1)
Crassinella varians (Carpenter, 1855) (1)
Cardita megastropha (Gray, 1825) (1)
Trigoniocardia guanacastense (Hertlein and Strong, 1947) (2)
Ventricolaria isocardia (Verrill, 1870) (2)
Semele sp. (1)
Corbula marmorata Hinds, 1843 (1)

Most of these species were found below 300 m—far below their normal habitat of the intertidal rocky shore.

The other group of dead shells is far more interesting. This assemblage of shells is very distinct and forms one of the most clear-cut associations of species. Of the nine species involved, only one was collected alive, and that only once, in the northern basins, although three more were taken alive on the upper slope of the central Gulf. The nine species of this group are (station occurrences in parentheses)—

GASTROPODS
Turritella sp. (cf. *T. cooperi* Carpenter, 1864) (6)
Nassarius miser Dall, 1908 (8)
LAMELLIBRANCHS
Nuculana hamata (Carpenter, 1864) (8)
N. taphria (Dall, 1897) (5)
Cardita barbarensis Stearns, 1890 (13)
Lucina tenuisculpta (Carpenter, 1864) (10)
Lucinoma annulata (Reeve, 1850) (14)
Nemocardium centifilosum (Carpenter, 1845) (20)
Hiatella arctica (Linné, 1767) (6)

Without exception, all of these species are found off the California coast; all are continental-shelf species not living in depths beyond 180 m, and most have not been recorded south of San Diego on the outer Pacific coast.

IX. UPPER SLOPE, CENTRAL AND SOUTHERN GULF, 121 TO 730 METERS

A slightly different fauna occurs between 121 and 730 m in the area separating the northern and central Gulf, south of the large islands. Twenty-four species were found to be common to the northern and southern Gulf, and 31 species were taken alive on 14 stations (Fig. 18). A considerable number of dead shallow-water mollusks were found on sand bottoms, probably as a result of slumping and a Pleistocene low stand of sea level. Some characteristic species from this region are shown in Plates 7 and 10; a complete list is given by Parker (1964). The living species taken at the 14 stations on the upper slope are listed below (number of stations in parentheses).

SPONGES
Poecillastra tricornis Wilson (1)
OCTOCORALS
Anthomuricea sp. (1)

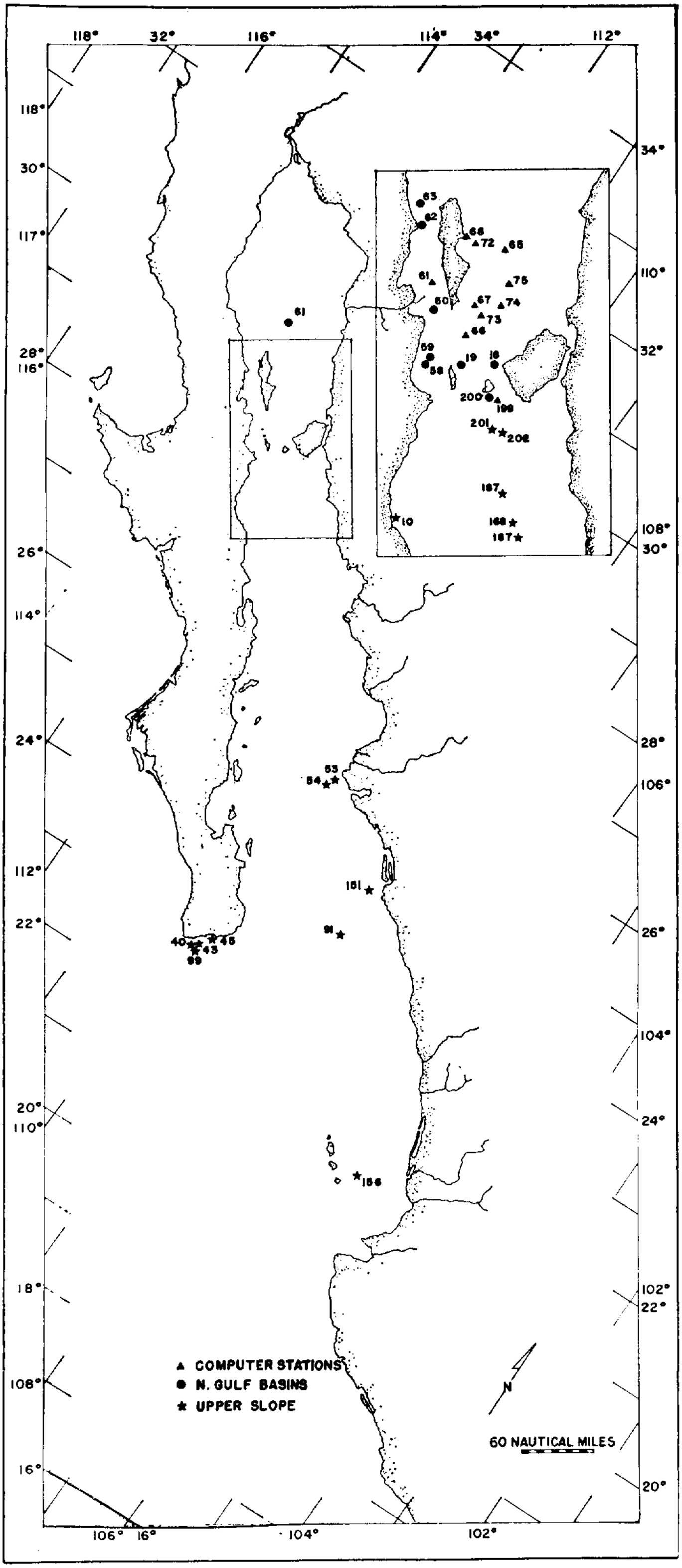


FIG. 18.—Location of characteristic stations (triangles) and all others of the basin environment of the northern Gulf of California, and of the upper slope environment.

BRACHIOPODS
- *Terebratula obsoleta* Dall (1)
- *Argyrotheca lowei* (1)

AMPHINEURA
- *Lepidopleurus?* (1)

SCAPHOPODS
- *Dentalium spendidulum* Sowerby, 1832 (1)
- *Cadulus californicus* Pilsbry and Sharp, 1898 (1)

GASTROPODS
- *Emarginula velascoensis* Shasky, 1961 (2)
- *Solariella permabilis* Carpenter, 1864 (1)
- *Calliostoma* sp. (1)
- *Polinices intemeratus* (Philippi, 1853) (1)
- *Nassarius insculptus gordanus* (Hertlein and Strong, 1951) (1)
- *N. miser* Dall, 1908 (1)
- *Fusinus colpoicus* Dall, 1915 (1)
- *Cancellaria?* sp. (1)
- *Clathurella thalassoma* (Dall, 1908) (2)

LAMELLIBRANCHS
- *Solemya valvulus* Carpenter, 1864 (1)
- *Nucula cardara* Dall, 1917 (2)
- *Amygdalum pallidulum* (Dall, 1916) (1)
- *Cyclopecten zacae* (Hertlein, 1935) (1)
- *Corbula ventricosa* Adams and Reeve, 1850 (1)
- *Pandora convexa* Dall, 1915 (1)

PYCNOGONIDS
- *Collosendeis bicincta* Schimkewitsch (1)

CRUSTACEANS
- *Sicyonia ingentis* (Burkenroad) (1)
- *Heterocarpus vicarius* Faxon (2)
- *Pleuroncodes planipes* Stimpson (3)
- *Paguristes holmesi* Glassell (1)
- *Cancer porteri* Rathbun (1)
- *Stenocionops beebei* Glassell (1)
- *Ethusa ciliafrons* Faxon (1)
- *Squilla* sp. (3)

HOLOTHURIANS
- *Pseudostichopus mollis* Theel, 1886 (1)

ASTEROIDS
- *Astropecten californicus* Fisher

OPHIUROIDS
- *Schizoderma diplax* Nielsen
- *Amenichondrius granulosus* Fisher

This list shows that the number of living species on the upper slope is sharply reduced with respect to the continental shelf. A partial explanation may be that, in the Gulf of California, this depth zone falls within the oxygen minimum area (Fig. 7). Moreover, sampling difficulties on steep slopes also may have contributed to the deficiency in species of this assemblage.

X. MIDDLE CONTINENTAL SLOPE, 731–1,799 METERS

The middle continental slope with its steep, dissected topography is possibly the most difficult environment in the Gulf to sample. Of the 12 stations occupied at this depth, only 4 were occupied in the Gulf of California. Two more were taken in the deep basins of the northern Gulf, but belong to a different environment. All others are from elsewhere along the Pacific coast south of San Diego and off Central America, where the conditions are nearly uniform (Stations 39, 84, 90, 127, 135, 138, 214, 215, 216, 221, 273; Figs. 1 and 2). Bottom-water temperatures in this lower bathyal zone range from 3° to 6°C, and much of the middle slope falls in the oxygen minimum zone (0.5 to 0.9 ml/L oxygen). Only 32 species have been identified in this environment; 6 of them were found only as dead shell. Only 3 species were taken twice—the crustaceans *Acanthephyra curtirostris* and *Paralomis multispina*, and the pelecypod *Solemya agassizi*. Low oxygen and inadequate sampling probably account for the poverty of the species list. A complete list is given below; some important mollusks are shown on Plate 8. Some of the mollusks taken in continental borderland basins off California (discussed in Parker, 1964) also are shown on Plate 8.

HEXACORALS
- *Cyathocerus* sp. (dead)

OCTOCORALS
- *Distichoptilum* n. sp.
- *Pennatula phosphorea californica* Kukenthal
- *Stachyptilum superbum* Studer
- *Swiftia* sp. (aff. *S. pacifica* [Nutting])

MONOPLACOPHORANS
- *Neopilina galatheae* Lemche, 1957 (dead)

GASTROPODS
- *Solariella nuda* Dall, 1896
- *Turcicula bairdii* Dall, 1889
- *Cocculina diomedae* Dall, 1908 (dead)

LAMELLIBRANCHS
- *Solemya agassizi* Dall, 1908
- *Lucinoma* n. sp.
- *Vesicomya lepta* (Dall, 1896)

CEPHALOPODS
- *Argonauta pacifica* Dall, 1896 (dead)

SOLENOGASTERS
- *Prochaetoderma* n. sp.

CRUSTACEANS
- *Benthesicymus tanneri* Faxon
- *Heterocarpus affinus* Faxon
- *Heterocarpus* n. sp.
- *Paracrangon areolata* Faxon
- *Glyphocrangon spinalosa* Faxon
- *Acanthephyra curtirostris* Faxon
- *Axiopsis (Calocarides)* n. sp.
- *Munidopsis* sp.
- *Parapagurus pilasimanus* Smith
- *Neolithodes diomedae* (Benedict)
- *Paralomis multispina* (Benedict)
- *Paralithodes rathbuni* (Benedict)
- *Gnathaphausia zoea* Sars

HOLOTHURIANS
- *Molpadia musculus* Risso (*violaceum* type)
- *M. musculus* (*musculus* type) Risso
- *Synallactes ishikawa* forma?

XI. ABYSSAL SOUTHERN BORDERLAND BASINS AND OUTER CONTINENTAL SLOPE, 1,800 TO 4,122 METERS

The abyssal region is markedly different from the previously discussed slope environments, because of the great diversity of its fauna and the large number of individuals. Although only 15 stations were occupied in abyssal depths, 77 species of benthonic invertebrates have been identified, and many more are still in the hands of specialists. Whereas in most of the shallower Gulf of California stations a species is generally represented by only a few individuals, the species in the abyssal stations generally were present with numerous individuals per station. The richness of the fauna is comparable to that of the inner portions of the continental shelf.

Bottom-water temperatures of this environment range from 1.2° to 2.6°C, and oxygen from 1 to 2.8 ml/L—high enough to support most forms of marine life. All stations except one have a silty clay bottom; the one exception at the mouth of the Gulf of California contains a substantial amount of manganese crust. The majority of the stations is less than 100 nautical miles from land, as the continental shelf is generally narrow along the Pacific coast of Central America. Upwelling and high primary surface productivity are common in the areas where sampling was carried out. As a result, organic matter accumulates in large quantities in the borderland basins, the continental slope, and the adjacent ocean floor (Parker, 1961; van Andel, this volume).

A complete list of the invertebrates identified so far in the 15 stations of this environment is given below (station occurrences in parentheses). Of the 77 species, only 5 also are found on the middle slope. Many typical mollusks are illustrated on Plates 9 and 10.

OCTOCORALS
- *Anthomastus ritteri* Nutting
- *Thouarella* sp.
- *Scleroptilum* cf. *durissimum* Studer

HEXACORALS
- *Caryophillia diomedaea* Von Marenzeller

POLYCHAETES
- *Maldane* sp.

BRACHIOPODS
- *Macandrevia americana diegenesis* (2)

POGONOPHORA
- *Galathealinum bruuni* Kirkegaard?

MONOPLACOPHORA
- *Neopilina galathaea* Lemche, 1957

GASTROPODS
- *Puncturella* cf. *expansa* Dall, 1896
- *Solariella ceratophora* Dall, 1896 (dead)
- *S. equatorialis* Dall, 1908 (2)
- Chitinous trochids?
- *Fusinus rufocaudatus* Dall, 1896
- *Tractolira sparta* Dall, 1896
- *Gemmula* n. sp. (aff. *G. exulans*)
- *Pleurotomella clarinda* Dall, 1908
- *Steiraxis aulaca* Dall, 1896

NUDIBRANCHS
- *Bathydoris aioca* E. and E. Marcus, 1962

SCAPHOPODS
- *Dentalium megathyris* Dall, 1889 (5)

LAMELLIBRANCHS
- *Solemya agassizi* Dall, 1908
- *Nucula panamina* Dall, 1908
- *N. agapea* (Dall, 1908)
- *Malletia truncata* Dall, 1908
- *Tindaria compressa* Dall, 1908
- *Arca corpulenta pompholynx* Dall, 1908
- *A. nucleator* Dall, 1908 (2)
- *Limopsis compressus* Dall, 1908 (6)
- *Chlamys latiaurata monotimeris* (Conrad, 1837) (2)
- *Cyclopecten* n. sp.
- *Vesicomya* sp. (dead)
- *Abra profundorum* E.A. Smith, 1885
- *Cuspidaria panamensis* Dall, 1908 (2)
- *Myonera garretti* Dall, 1908 (2)
- *Poromya perla* Dall, 1908

CRUSTACEANS
- *Storthyngura* aff. *pulchra* (Hansen, 1897)
- *Paropsurus giganteus* Wolff, 1962
- *Benthesicymus altus* Bate (2)
- *Hymenopenaeus doris* Faxon (2)
- *Sergestes phorcus* Faxon
- *Pandalopsis ampla* Bate
- *Pontophilus occidentalis* Faxon
- *Glyphocrangon* n. sp. (aff. *G. longirostris*)
- *Lebbeus* sp. (2)
- *Nematocarcinus cf. ensifer* Smith
- *Acanthephyra curtirostris* Faxon (2)
- *A. brevirostris* Smith
- *A.* n. sp. (aff. *sibogae*)
- *Munidopsis* sp.
- *M. bairdii* (Smith) (2)
- *Parapagurus pilosimanus* Smith (3)
- *Parolomis verrilli* (Benedict)
- *Ethusina faxonii* Rathbun

PYCNOGONIDS
- *Collosendeis angusta* Sars (2)
- *C. bicincta* Schimkewitsch
- *C. collossea* Wilson
- *C. macerrima* Wilson
- *Pallenopsis californica* Schimkewitsch
- *Ascorhynchus agassizi* Schimkewitsch

HOLOTHURIANS
- *Bathyplotes* sp.
- *Pseudostichopus mollis* Theel, 1886
- *Oneirophonta mutabilis* Theel, 1886
- *Peniagone* sp.
- *Benthodytes sanguinolenta* Theel, 1886 (4)
- *Psychropotes raripes* Ludwig, 1894
- *P. dubiosa* Ludwig, 1894
- *Abyssicucumis abyssorum* (Theel, 1886) (3)

Sphaerothuria bitentaculata Ludwig, 1894
Molpadia granulosa Ludwig, 1875
M. musculus Risso, 1826 forma *musculus*
M. musculus Risso, 1826 forma *violaceum*
M. musculus Risso, 1826 forma *spinosum*

ECHINOIDS
Aporocidaris milleri (A. Agassiz) (3)
Kamptosoma asterias (A. Agassiz)
Tromikosoma panamense (A. Agassiz) (2)
T. hispidum (A. Agassiz)
Urechinus loveni (A. Agassiz)
Brisaster latifrons (A. Agassiz)

ASTEROIDS
Eremicaster pacificus (Ludwig)

OPHIUROIDS
Ophiura irrorata Lyman
Ophiomusium glabrum Lütken and Mortensen
O. lymani W. Thomsen
Ophiocantha setosa Lyman
Amphiura seminuda Lütken and Mortensen
Amphiodia digitata Nielsen
Amphilepis patens Lyman
Amphioplus hexacanthus H.L. Clark

DISCUSSION

The presence of distinct faunas in the 11 environments described above (Fig. 19) is a function not only of the physical characteristics of the environments themselves, but also of the geological history of the region and of the biology of the principal species. An evident correlation exists between simple physical and chemical factors such as temperature, depth, sediment distribution, turbulence, salinity, and dissolved oxygen, and the distribution of macro-invertebrate assemblages. However, the presence of some species, or even of entire assemblages, may not be determined by the environmental parameters alone, but also by biological factors such as food preferences and feeding mechanisms, food competition, predator-prey relationships, reproductive capacity and larval development, and commensal or parasitic relationships. The basic organization of animal communities results from interdependence of biological factors and an over-all dependence upon the physical and chemical environment. Thorson (1957) has stated that parallel bottom communities, characterized by the same or closely related genera of dominants, exist wherever environmental conditions are similar. It has also been proposed that perhaps these communities are not so much similar in generic composition as they are comparable in biological organization. Communities found in all waters with similar environmental conditions may be characterized by similar feeding types and dominated by animals with characteristic kinds of reproduction or larval development. It is not necessary that the genera, or even families, be the same for the dominants in two communities in the same environment, so long as the dominants perform the same function within the commmunity. For this reason, a preliminary analysis of the feeding types to which the characteristic animals of each environment belong was made (Fig. 20). In the following pages both biological and environmental aspects of the faunal assemblages will be discussed; a more detailed treatment can be found in Parker (1964).

I. THE INTERTIDAL ROCKY SHORES

The rocky-shore assemblage is entirely an epifaunal group, dominated by algal and suspension feeders (Fig. 20), accompanied by a number of predatory species. Because little sediment normally accumulates, deposit feeders are absent. The same composition of feeding types was observed in the Okhotsk Sea by Savilov (1961). The majority of the gastropods are adapted to living in a rigorous environment, and nearly all lamellibranchs possess byssal threads which attach them to the rocks. Most forms have rather long, planktonic larval stages. Many of the characteristic genera are widespread in this environment (*Littorina*, *Ostrea*, *Mytilus*, *Fissurella*, *Balanus*, and *Bugula*, a bryozoan), although tropical shores commonly are characterized by more genera and species and fewer individuals than temperate or boreal regions. The principal environmental factors influencing this assemblage are the rocky substrate, great turbulence, extreme temperature range, high oxygen, and normal oceanic salinity.

The fossil assemblages known from the Baja California and Gulf of California regions, largely of Pleistocene to Pliocene age, generally consist of a mixture of the rocky shore and nearshore shelf assemblages (Emerson, 1960; Hertlein and Emerson, 1959; Durham, 1950). Of the 34 species from the Pleistocene of Ceralvo Island described by Emerson, 12 belong to the rocky-shore assemblage; the others are from the nearshore shelf group. The entire fauna is, as Emerson states, a reworked suite. The Pleistocene fauna

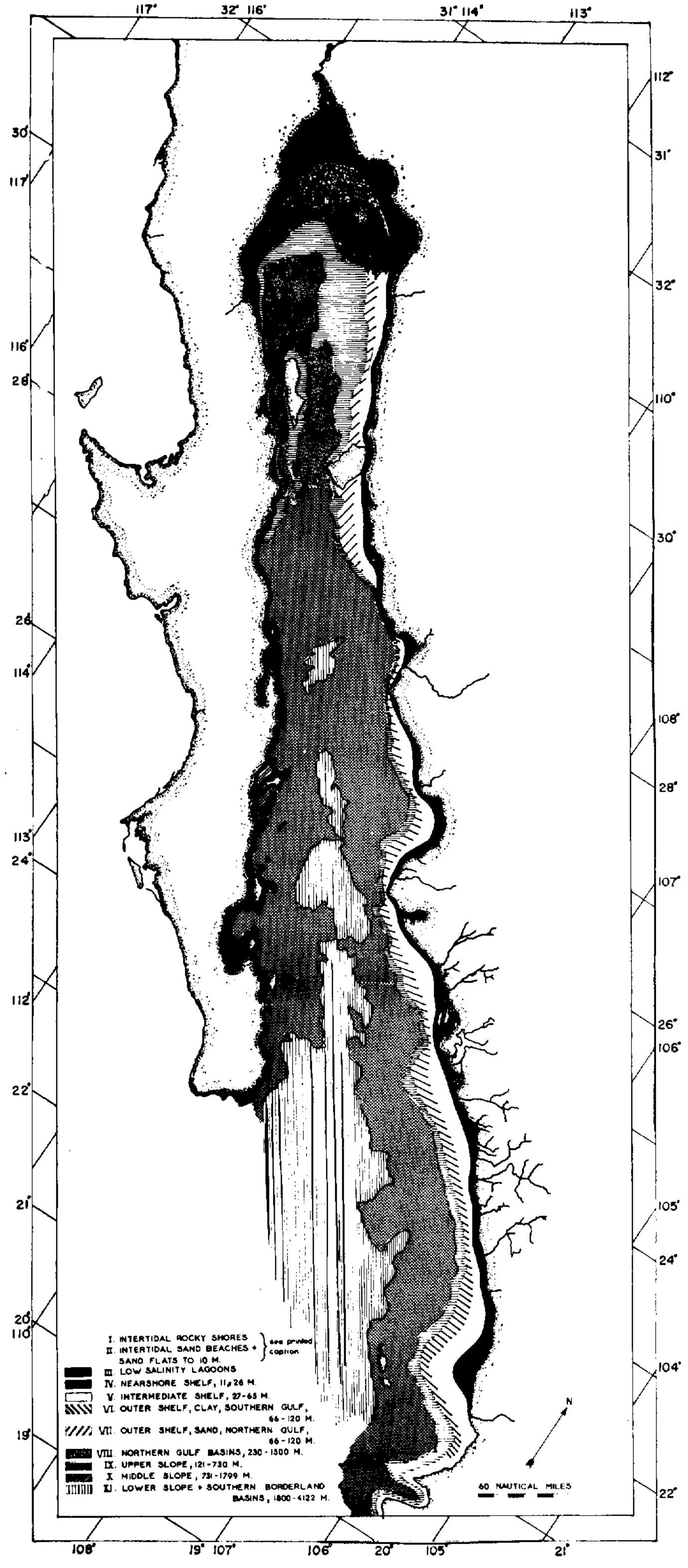


FIG. 19.—Regional distribution of Gulf of California faunal assemblages and environments. The distribution of the intertidal environments is shown in Fig. 12. Stippled area at the head of the Gulf has been sampled inadequately and does not represent a specific environment.

from María Cleofas Island, in the Tres Marías group, is primarily a level-bottom fauna (Hertlein and Emerson, 1959). Of the 28 species, 8 are attaching forms generally found in intertidal rocks. Few of the members of the rocky-shore community living at present in the Gulf are found as fossils in Pleistocene outcrops along the northwestern Baja California coast; the majority of the fossils are rock-living species normally found on the Californian coast (Emerson, 1956; Addicott and Emerson, 1959; Emerson and Addicott, 1958).

II. INTERTIDAL SAND BEACH AND SAND FLATS TO 10 METERS

The assemblage of sand flats and sand beaches is similar throughout the warm-temperate and tropical regions of the world (Pearse, Humm, and Wharton, 1942; Gauld and Buchanan, 1956). A great many similarities exist, for example, between the surf-zone and inner-shelf assemblage of the Gulf of Mexico (Parker, 1960, p. 320–321) and that of the Gulf of California, especially at the subgeneric level of mollusks and crustaceans. Many of the species of the two regions are nearly identical and have common ancestors in the Miocene and Pliocene of Panamá and Colombia (Olsson, 1961). However, the Gulf of California fauna is richer, possibly because of the more restricted air temperature range (15° to 30°C), as compared with the Gulf of Mexico (−5° to 40+° C).

The dominant feeding type among the lamellibranchs is suspension feeding (Fig. 20), because an abundant supply of suspended organic matter and living organisms is provided by the high turbulence and longshore-current transport. Predators are predominant among the gastropods and probably are dependent upon the lamellibranch population. The relative absence of deposit-feeding mollusks and the lack of selective deposit feeders among the echinoids can be attributed to the lack of organic detritus, which is not easily deposited in the agitated bottom water. Most of the inhabitants of this environment have long, pelagic larval stages, with the exception of the very large prosobranch gastropods, whose large larvae contained in egg capsules can withstand the turbulence. The long pelagic development and the mobility of most of the inhabitants of the sand flat environment may explain the uniformity of this assemblage over long stretches of coastline, even where interrupted by considerable portions of rocky shore.

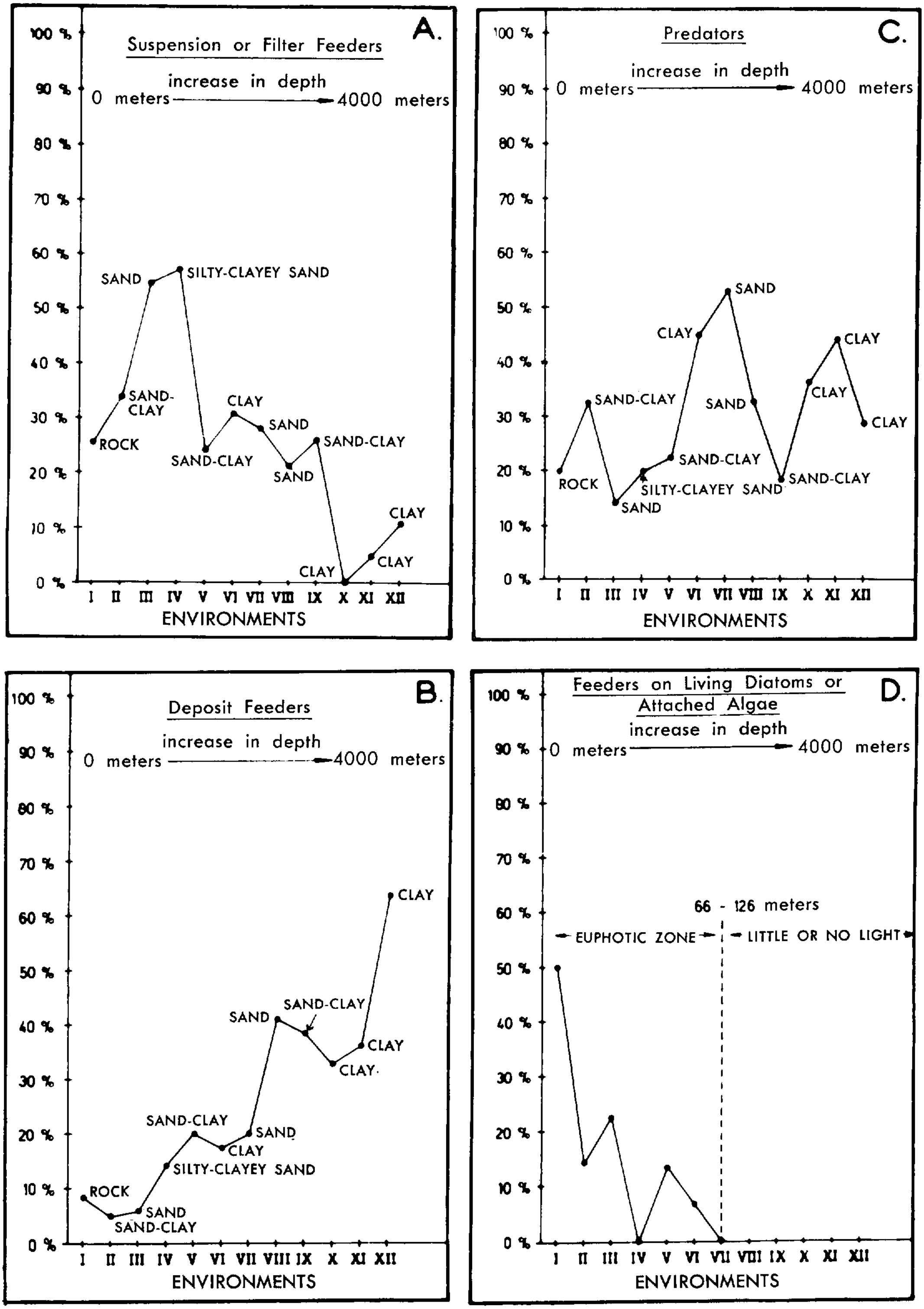
This assemblage has been important in the interpretation of the late Quaternary history of the continental shelf. Fossil assemblages, indicative of lower sea-level positions than the present one, have been found at various depths on the continental shelf, and dating of the shells by radiocarbon has aided in the understanding of history of the post-Pleistocene trangression. This assemblage, composed of sturdy and commonly large specimens, is resistant to destruction and common in Pleistocene deposits of the Gulf of California (Emerson, 1960; Hertlein and Emerson, 1959).

III. LOW SALINITY LAGOONS AND MANGROVE MUD FLATS

This assemblage, with its abundant populations of oysters, *Rangia*, mytilids, corbiculids, and penaeid shrimp, closely resembles the low-salinity, river-influenced assemblage of the northwestern Gulf of Mexico, discussed in detail by Parker (1956, 1959, 1960). Of the 19 species listed for the Gulf of California, 11 have their counterparts in the Gulf of Mexico lagoons, although the large *Anadara tuberculosa* and the large corbiculids are typical for the Gulf of California alone. Many of the genera and subgenera also are known from similar environments in South America, Africa, and tropical, subhumid Asia.

Little is known about the feeding types and larval stages of this assemblage. Suspension feeders predominate even in these turbid waters and on fluid mud bottoms (Fig. 20). Virtually all of the large lamellibranchs from this environment have planktonic larvae which settle to the bottom comparatively rapidly.

This assemblage is rare in the older deposits of the Gulf of California region, but is very common in the prehistoric shell middens of the southern part of the Gulf. Occasional specimens of some of the characteristic species were found in outer-shelf sand deposits. The species characteristic of this environment also are excellent climatic indicators.


A.
Suspension or Filter Feeders
increase in depth
0 meters
4000 meters
100 %
90 %
80 %
70 %
60 %
50 %
40 %
30 %
20 %
10 %
0 %
ROCK
SAND-CLAY
SAND
SILTY-CLAYEY SAND
SAND-CLAY
CLAY
SAND
SAND
SAND-CLAY
CLAY
CLAY
CLAY
I II III IV V VI VII VIII IX X XI XII
ENVIRONMENTS
C.
Predators
increase in depth
0 meters
4000 meters
ROCK
SAND-CLAY
SAND
SILTY-CLAYEY SAND
SAND-CLAY
CLAY
SAND
SAND
SAND-CLAY
CLAY
CLAY
CLAY
I II III IV V VI VII VIII IX X XI XII
ENVIRONMENTS
B.
Deposit Feeders
increase in depth
0 meters
4000 meters
ROCK
SAND
SAND-CLAY
SILTY-CLAYEY SAND
SAND-CLAY
CLAY
SAND
SAND
SAND-CLAY
CLAY
CLAY
CLAY
I II III IV V VI VII VIII IX X XI XII
ENVIRONMENTS
D.
Feeders on Living Diatoms or Attached Algae
increase in depth
0 meters
4000 meters
66 - 126 meters
EUPHOTIC ZONE
LITTLE OR NO LIGHT
I II III IV V VI VII VIII IX X XI XII
ENVIRONMENTS

IV. NEARSHORE SAND TO SAND-MUD, 11 TO 26 METERS

This environment corresponds closely to the shallow and nearshore shelf off the Mississippi Delta (Parker, 1956) and to portions of the nearshore and intermediate shelf off Texas (Parker, 1960). Of the assemblage off the Mississippi Delta, 8 of the 11 gastropod species, 15 of the 25 Pelecypoda, all echinoderms, and a large number of the crustaceans have counterparts on the subgeneric level in the equivalent environment of the Gulf of California. Most of these species also were found off Texas in similar depths. On the other hand, similar environments in India (Samuel, 1944), the Persian Gulf (Thorson, 1957), and Ghana, West Africa (Buchanan, 1958), show much less faunal diversity for similarly sized samples for comparable areas, and do not have the same dominant species (Parker, 1964).

The diversity of animal life in this environment in the Gulf of California is great. Each new grab sample or dredge haul produced an almost completely new set of species (Fig. 21-A, B). Five 0.1 m^2 Petersen grab samples were taken at a single locality (Fig. 21-C), four of which produced 2 to 5 new species (of a total 11) for each new sample taken. On the other hand, consecutive samples from Danish (Petersen and Boysen Jensen, 1911) and English (Holme, 1953) waters proved to be fairly uniform (Fig. 21-D). Complete data on these samples can be found in Parker (1964). This lack of species dominance, due to both geological and biological causes, is not confined to the recent assemblage. A similar variety can be found in the Pliocene of Florida (Dall, 1890b–1903), in a thin horizon of the Miocene of Florida (Dall, 1915), and in large lists of mollusks from the older Tertiary of North and South America (Gardner, 1926 to 1947; Woodring, 1925, 1928, 1957, 1959; Olsson, 1922). Apparently 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, the warm-temperate to boreal faunas of the middle Atlantic Miocene (Dall, 1904) and Danish Miocene (Sorgenfrei, 1958) possess only a comparatively small number of species.

One explanation for the great variety of mollusks in the Gulf of California may be found in its geological history. In middle Tertiary time, the relatively deep marine connections between the Caribbean and the Pacific permitted mixing of the two faunas, the principal migration taking place from east to west (Ekman, 1953) and adding a large number of species to the already rich and continually evolving eastern Pacific fauna. In addition, there has been a continuous renewal of species from the Indo-Pacific area. During the Pleistocene, a southward migration of some species from the California province also took place. With the high productivity of the Gulf, the availability of a great variety of ecological niches, and the comparative stability of the physio-chemical environment, virtually all species from these various zoogeographic regions have successfully maintained themselves.

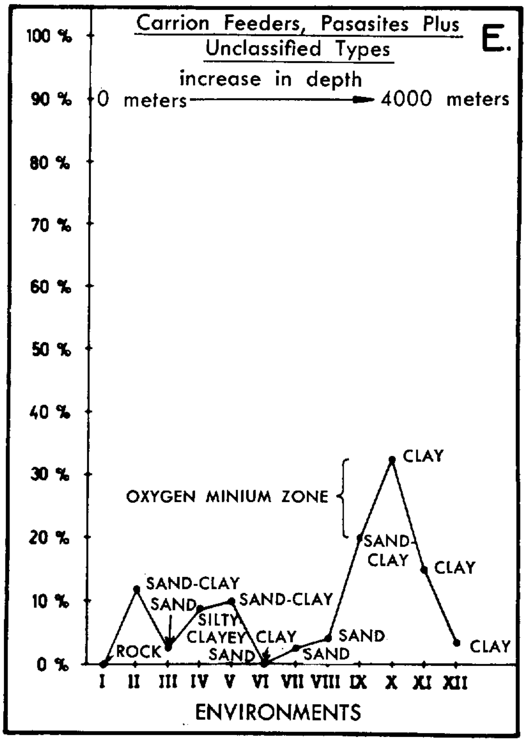
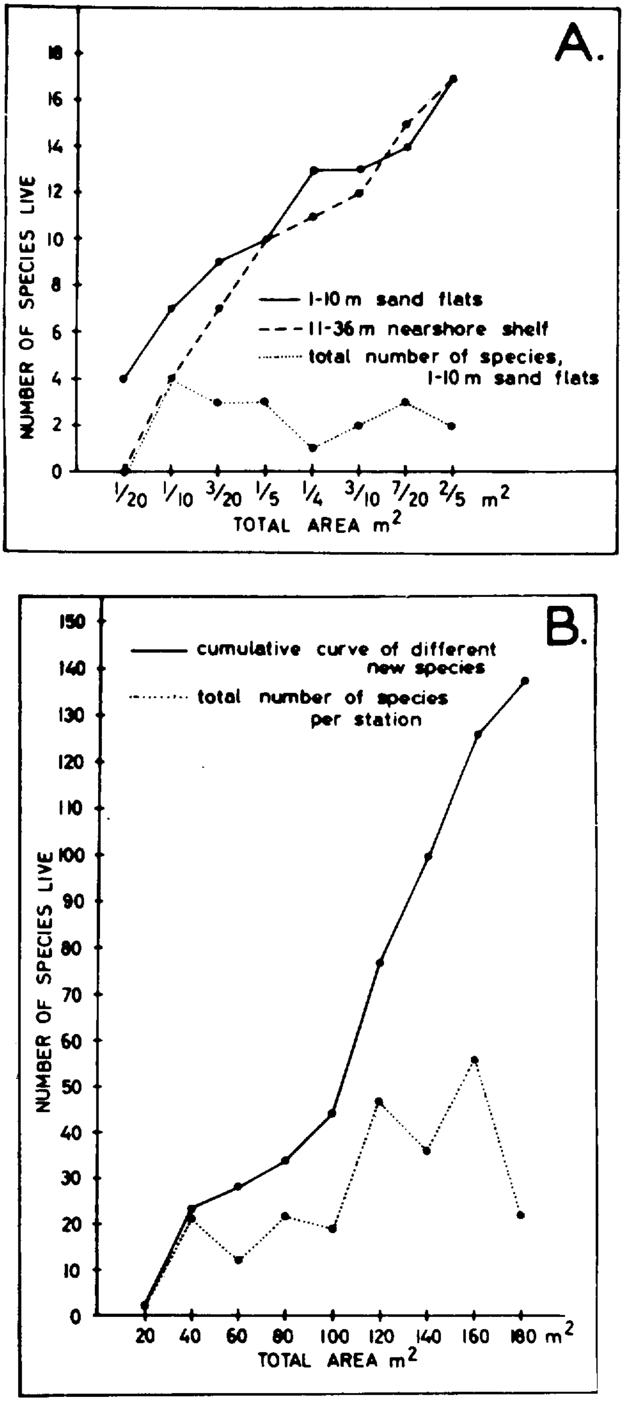


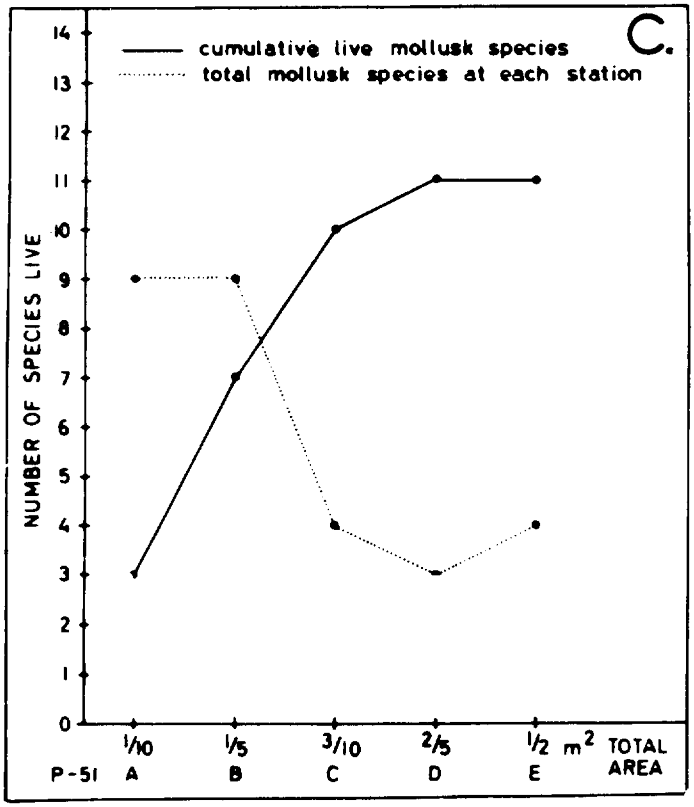
FIG. 20.—Distribution of feeding types of invertebrates in all environments discussed in this paper. Roman numerals refer to sections of the discussion.



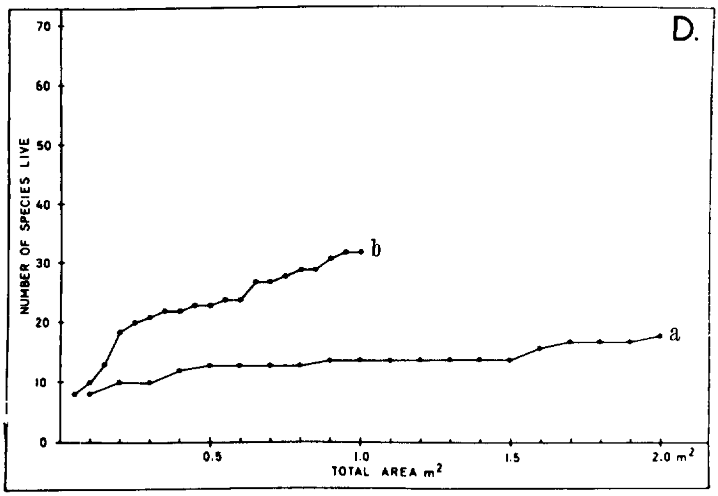
A. Curves of 1/20 m² Van Veen samples in two shallow environments in the southern Gulf of California region.

B. Curve of 9 successive samples from the northern shelf region, taken with a small shell dredge, covering roughly 20 m² per sample.

FIG. 21.—Cumulative curves of appearances of new species in successive samples from various localities in the Gulf of California and northwestern Europe.



C. Curve of mollusk species only, from 5 equal-sized samples in one spot off Topalabompo, Mexico, in a depth of 17 m, using a 1/10 m^2 Petersen Grab.



D. Cumulative curves of species diversity in 20 consecutive stations each from (a) Denmark (Petersen and Boysen Jensen, 1911. First 20 stations with 1/10 m^2 Petersen Grab. Thisted Bredning 14–27 m); and (b) England (Holme, 1953. 20 stations with 1/20 m^2 Scoop Sampler. Whitsand Bay 16.5 m).

Of the living species at the 9 closely associated stations of Figure 13, 45 per cent are suspension feeders, 30 per cent are predators or scavengers, 19 per cent are deposit feeders, 4 per cent are algae feeders, and 2 per cent are parasitic or commensal (Fig. 20). Similar feeding types characterize the same environment in Long Island Sound and Buzzards Bay (Sanders, 1958, 1960). Two-thirds of the characteristic species appear to have a planktonic larval development.

V. INTERMEDIATE SHELF, 27 TO 65 METERS

The assemblage characterizing this environment becomes a distinct entity at depths below approximately 40 m, especially in the southern Gulf. In the northern Gulf, the transition between this assemblage and the previous one is more gradual. In the intermediate zone, from 27 to 40 m, there is considerable overlap in depth ranges, and there is a considerable reduction in number of species and individuals. The transition zone is well developed only on finer sediments, especially on those inshore of relict sands resulting from the post-Pleistocene transgression. The zone also was observed in the northwestern Gulf of Mexico (Curray, 1960; Parker, 1960). In the Gulf of Mexico, the standing crop, mainly consisting of deposit feeders, was much lower (an average of 2.2 individuals per 0.2 m^2 grab sample) than in the Gulf of California (an average of 25.2 individuals per 0.2 m^2), where the primary productivity is much higher.

The sand-bottom assemblage between 39 and 65 m is the most distinct of the intermediate shelf faunas. It occurs, in part, on reworked relict nearshore sediments and in this respect is similar to faunas off the Texas coast in waters from 36 to 63 m (Parker, 1960, p. 322–323). Closely related or twin species are found in the Gulf of Mexico and in the Gulf of California, which have common origins in the Miocene and Pliocene shallow seas of Central America. A large number of these species, or their precursors, also can be found in the middle Tertiary of Central and South America (Olsson, 1961) and of Florida (Dall, 1890b–1903) and the Caribbean (Woodring, 1925, 1928).

Suspension and detritus feeders and predators are almost equally represented in the modern fauna of the Gulf of California (Fig. 20). Generally, a sand bottom is inhabited by an excess of suspension feeders, but the sands in deeper water are relatively quiet and organic detritus can accumulate. A high percentage of the mollusks have nonplanktonic larvae, but most of them are gastropods. The majority of the intermediate shelf lamellibranchs have planktonic larvae.

VI. OUTER SHELF, 66 TO 120 METERS, CLAY BOTTOM, SOUTHERN GULF

The fauna found in this environment is very similar to that of the same environment in the Gulf of Mexico. The large number of closely related species indicates a persistence of clay bottoms to 100 m depth across Central and South America in Tertiary time. Of the 21 typical species taken between 70 and 120 m in the Gulf of Mexico, 13 have exact counterparts in the Gulf of California, and an additional 6 were taken at slightly different depths. These closely related species also are predominant in both areas.

Most of the lamellibranchs are deposit feeders or suspension feeders, feeding nonselectively on detrital material; the majority of the gastropods are predators (Fig. 20). Savilov (1961) also found that nonselective deposit feeders reach their greatest development in zones of rapid deposition of fine sediment on the upper slope. The majority of the mollusks have pelagic larvae which are well adapted to the rather uniform environment.

VII. OUTER SHELF, 66 TO 120 METERS, SAND BOTTOM, NORTHERN GULF

No exact counterpart of this assemblage is known from any other part of the world, because deep, uniform, terrigenous sand deposits are relatively uncommon. The composition of the fauna in this environment is very patchy, in contrast to the uniform distribution of the assemblage described above, and few mollusk species were taken more than twice in 18 stations. The crustaceans were by far the most abundant, and many were taken at four or five stations, but they also are distributed rather uniformly in this region from shore to shelf edge. This environment is a transition zone rather than a distinct entity. The majority of the lamellibranchs probably are suspension feeders, whereas 20 of the 24 living gastropods are predators (Fig. 20). An abundant supply of organic matter is available, because primary production in the region is high. The breakdown of the thermocline in this region, as a result of intense tidal turbulence, may contribute to the transitional nature of the assemblage. A number of lamellibranch species proved to have a direct or lecithitrophic larval development, differing from those of previous environments.

VIII. NORTHERN GULF BASINS AND TROUGHS, 230 TO 1,500 METERS

This environment is characterized by its vertical uniformity and resulting high bottom-water temperatures and oxygen values. Vertical stratification of the benthic fauna is lacking. Similar environments may exist elsewhere, but the only possible case studied—the Red Sea (Fuchs, 1901)—seems to possess a normal faunal sequence somewhat similar to that of the southern Gulf of California. A similar ancient environment has been assumed by Baldi (1961) for parts of the Miocene in Hungary; others may occur in Southern California and Venezuela.

A striking feature of the fauna in this environment is the occurrence of numerous shells of species now extending nó farther south than the California province on the Pacific coast. The present bottom-water temperature in the northern Gulf basins ranges from 11° to 14°C, which is comparable to the temperature range of the California shelf. Many of the cold, shallow-water species were taken in the Gulf from sand layers in piston cores and may have been displaced from an original shelf position. Others have been collected as dead shell from the region around Cape San Lucas in depths of 200 to 800 m. It may be assumed that during the late Pleistocene, when sea level stood approximately 100 m lower than at present (substantiated by the dating of nearshore mollusk shells found in 110–115 m off San Blas, Mexico, which were 17,000–19,000 years old), the California-province species invaded the Gulf along the upper slope, and the basin floors in the northern Gulf now are in the only environment in which survival is possible.

All of the pelecypod species occurring in this environment are deposit feeders; the gastropod is a predator, and the echinoids and scaphopods are deposit feeders, feeding on the abundance of organic matter resulting from high surface productivity. The dead shallow-water species found in the bottom of the deep troughs are suspension and algae feeders, which agree with the feeding types of the nearby rocky-shore assemblage. The California-province species found as dead shell are predominantly deposit feeders, indicating an environment rich in organic detritus similar to the present one. Most of the species have a pelagic larval stage, although a few lamellibranchs prove to have brood-protection for their larvae.

IX. UPPER SLOPE, CENTRAL AND SOUTHERN GULF, 121 TO 730 METERS

Few living organisms were taken on the upper slope, much of which lies in the oxygen minimum zone. Several parts of the region appear devoid of life. The only animals that were at all common were several species of stomatopod shrimp (*Squilla*) and occasionally large numbers of *Munida* and *Pleuroncodes planipes*, both galatheid shrimp, all carrion feeders and well adapted to this environment of great accumulation of organic detritus.

Assemblage studies of this environment elsewhere in the world do not exist, although taxonomic monographs are abundant (Dall, 1886, 1889, 1890a, 1908; *Albatross*, *Challenger*, and *Galathea* Reports; Ekman, 1953). The majority of the animals are deposit feeders or scavengers, but a rather high percentage (27 per cent) can be classified as suspension feeders, probably subsisting on the rain of planktonic material. W.K. Ocklemann of the Marine Biological Laboratory, Helsingør, Denmark, and this author, indicate that the majority of species have lecithitrophic or direct (nonpelagic) development. In general, the number of mollusk species with nonpelagic larval development increases with increasing depth below the shelf edge.

X. MIDDLE CONTINENTAL SLOPE, 731 TO 1,799 METERS

The mid-slope assemblage is a typical deep-sea fauna, composed of lower bathyal and upper abyssal components. Three of the eight species of mollusks taken in this environment are listed as abyssal by Clarke (1962), and all genera are primarily abyssal in distribution. Bottom-water temperatures are between 3°C and 6°C, but there are no definite depth or temperature criteria on which the boundary between abyssal and bathyal can be based. Monographs of a taxonomic nature on slope animals are common in the literature, but community and ecological studies concerned with the bathyal-abyssal environment are very rare.

All but five of the mollusks collected alive are deposit feeders, but the corals can be considered suspension-feeding predators. The shrimp and large decapod crabs are most probably scavengers, but nothing certain is known of their feeding habits. The suspension feeders probably live off the rain of plankton from the high surface productivity along the Pacific Coast. A few of the mollusk species related to those occurring in this assemblage have been found in the Miocene and Pliocene of the west coast of North America (Grant and Gale, 1931), and in Tertiary sediments of Panamá, Costa Rica, and Ecuador (Olsson, 1942).

XI. ABYSSAL SOUTHERN BORDERLAND BASINS AND OUTER CONTINENTAL SLOPE, 1,800 TO 4,122 METERS

Notwithstanding the great depth and low temperature (1°–2.5°C) of this environment, the richness and complexity of the fauna are not equalled elsewhere in the deep sea, and not commonly even on the continental shelf. Similar rich development on the outer slope region has been observed elsewhere (Wolff, 1961; Sanders, personal communication). In Wolff's paper, 54 species of invertebrates are listed from one station in the Gulf of Panama, and some material is not yet identified. Similarly, incomplete determinations from the 15 stations off Mexico and Guatemala show 86 species. Only 11 species of invertebrates were taken in common by the two programs. Elements of this fauna have been found in Tertiary sediments of Panamá, Costa Rica, and Ecuador (Olsson, 1942).

The majority of the animals living in this environment are deposit feeders, whereas most of the others probably are scavengers and predators. Many of the species, however, have no shallow-water relatives, and it is almost impossible to deduce their feeding habits or larval development from the present material. More sophisticated sampling techniques and emphasis on the biology rather than on the taxonomy of deep-sea animals are urgently needed.

SUMMARY AND CONCLUSIONS

The data obtained in this study have contributed to the knowledge of shallow-water faunas in a somewhat unusual subtropical and tropical region and have provided considerable information on the composition of deep-sea assemblages. Many of the environments and assemblages of the Gulf of California have counterparts elsewhere in the world, but some, especially those of outer-shelf to bathyal depth in the northern Gulf, appear to be almost unique.

The density of animals in the tropical and subtropical region studied appears to be smaller than in boreal and temperate regions. Moreover, the density decreases with increasing depth, with the exception of the lower slope. On the other hand, the diversity of animals in level-bottom communities seems to be greater in the tropics than in more northerly climates. Thorson (1957) disagrees with this statement, but he does admit that the diversity of epifaunal habitats is greater in the tropics because many more niches are available, particularly on coral reefs. Neither this study nor other studies of the tropical region provides enough quantitative data, however, for a significant comparison between warm- and cold-water faunas.

The study has provided additional information for the interpretation of ancient environments, particularly those of deeper water, and many similarities have been noted between the living faunas of the area studied and the Tertiary assemblages of Central America and the Caribbean region.

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APPENDIX

TABLE I. CHECK-LIST OF CHARACTERISTIC INVERTEBRATE SPECIES IN GULF OF CALIFORNIA ENVIRONMENTS
(Key to class symbols at bottom of page)

Species	*Class*[1]	I	II	III	IV	V	VI	VII	VIII	IX	X	XI[2]
		Environments										
Acmaea discors	G	X										
Tegula ligulata	G	X										
Turbo fluctuosus	G	X										
T. squamiger	G	X										
Nerita scabricosta	G	X										
Littorina aspersa	G	X										
L. conspersa	G	X										
Vermicularia pellucida	G	X										
Diodora alta	G	X										
Cerithium stercusmuscarum	G	X										
C. sculptum	G	X										
Jenneria pustulata	G	X										
Acanthina lugubris	G	X										
Morula ferruginosa	G	X										
Purpura patula pansa	G	X										
Pyrene fuscata	G	X										
Nassarius tiarula	G	X										
Marginella californica	G	X										
Onchidiella binneyi	PUL	X										
Siphonaria maura	PUL	X										
Arca pacifica	P	X										
Barbatia reeveana	P	X										
Arcopsis solida	P	X										
Brachidontes multiformis	P	X										
Isognomon chemnitzianus	P	X										
Ostrea conchophila	P	X										
Anomia adamas	P	X										
A. peruviana	P	X										
Cardita affinus californica	P	X										
Grapsus grapsus	CR	X										
Tetraclita stalactifera	CR	X										
Diadenum mexicanum	E	X										
Heliaster kubiniji	AS	X										
Athyone glanelli	HO	X										
Brandtothuria impatians	HO	X										
Cerithium maculosum	G		X									
Cerithidea albonodosus	G	X	X									
Neritina luteofasciata	G		X	X								
Turritella gonostoma	G		X									
T. leucostoma	G		X									
Natica chemnitzii	G		X		X							
Cypraea arabicula	G		X									
Strombus granulatus	G		X									
S. gracilior	G		X		X							
Oliva spicata	G		X									
Olivella anazora	G		X									
Nassarius angulicostus	G		X									
Bulla gouldiana	G		X	X								
Cadulus austinclarki	SC		X									
Anadara labiosa	P		X									
A. multicostata	P		X									
Glycymeris delessertii	P		X									
G. gigantea	P		X									
Cardita grayi	P		X									
C. megastropha	P		X									
Codakia distinguenda	P		X									
Trachycardium procerum	P		X									
Papyridea aspersa	P		X									
Diplodonta subquadrata	P		X			X						
Tivela byronensis	P		X									
Transanella puella	P		X									
Pitar concinna	P		X									
P. lupanaria	P		X									
Megapitaria squalida	P		X		X							
Dosinia dunkeri	P		X									
D. ponderosa	P		X									

[1] Key for letter symbols under *Class* column
AN—Anthozoa
BR—Brachiopoda
MON—Monoplacophora
G—Gastropoda
PUL—Pulmonata
SC—Scaphopoda
P—Pelecypoda
PO—Polychaeta
CR—Crustacea
PYC—Pycnogonida
POG—Pogonophora
HO—Holothuroidea
E—Echinoidea
AS—Asteroidea

[2] Roman numeral headings under the environments correspond to the same numbers used for the environments throughout the text.

TABLE I—(*continued*)

Species	*Class*[1]	I	II	III	IV	V	VI	VII	VIII	IX	X	XI[2]
		Environments										
Chione californiensis	P		X									
C. picta	P		X									
Anomalocardia subimbricata	P		X									
A. subimbricata tumens	P		X									
Protothaca metadon	P		X									
Mulinia pallida	P		X									
Tellina felix	P		X		X							
Macoma pacis	P		X									
Donax assimilis	P		X									
D. californiensis	P		X									
D. carinatus	P		X									
D. punctostriatus	P		X									
Heterodonax bimaculatus	P		X									
Tagelus affinus	P		X									
Semele guaymasensis	P		X		X							
Pholas chiloensis	P		X									
Uca crenulata	CR		X									
Clibanarius diguetii	CR		X									
Ocypode occidentalis	CR		X									
Neopanope petersenii	CR		X									
Encope grandis	E		X									
E. californica	E		X									
Echinometra vanbruntii	E		X									
Brissus latecarinatus	E		X									
Selenkothuria lubrica	HO		X									
Thyone parafusus	HO		X									
Neothyone gibbosa	HO		X									
Cerithidea mazatlanica	G			X								
C. montagnii	G			X								
Littoridina sp.	G			X								
Melampus olivaceous	PUL			X								
Anadara tuberculosa	P			X								
Mytella falcata	P			X								
Ostrea columbiensis	P			X								
O. corteziensis	P			X								
Polymesoda mexicana	P			X								
P. olivacea	P			X								
Rangia mendica	P			X								
Architectonica placentalis	G				X							
Calyptraea conica	G				X							
Crepidula arenata	G				X							
C. excavata	G				X							
C. perforans	G				X							
Crucibulum serratum	G				X		X					
C. spinosum	G				X	X						
Polinices reclusianus	G				X							
Sinum debile	G				X							
Hexaplex erythrostomus	G				X							
Nassarius versicolor	G				X							
Oliva incrassata	G				X							
O. spicata polposta	G				X							
Olivella fletcherae	G				X							
Mitra hindsii	G				X							
Cancellaria balboae	G				X							
Clathrodrillia pilsbryi	G				X							
Hormospira maculosa	G				X	X						
Conus perplexus	G				X							
Terebra specillata	G				X							
T. variegata	G				X							
Dentalium oerstedii oerstedii	SC				X		X					
Nuculana impar	P				X							
Adrana penascoensis	P				X							
Barbatia alternata	P				X							
Anadara nux	P				X							
A. obesa	P				X							
Lioberus salvadoricus	P				X							
Chlamys circularis	P				X	X						
C. tumbezensis	P				X							
Crassatella gibbosa	P				X	X						
Lucina prolongata	P				X							
Trachycardium panamense	P				X							
Trigoniocardia granifera	P				X							
Laevicardium elatum	P				X	X						
L. elenense	P				X							
Pitar newcombianus	P				X							
Chione mariae	P				X	X						
Mactra californica	P				X							
Tellina tabogensis	P				X							
Donax gracilis	P				X							
Ensis californicus	P				X							
Pandora claviculata	P				X							

TABLE I—(*continued*)

Species	Class[1]	I	II	III	IV	V	VI	VII	VIII	IX	X	XI[2]
		Environments										
Lyonsia gouldii	P				X							
Balanus concavus mexicanus	CR				X	X	X					
Dardanus sinistripes	CR				X	X						
Petrochirus californicus	CR				X	X						
Pylopagurus varians	CR				X							
Encope micropora	E				X							
Lovenia cordiformis	E				X	X						
Moira clotho	E				X							
Heterocyathus aequicostatus	AN					X						
Calliostoma bonita	G					X						
C. nepheloide	G					X						
Astele rema	G					X						
Solariella triplostephanus	G					X						
Architectonica nobilis	G					X						
Natica broderipiana	G					X						
N. grayi	G					X						
Polinices uber	G					X						
Cassis centiquadrata	G					X						
Distorsio decussatus	G					X						
Bursa nana	G					X						
Murex recurvirostris	G					X						
Hexaplex brassica	G					X						
Eupleura muriciformis	G					X						
Coralliophila hindsii	G					X						
Strombina fusinoidea	G					X						
Cantharus capitaneus	G					X						
Hindsia acapulcana	G					X						
Nassarius pagodus	G					X						
Mitra erythrogramma	G					X						
Fusinus dupetithouarsi	G					X						
Harpa crenata	G					X						
Clavus roseolus	G					X						
Pleuroliria oxytropis albicarinata	G					X		X				
P. picta	G					X						
Glycymeris tessellata	P					X						
Cyclopecten pernomus	P					X						
Plicatula inezana	P					X						
Anodontia edentuloides	P					X						
Trachycardium belcheri	P					X						
Nemocardium pazianum	P					X						
Cyclinella kroyeri	P					X						
C. saccata	P					X						
Macoma siliqua	P					X						
Solecurtus guaymasensis	P					X						
Semele paziana	P					X						
Clypeaster europacificus	P					X		X				
Munida tenella	CR					X		X		X		
Porcellana cancrisocialis	CR					X						
Clibanarius panamensis	CR					X						
Paguristes bakeri	CR					X						
P. praedator	CR					X		X				
Pagurus gladius	CR					X						
Hypoconcha loweii	CR					X						
Calappa sausserei	CR					X		X				
Cyclöes bairdii	CR					X						
Hepatus kossmanni	CR					X						
Iliacantha hancocki	CR					X						
Persephone townsendi	CR					X						
Randallia americana	CR					X		X				
R. buligera	CR					X						
Euphylax robustus	CR					X						
Portunus acuminatus	CR					X						
P. affinus	CR					X						
P. pichilinquei	CR					X						
Cancer amphioetus	CR					X						
Medaeus lobipes	CR					X						
Leiolambrus punctatissimus	CR					X						
Mesorhea belli	CR					X						
Collodes gibbosus	CR					X						
C. tenuirostris	CR					X		X				
Euprognatha bifida	CR					X		X				
Paradasygius depressus	CR					X		X				
Pyromaia tuberculata	CR					X		X				
Stenorhynchus debilis	CR					X						
Cymopolia zonata	CR					X						
Protula superba	PO						X					
Crepidula incurva	G						X					
Crucibulum n. sp.	G						X					
Polinices intemerata	G						X					
Nassarius cattatus	G						X			X		
Conus arcuatus	G						X					

TABLE I—(*continued*)

Species	*Class*[1]	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
		Environments										
Anadara mazatlanica	P						X					
Chione kellettii	P						X					
Corbula luteola	P						X					
Periploma carpenteri	P					X	X					
Pleuroncodes planipes	CR						X			X		
Ceratotrochus franciscana	AN							X				
Polinices otis	G							X				
Cymatium amictum	G							X				
Pleuroliria nobilis	G							X	X			
P. oxytropis oxytropis	G							X				
Lucinoma annulata	P							X	X	X		
Nemocardium centrifilosum	P							X	X			
Corbula ventricosa	P							X				
Stenocionops beebei	CR							X				
S. ovata	CR							X				
Libinia mexicana	CR							X				
Cymopolia zacae	CR							X				
Ethusa lata	CR							X				
Parastichopus californicus	HO							X				
Vaneyothuria zacae	HO							X				
Balanophyllia sp.	AN								X			
Desmophyllum crista-galli	AN								X			
Acanthogorgia n. sp.	AN								X			
Terebratalia obsoleta	BR								X	X		
Morrisia hornei	BR								X			
Calliostoma variegatum (dead)	G								X			
Turritella cf. *cooperi* (dead)	G								X			
Boreotrophon n. sp. (dead)	G								X	X		
Nassarius insculptus gordanus	G								X	X		
Fusinus traski	G								X			
Pleuroliria artia	G								X			
Acila castrensis	P								X			
Nuculana hamata (dead)	P								X			
N. taphria	P								X			
Glycymeris corteziana (dead)	P								X			
Cyclopecten vancouverensis (dead)	P								X			
Cardita barbarensis (dead)	P								X	X		
Lucina tenuisculpta (dead)	P								X	X		
Trigoniocardia guanacastense (dead)	P								X			
Tellina carpenteri (dead)	P								X			
T. tabogensis (dead)	P								X			
Macoma siliqua spectri	P								X			
Hiatella arctica (dead)	P								X			
Dentalium vallicolens (dead)	SC								X			
Cadulus perpusillus (dead)	SC								X			
Hesperocidaris perplexa	E								X			
Brisaster townsendi	E								X			
Emarginula velascoensis	G									X		
Solariella permabilis	G									X		
Nassarius miser	G									X		
Fusinus colpoicus	G									X		
Daphnella imparella	G									X		
Clathurella thalassoma	G									X		
Solemya valvulus	P								X	X		
Nucula cardara	P									X		
Nuculana callimene	P									X		
Amygdalum pallidulum	P								X	X		
Cyclopecten zacae	P									X		
Pandora convexa	P									X		
Pseudostichopus mollis	HO									X		
Pennatula phosphorea californica	AN										X	
Stachyptilum superbum	AN										X	
Solariella nuda	G										X	
Turcicula bairdii	G										X	
Solemya agassizi	P										X	X
Lucinoma n. sp.	P										X	
Vesicomya lepta	P										X	
Collosendeis bicincta	PYC										X	X
Paracrangon areolata	CR										X	
Heterocarpus affinus	CR										X	
Acanthophyra curtirostris	CR										X	X
Parapagurus pilosimanus	CR										X	X
Neolithodes diomedaea	CR										X	
Paralomis multispina	CR										X	
Paralithodes rathbuni	CR										X	
Synallactes ishikawa	HO										X	

TABLE I—(*continued*)

Species	*Class*[1]	I	II	III	IV	V	VI	VII	VIII	IX	X	XI[2]
		Environments										
Molpadia musculus	HO										X	X
Caryophillia diomedaea	AN											X
Anthomastus ritteri	AN											X
Galathealinum bruunei	POG											X
Macandravia americana diegensis	BR											X
Neopilina galathaea	MON											X
Puncturella expansa	G											X
Solariella equatorialis	G											X
Tractolira sparta	G											X
Pleurotomella clarinda	G											X
Steiraxis aulaca	G											X
Dentalium megathyris	SC											X
Nucula panamina	P											X
Malletia truncata	P											X
Tindaria compressa	P											X
Arca corpulenta pompholynx	P											X
A. nucleator	P											X
Limopsis compressus	P											X
Abra profundorum	P											X
Cuspidaria panamensis	P											X
Myonera garretti	P											X
Poromya perla	P											X
Colossendeis angusta	PYC											X
Pallenopsis californica	PYC											X
Benthesicymus altus	CR											X
Hymenopenaeus doris	CR											X
Pandalopsis ampla	CR											X
Munidopsis bairdii	CR											X
Paralomis verrilli	CR											X
Aporocidaris milleri	E											X
Tromikosoma hispidum	E											X
T. panamense	E											X
Urechinus loveni	E											X
Brisaster latifrons	E											X
Abyssicucumis abyssorum	HO											X
Benthydotes sanguinolenta	HO											X
Psychropotes dubiosa	HO											X
P. raripes	HO											X

(*For Table II, please turn the page.*)

TABLE III. FAUNAL CHARACTERISTICS OF THE TIBURÓN SUBGROUP OF THE NEARSHORE SAND-MUD ASSEMBLAGE

	Per cent of Occurrences in Stations Alive	*Per cent of Total Live Occurrences in Whole Gulf*	*Index*
Leavicardium elatum	88	71	80
Hexaplex erythrostomus	44	100	72
Donax gracilis	44	100	72
Ensis californicus	44	100	72
Strombus gracilior	33	100	66
Tellina tabogensis	33	100	66
Polinices reclusianus	66	60	63
Trachycardium panamense	66	50	58
Olivella fletcherae	55	60	58
Crepidula excavata	55	57	56
Terebra specillata	44	66	55
Lioberus salvadoricus	33	75	54
Anadara obesa	33	75	54
Laevicardium elenense	60	40	50
LESSER IMPORTANCE, LIVING			
Trigoniocardia granifera	44	50	47
Crepidula arenata	20	60	43
Nassarius versicolor	44	40	42
LESSER IMPORTANCE, DEAD			
Barbatia alternata	55	55	55
Semele guaymasensis	55	36	45
Lucina prolongata	33	43	38
Mactra californica	33	33	33

TABLE IV. FAUNAL CHARACTERISTICS OF THE SOUTHERN GULF SUBGROUP OF THE INTERMEDIATE SHELF ASSEMBLAGE

	Per cent of Occurrences in Stations	*Per cent of Total Occurrences In Whole Gulf*	*Index*
CRUSTACEANS			
Iliacantha hancocki Rathbun	86	66	76
Portunus acuminatus Stimpson	71	71	71
Persephone townsendi (Rathbun)	71	71	71
Stenorhynchus debilis Smith	71	62	66
Medaeus lobipes Rathbun	71	62	66
Dardanus sinistripes (Stimpson)	86	38	62
Pyromaia tuberculata (Lockington)	86	27	57
Paradysygius depressus (Bell)	57	44	51
Randallia bulligera Rathbun	43	60	51
Leilolambrus punctatissimus (Owen)	43	60	51
Hepatus kossmanni Newman	43	43	43
GASTROPODS			
Distorsio decussatus (Broderip, 1833)	100	86	93
Cantharus capitaneus (Berry, 1957)	100	53	76
Calliostoma bonita Strong, Hanna, and Hertlein, 1933	57	66	61
Architectonica nobilis Röding, 1789	57	50	53
Crucibulum spinosum (Sowerby, 1824)	86	17	51
Hexaplex brassica (Lamarck, 1822)	43	60	51
Strombina fusinoidea Dall, 1916	57	44	50
Hormospira maculosa (Sowerby, 1834)	71	26	48

TABLE II. SPECIES AND ENVIRONMENTAL CONDITIONS OF THE NEARSHORE SAND AND SAND-MUD ASSEMBLAGES

Species	*Index Group Numbers* 2	3	7	64	74
GASTROPODS					
Crepidula arenata			X		
C. excavata				X	
Polinices intemerata				X	
P. reclusianus			X		
Strombus gracilior (Index species grp. 64)				X	
Hexaplex erythrostomus				X	
Distorsio decussatus	X				
Nassarius versicolor			X		
Strombina gibberula		X			
Olivella fletcherae			X		
Terebra specillata		X			
Acteocina angustior			X		
PELECYPODS					
Nuculana elenensis					X
Barbatia alternata				X	
Anadara obesa	X				
Lioberus salvadoricus		X			
Chlamys circularis (Index species grp. 2)	X				
Lucina prolongata		X			
Ctena mexicana	X				
Laevicardium elatum				X	
L. elenense (Index species grp. 7)			X		
Trachycardium panamense			X		
Trigoniocardia biangulata			X		
Megapitaria squalida			X		
Dosinia dunkeri			X		
Chione mariae			X		
Tellina amianta			X		
T. inaequistriata		X			
Macoma siliqua	X				
Semele guaymasensis			X		
Donax gracilis (Index species grp. 74)					X
Ensis californica (Index species grp. 3)		X			
CRUSTACEANS					
Portunus pichelinqui		X			

Physical Factors

Station Numbers	*Depth in Fathoms*	*Temp. in °C*	*Oxygen in ml/L*	*Sediment Type*	2	3	7	64	74
24	13	16	2.5	sand			X		
114	4	30	4.0	sand	X				
163	1	20	4.0	sand				X	
172	7	20	3.0	shell sand	X				
175	14	13	1.2	mud sand	X				
179	1	14	3.0	sand			X		X
181	9	18	3.0	sand		X		X	
184	9	14	3.0	sand		X	X		X
185	31	13	2.4	sand			X		X
190	7	20	3.0	sand					X
191	14	15	3.0	mud sand				X	
194	7	20	3.0	mud sand	X	X	X		
195	12	18	3.0	mud sand	X		X		
196	13	16	3.0	sand	X	X	X	X	X
208	7	19	2.6	sand	X			X	
212	31	13	2.4	sand		X	X		

Average environmental conditions		2	3	7	64	74
	Depth in fathoms	10.6	19.0	16.6	7.4	9.4
	Temperature in °C	17.0	14.3	14.0	19.2	18.0
	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