# THE DISTRIBUTION AND ABUNDANCE OF THE INARTICULATE BRACHIOPOD GLOTTIDIA ALBIDA (HINDS) ON THE MAINLAND SHELF OF SOUTHERN CALIFORNIA

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## INTRODUCTION

The inarticulate brachiopod *Glottidia albida* (Hinds, 1844) (Figure 1) is a member of the geologically ancient family Lingulidae. *Lingula*, the only other living genus of this family, is known since the Ordovician (Hyman, 1959). *Glottidia albida* is reported from the Upper Eocene (*?albida*), Miocene, Pliocene, Pleistocene and Recent of California (Hertlein and Grant, 1944). The recent geographic range of this species is from Monterey Bay, California to Acapulco Bay, Guerrero, Mexico. Its depth range is given as low water to 80 fathoms (146.2 meters) (Dall, 1920; Hertlein and Grant, 1944; Ricketts and Calvin, 1948; and Smith and Gordon, 1948). In the Gulf of California a closely related species, *Glottidia palmeri* Dall, replaces *Glottidia albida* (see Hertlein and Grant, 1944).

During the past decade marine scientists of the Allan Hancock Foundation, University of Southern California, have made extensive collections off southern California, using large-scale methods of the quantitative study of the sea-bottom (Durham, 1955; Barnard and Jones, 1960). More than 2000 quantitative benthic samples have been collected from the offshore region of southern California aboard the research vessel *Velero IV*.

The first study in this series, a quantitative survey of the benthos of San Pedro Basin (including the San Pedro Bay shelf, the San Pedro deep basin, Lasuen Seamount, and the eastern shelf of Santa Catalina Island) was initiated in 1952 (Hartman, 1955). In this work Hartman recorded the biological components of 267 samples. *Glottidia albida* was present in 15 of these samples from the San Pedro shelf in a depth range from 11 to 54 fathoms (20.5 to 98.8 meters) (mean depth, 20 fathoms) (36.6 meters); the maximum number of specimens per sample was 12. Three samples from the eastern shelf of Santa Catalina Island yielded specimens of *Glottidia*. These were collected in a range of 19 to 44 fathoms (34.7 to 80.5 meters) with a mean depth of 30 fathoms (47.5 meters). Dall (1920) and Mattox (1955) also have reported this species from Santa Catalina Island. It is to be expected that *G. albida* also is present on the shelves bordering the other offshore islands and perhaps on some of the offshore banks.

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Hartman (1956) extended her analysis of the southern California benthos with a study of the fauna of Santa Monica Bay where twenty-two of 144 samples (15.2%) yielded *Glottidia* in a depth range of 7 to 261 fathoms (12.8 to 477.0 meters) with a mean depth of 32 fathoms (97.5 meters). The maximum number of specimens per sample was 23.

Whereas *Glottidia albida* may extend down into the numerous submarine canyons that dissect the mainland and island shelves, it was absent from the 152 samples examined by Hartman and Barnard (1958, 1960) in their study of the deep basins off southern California.

Beginning in 1956 the sampling program of the Allan Hancock Foundation was extended to cover the mainland shelf of southern California from Point Conception to the Mexican border under a contract with the California Water Pollution Control Board. The present paper on the recent distribution and abundance of *Glottidia* is based upon these samples.

## Methods

Deep-water bottom samples were obtained by a modified Hayward Standard orange-peel bucket (OPB) with an areal coverage of 2.6 square feet (about 0.25 square meters). The nearshore portion of the shelf, in water depths of 8 to 33 feet (2.4 to 10.1 meters), was sampled from the motor launch of the R/V *Velero IV* using a 0.1 square meter Van Veen Grab. Collection of the animals was controlled by the size of the mesh through which the sediment was screened aboard ship before preservation and sorting. The screen is commonly known as 1 millimeter mesh, with square openings of 0.7 millimeters (Durham, 1955; Barnard and Jones, 1960).

Our analysis is based partly upon a stratified model of 176 OPB samples chosen for their geographic and depth distribution. The arrangement of the sample sites forms an imperfect grid system that encompasses the depths of 5 to 100 fathoms (9.1 to 182.8 meters) between Point Conception and the Mexican border. Later, the grid was expanded to include 348 samples.

This grid system was devised in the following manner:

(1) The shelf was arbitrarily divided into eight geographic areas which were separated, as much as possible, by natural differences in orientation, general shape, sediment character, topography, steepness of slope, and relative depth. Submarine canyons or prominent headlands or points were used to delimit the boundaries. The geographic features selected as boundaries do not necessarily form biological barriers but represent convenient markers by which the shelf may be subdivided logically (Figure 2).

(2) Each geographic area was further subdivided into depth classes. Because the survey was based on Coast and Geodetic Survey Charts 5101 and 5202, with depths in fathoms rather than meters,

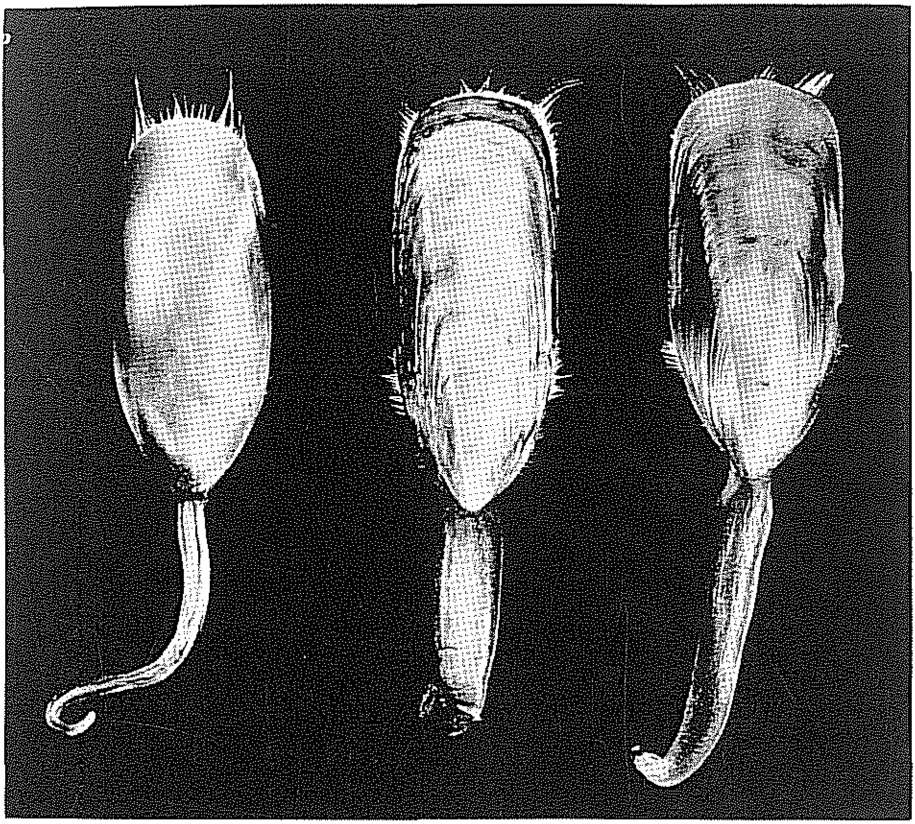

Fig. 1. *Glottidia albida* (Hinds), two dorsal views above and one ventral view below, × 2.5.

the depths were chosen in multiples of 10 fathoms (18.2 meters) resulting in classes of 10, 20, 30, 40, 50 and 100 fathoms (18.2, 36.4, 54.6, 72.8, 91.4 and 182.8 meters).

(3) The area of each geographic subdivision and each depth class within any given subdivision was determined by a simple planimetric analysis (Barnard and Jones, 1960, p. 418). In each case the number of samples assigned to represent any of the eight geographic subdivisions of the shelf or of any depth increment within any subdivision, is proportional to the area of the unit involved.

By utilizing such a system it is possible to calculate from a relatively small number of samples the distribution and abundance of benthic species, although each sample represents an area of more than 3 nautical square miles. Sediment data were available for 320 of the 348 biological samples utilized in these calculations.

Bathythermograph data in Figures 13 and 14 were supplied by Drs. Stevenson and Tibby of the Hancock Foundation. These include only those records obtained when the instrument came within 25 feet (7.6 meters) of the bottom. Data from November 1956 to February 1960 are included in the analysis. Bottom water temperatures of the mainland shelf had been highly variable during that period because of a warming trend followed by a sudden return of cool water in 1960. Hence, bottom water temperatures at hand may not be representative of the average shelf conditions in this area.

Figure 14 is based on 151 records from the Santa Barbara area and 308 records from the San Pedro area. Mud temperatures were taken from November 1956 to July 1958 by inserting a thermometer deeply into the large sediment samples collected with the Hayward grab after they had reached the deck. Because of the large volume of these samples, the rapid ascent of the grab from the relatively shallow depths of the study area, and the somewhat low thermal conductivity of the sediments (excluding sands which were not measured) this method provides a fairly accurate indirect measure of bottom sediment temperature. Sediment temperatures are based on 176 samples from the entire mainland shelf. A full year of temperature data from the San Pedro area is shown in Figure 13.

## Area

The complex offshore area of southern California is noted for its islands, banks, ridges, basins and troughs and is designated a "continental borderland" by Shepard and Emery (1941). The borderland system is composed of basins and ridges with an east-west (in the north) to a north-south (in the south) orientation more or less paralleling the adjacent land topography. The topographic highs are formed of deeply submerged sills, shallow flat-topped banks or islands projecting above the sea surface. These high areas enclose thirteen basins and several open troughs. Numerous submarine canyons dissect the mainland and island shelves and some of these descend into the basins. The narrow strip of bottom immediately adjacent to the continent is designated the mainland shelf; it forms only 6.2% of the area of the continental borderland (Emery, 1960).

The southern California shelf region comprises 1061 square miles of depths of 0 to 100 fathoms (182.8 meters). Eighty-six percent (or 916 square miles) of this area is shallower than 50 fathoms, which is approximately the average depth of the shelf edge, but the limits vary between 40 and 70 fathoms (73.2 and 128.0 meters).

The shelf area shallower than 50 fathoms is partitioned into five arbitrary depth classes of 0-10, 11-20, 21-30, 31-40, and 41-50 fathoms as follows: 26.7%, 24.6%, 18.4%, 15.9% and 14.2%, (determinations by planimetric method, Barnard and Jones, 1960).

The width of the mainland shelf varies between 11.9 and 0.5 nautical miles (distance seaward to the 50 fathom [91.4 meter] contour). The broader portions are known as the Santa Barbara shelf (maximum width,

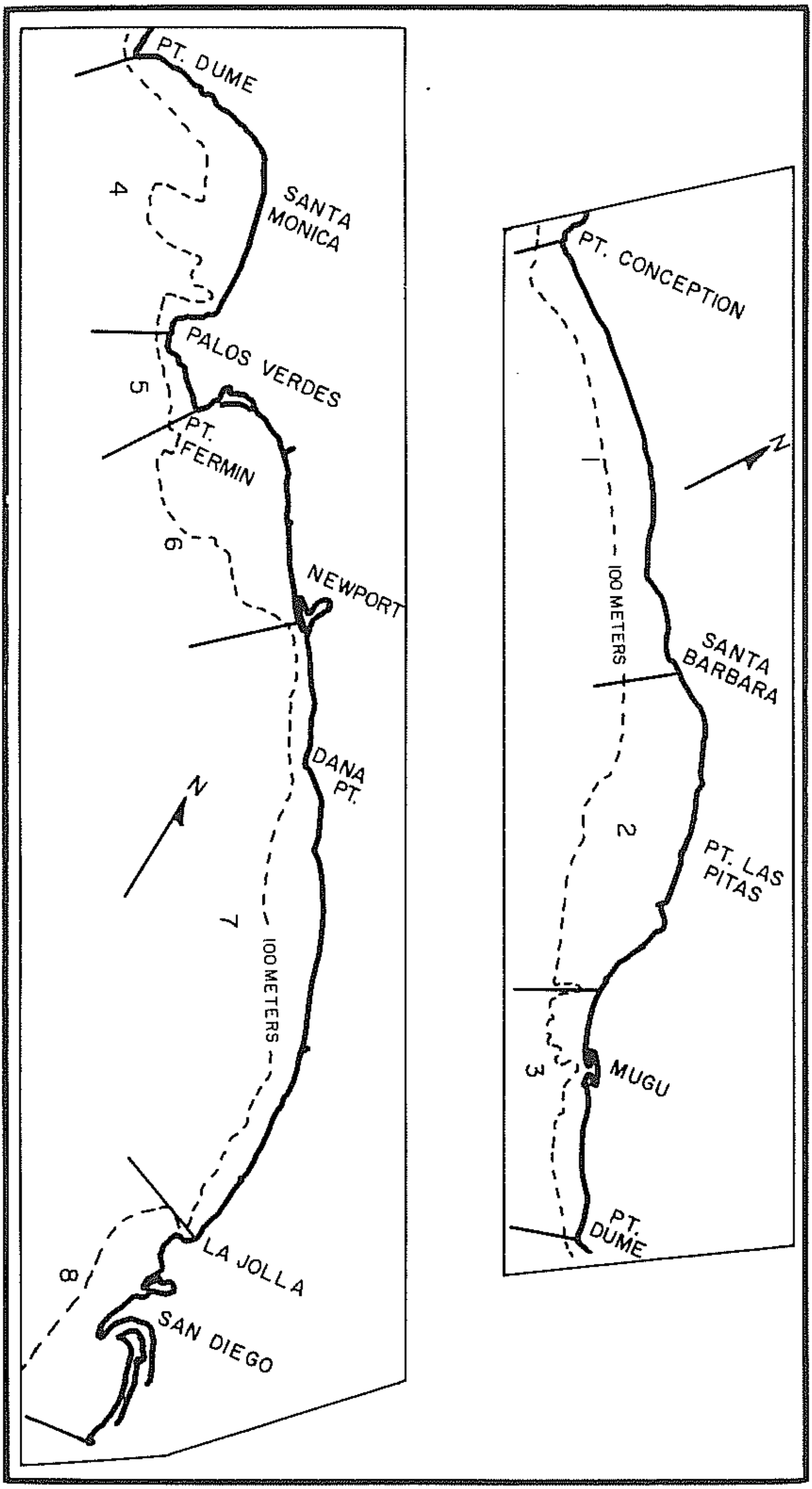


Fig. 2. Subdivisions of the mainland shelf of southern California.

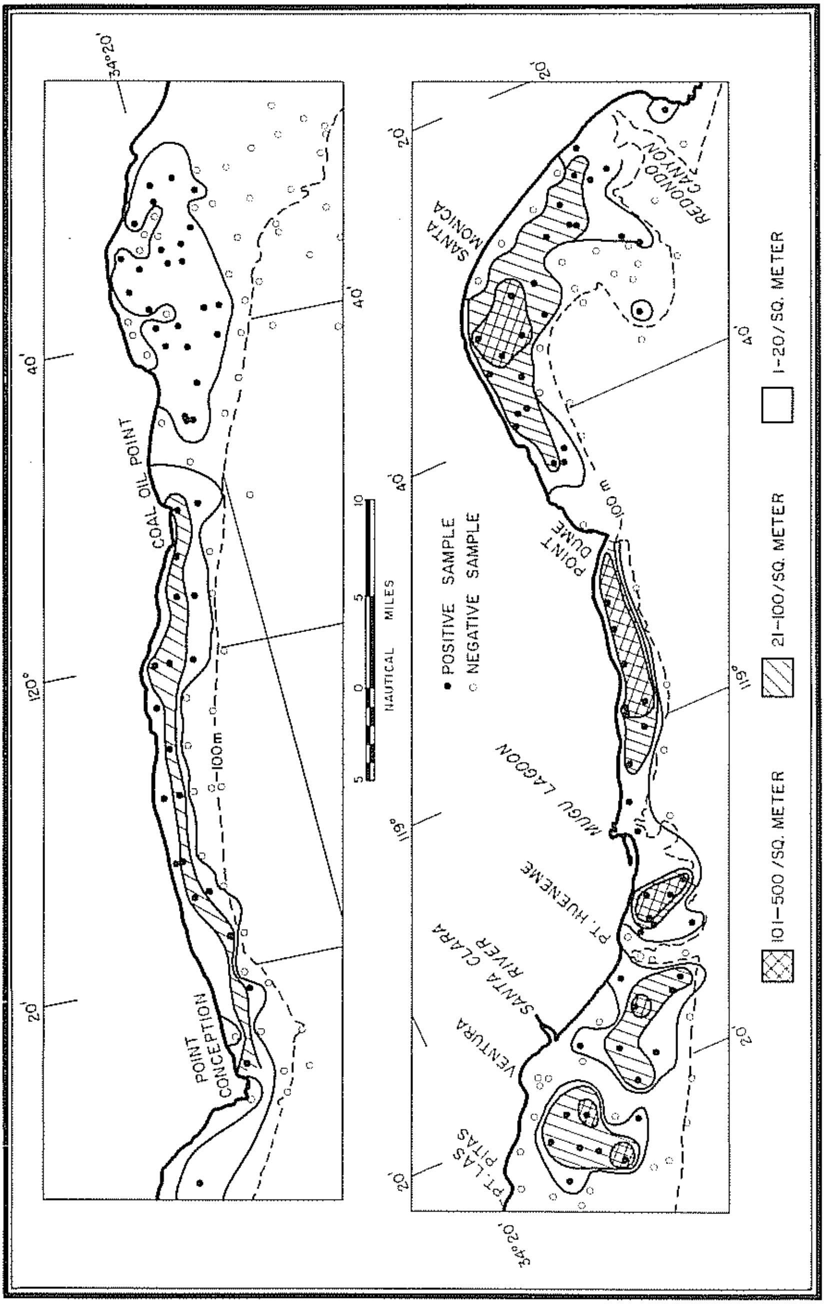


Fig. 3A. Distribution of *Glottidia albida* on the mainland shelf of southern California.

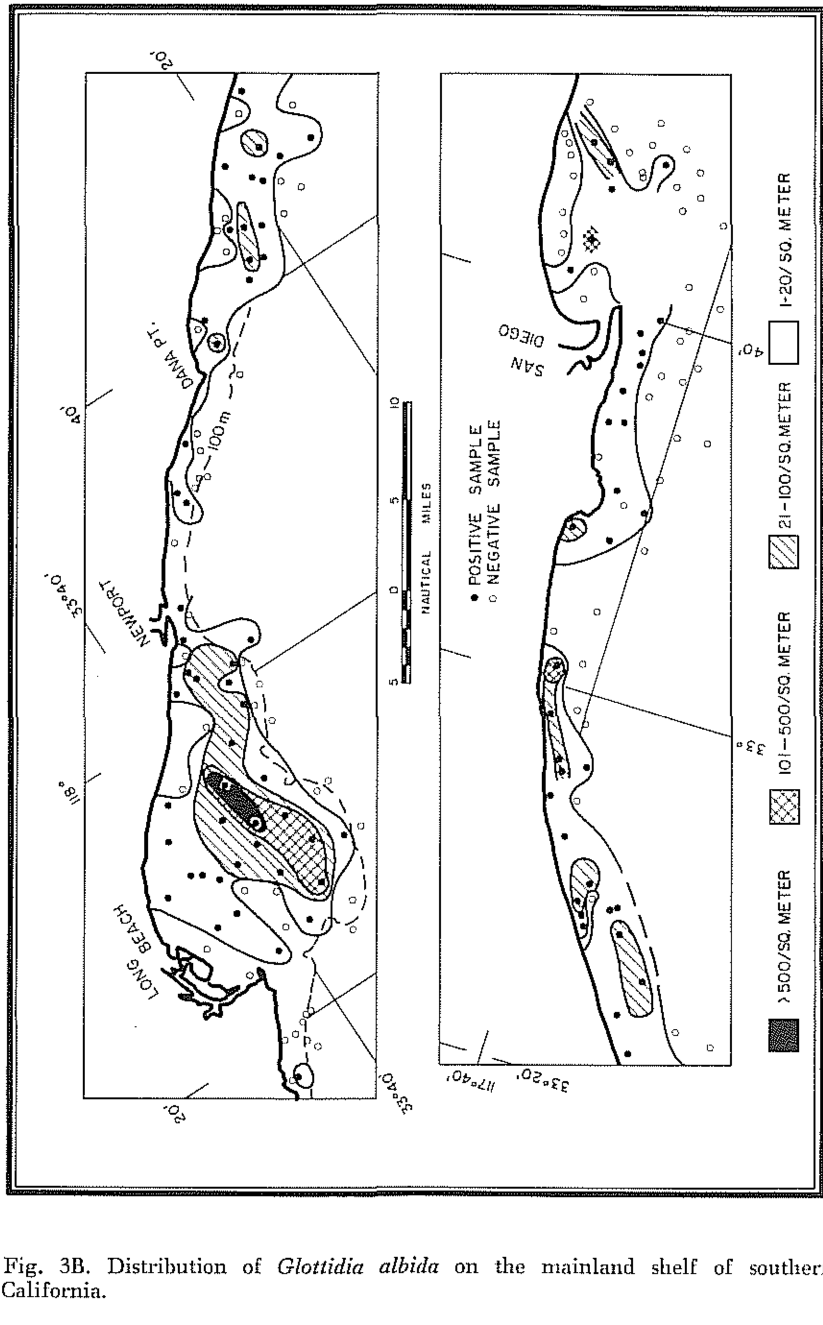


Fig. 3B. Distribution of *Glottidia albida* on the mainland shelf of southern California.

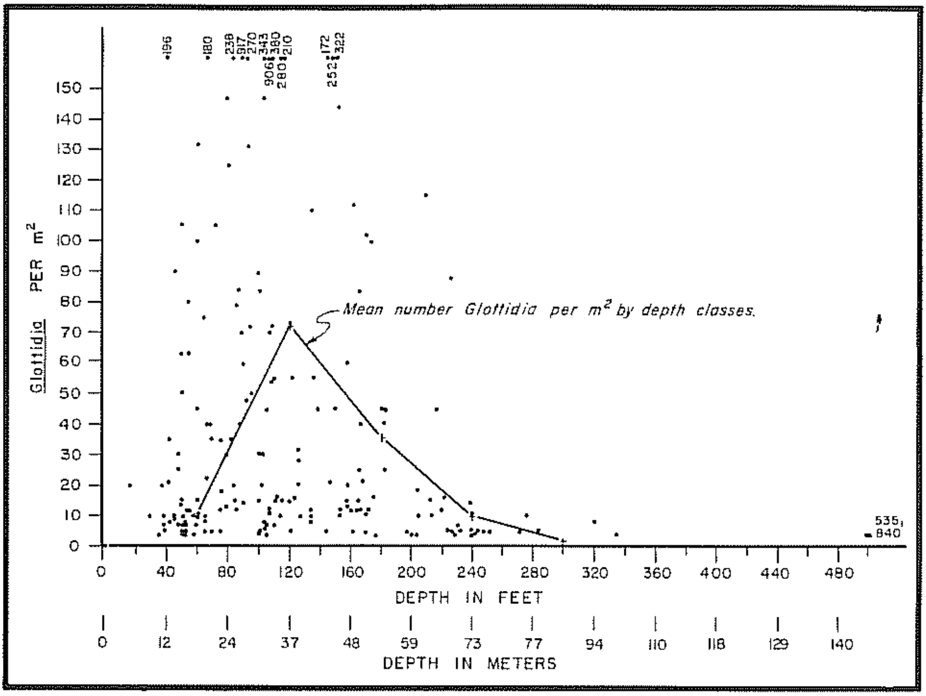


Fig. 4. Scatter diagram of *Glottidia* samples in relation to depth and number of specimens. The two left dots show the only 2 of 100 Van Veen samples returning *Glottidia*. All other samples were taken by an orange-peel-grab. All specimens were alive at the time of collection. The curve shown is based on the mean number of individuals per square meter for each of the depth classes and is calculated on the basis of the stratified sample of 348 stations.

9.5 miles), the Santa Monica shelf (maximum width, 9.7 miles), the San Pedro shelf (maximum width, 11.9 miles), and the San Diego shelf (maximum width, 8.8 miles).

The areal distribution of sediments is as follows: rock, 5.1%; olive-green gravelly sand, less than 0.1%; olive-green medium to fine sand, 29.1%; coarse gray sand, 1.5%; coarse red sand, 3.7%; olive-green silty sand, 31.8%; olive-green sandy silt, 19.5%; gray sandy silt, 1.2%; black sandy silt, less than 0.1%; and olive-green silt, 8.1% (based on a planimetric analysis of Figures 12, 17, and 20 of Stevenson, Uchupi and Gorsline, 1959). Thus, sands, silty sands and sandy silts comprise more than 80% of the substrate of the mainland shelf.

The hydrography of the southern California continental borderland has been summarized by Emery (1960). The surface pattern is dominated by the sinuous cold California Current trending southeastward, but nearshore waters are dominated by a large slowly-moving eddy forming a countercurrent. Water at intermediate depths is of southern origin; it spreads over the continental borderland where most of it is blocked by the Santa Rosa-Cortes Ridge. Entrainment of water by the California Current across this ridge causes upwelling of the intermediate water. Northwesterly winds, particularly in the northern part of the area, near Point Conception, also cause upwelling.

## DISTRIBUTION AND ABUNDANCE OF GLOTTIDIA

### Geographical

The general distribution of *Glottidia albida* on the mainland shelf of southern California is illustrated in Figures 3A and 3B[1]. Solid dots mark the locations of 189 sampling locations at which this species was present. Altogether, 10,142 living specimens were collected. Empty circles mark the locations of 193 sampling locations where this species was absent. Population densities are indicated by the contour intervals of 1-20 individuals per square meter, 21-100 per square meter, 101-500 per square meter, and more than 500 per square meter. *Glottidia albida* occurs along the full length of the mainland shelf of southern California, but its distribution is not continuous; areas of high population density are separated by areas of low density or areas apparently devoid of this species. Generally, *Glottidia* is more widely distributed and more abundant on the northern and central portions of the shelf (north of Newport, California).

Samples on the Point Conception shelf showing a population density of 21 to 100 per square meter form a rectangle extending from a point just east of Point Conception to Coal Oil Point. East of Coal Oil Point a large area of low density exists and broadens to encompass the full western portion of the Santa Barbara shelf. This low-density area coincides at least in part with the large silt deposit reported by Stevenson, Uchupi and Gorsline (1959). The benthos of this region is populated principally by two assemblages, the *Listriolobus* community and the *Amphiodia-Cardita* community (Barnard and Hartman, 1959).

Sediments on the eastern portion of the Santa Barbara shelf, off Ventura, are much coarser than those to the west; sand bottoms of this region are populated by benthic associations dominated by *Nothria* and *Tellina* (the "Gray Sand Faunas", Barnard and Hartman, 1959). Two areas of high *Glottidia* population density (101-500 per square meter) occur there; the narrow separation between these shown in Figure 3A may be due to sampling frequency.

[1]Distributional maps, in contrast with other figures, are not based on the stratified sample of 348 OPB hauls, but on 382 completely sorted and analyzed samples selected without regard for areal representation. The 52 Van Veen samples collected from the shallow nearshore portion of the shelf are not shown in Figures 3A and 3B.

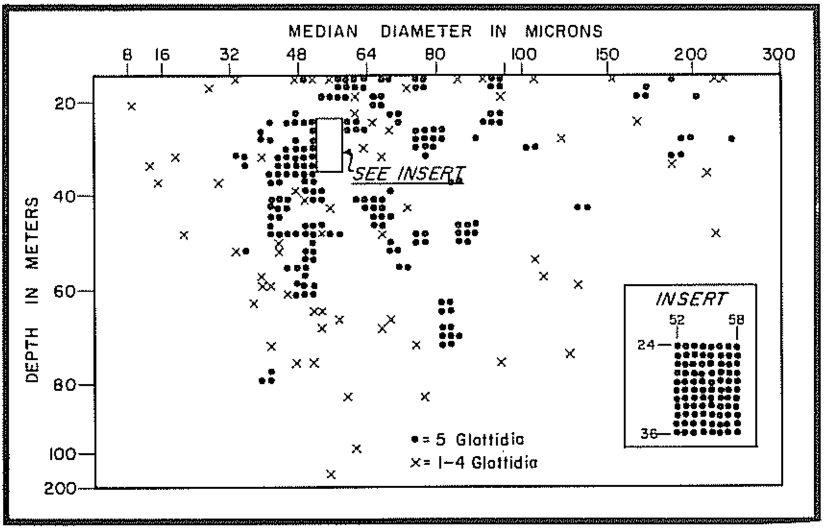


Fig. 5. Density scatter-diagram of living *Glottidia albida* in relation to depth and median diameter of sediments. Each dot represents 5 specimens plotted at the depth and sediment they were collected. Crosses indicate positive collections of less than five specimens. Based on 348 samples.

The Mugu shelf also has two regions of high population density (101-500 per square meter), lying at opposite ends of the shelf and separated by areas of sparseness off Mugu lagoon. The smaller westernmost one is separated by Hueneme submarine canyon from the adjacent high-density area of the Ventura shelf.

In Santa Monica Bay a large high-density region on the shelf begins east of Point Dume and extends to the northern wall of Redondo submarine canyon. Density is highest off Santa Monica (101-500 per square meter).

The largest and densest area of *Glottidia*, over 500 per square meter, is on the broad shelf of San Pedro Bay. Its geographic location coincides with the location of the *Amphioplus hexacanthus* community (Figure 4, Barnard and Ziesenhenne, 1961).

South of Newport, California, only nine small and scattered areas of dense population were discovered. Two of these lie off San Diego, but for the most part populations of this species are sparse on that broad shelf. Lack of continuity in the region south of Newport and particularly off San Diego, may be due in part to low sampling frequency. A large unsampled area exists in the center of the San Diego shelf; this is due in part to U. S. Naval restrictions limiting the use of certain types of equipment including devices for benthic sampling (see Coast and Geodetic Chart 5101).

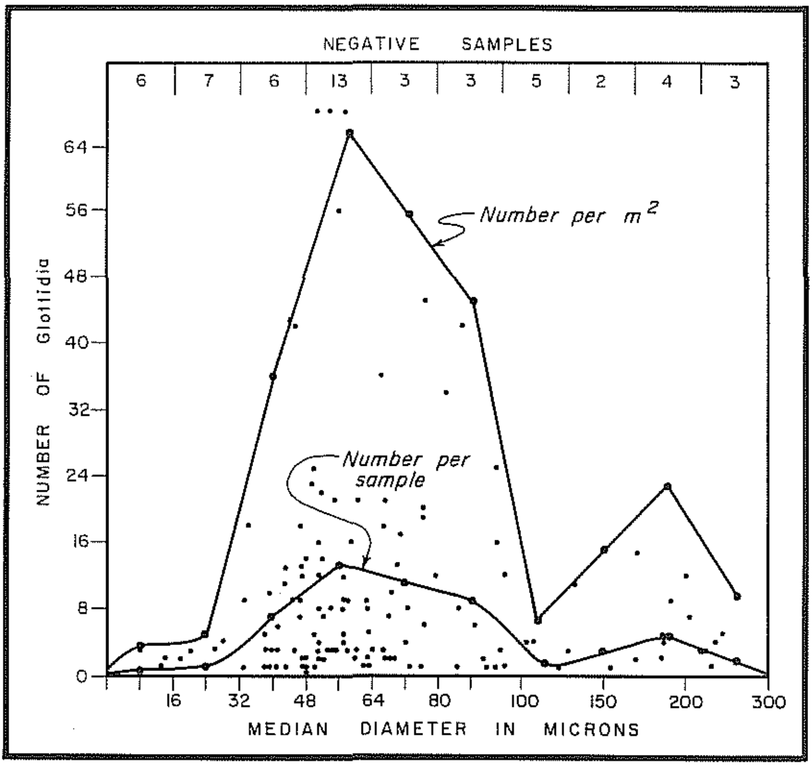


Fig. 6. The number of *Glottidia albida* per sample in relation to median diameter of sediments in depths of 18-64 meters. Negative samples are listed across the top of the diagram. Dots represent specimens per sample. The curves are the mean number of specimens per sample (bottom) and the mean number of specimens per square meter (top).

## Distribution with Depth

Generally, *Glottidia albida* occurs at low population density on bottoms shallower than 12 meters and deeper than 64 meters and reaches its peak of abundance at about 34 meters (Figure 4). The 189 *Glottidia*-positive samples had a mean depth of 38.7 meters (range, 9.1 to 256.0); the deepest positive sample, *Velero* station 4723, with the depth of 256.0 meters, is at the edge of the San Pedro Bay shelf off Newport, California. The 193 negative stations had a mean depth of 80.0 meters (range, 10.0 to 396.9).

*Glottidia* was not abundant in samples from the shallow nearshore regions of the mainland shelf collected in this study, in the 52 samples made from the motor launch of the R/V *Velero IV*. In depths of 2.4 to 10.1 meters only two samples contained this species. Two specimens were found at station 6301 in 5.5 meters of water and one specimen was collected at station 6304 in 8.8 meters of water. Both stations were part of a transect off Santa Barbara, California.

## Distribution in Relation to Sediments

That a relationship exists between *Glottidia* and the sedimentary characteristics of the bottoms on which it lives is not immediately apparent by a simple comparison of samples in which it does or does not occur (Table 1).

Table 1

Sediment characteristics for samples from the mainland shelf of southern California showing positive or negative occurrence of *Glottidia.*

| | Positive Occurrence | | | Negative Occurrence | | |
|---|---|---|---|---|---|---|
| | Stations | Mean | Range | Stations | Mean | Range |
| Percent sand | 162 | 45.0 | 1.4-98.9 | 160 | 43.0 | 0.2-99.5 |
| Percent silt | 161 | 49.0 | 1.1-93.5 | 158 | 48.8 | 0.8-94.7 |
| Percent clay | 152 | 5.4 | 0.5-29.0 | 137 | 7.5 | 0.4-51.5 |
| Median diameter, microns | 161 | 76.0 | 8-361.0 | 158 | 97.0 | 8-628.0 |
| Sorting (Trask) | 161 | 1.48 | 1.06-4.80 | 158 | 1.62 | 1.06-4.54 |

*Glottidia* inhabits a wide variety of sediments as shown by the range of compositions of sand, silt and clay. Corresponding ranges for the negative grouping are equally broad. The accompanying means for these attributes are similar for the two groupings. However, median diameters differ: 76 microns for the positive compared with 97 microns for the negative grouping, and the range for the negative grouping extends farther at the coarse extreme. Sediments at stations where *Glottidia* was found were better sorted, mean of 1.48, than where it was absent, 1.62, but the ranges for these two groupings are almost identical, 1.06 - 4.80 compared to 1.06 - 4.54.

If the two ecologic factors of depth and sediment character (median diameter) are considered simultaneously, as in Figure 5, a definite clustering effect is noted. *Glottidia* is abundant within the depth and sediment limits of 18 and 64 meters and 32 to 100 microns. This relationship is amplified in Figures 6 and 7, showing that *Glottidia* reaches its peak density in depths of 22-47 meters and on sediments with median diameters ranging from 40 to 64 microns.

A comparison is made in Figure 8 of the mean number of *Glottidia albida* per square meter at each of the 8 geographic subdivisions in depth of 29 to 73 meters. At both ends of the shelf the sediments are coarse and population densities low; in the Santa Barbara area where median diameters are lowest the densities are lowest. This is the only shelf area exhibiting a sharp decrease in density for this species (Table 2). South of this area median diameters increase and densities also increase.

Table 2

Sediment characteristics for samples from the Santa Barbara shelf (Area II), showing positive or negative occurrence of *Glottidia*.

| | Positive occurrence | | | Negative occurrence | | |
|---|---|---|---|---|---|---|
| | Stations | Mean | Range | Stations | Mean | Range |
| Percent sand | 18 | 43.6 | 1.9-87.7 | 33 | 16.8 | 0.2-75.5 |
| Percent silt | 18 | 45.6 | 9.4-93.9 | 33 | 66.3 | 3.5-93.0 |
| Percent clay | 18 | 10.7 | 3.0-23.8 | 33 | 14.2 | 4.1-51.5 |
| Median diameter, microns | 17 | 65.0 | 13-133 | 33 | 34.0 | 8-142 |
| Sorting (Trask) | 17 | 1.98 | 1.34-3.61 | 33 | 2.1 | 1.22-3.46 |

## Size Class Data

In order to determine the size relationship within the *Glottidia* population on the mainland shelf, 8976 specimens were measured. Based on valve length these specimens were distributed as follows:

| | No. of specimens | Percent | Range for shelf divisions |
|---|---|---|---|
| Less than 5 millimeters | 7721 | 86.0 | (72-95%) |
| 5 to 10 millimeters | 887 | 9.9 | (4-23%) |
| 11 to 20 millimeters | 272 | 3.1 | (1-7%) |
| 21 to 50 millimeters | 96 | 1.0 | (0-3%) |

With respect to this one factor little variation was noted among the subdivisions of the shelf. For example, the ranges show that the 5 mm. class was never less than 72% and never greater than 95% of the total population.

A relationship of size classes to depth is shown in Figure 9 where the percentage of specimens 5 mm. and smaller declines with depth. A relationship to median diameter of sediments is shown in Figure 10, where the percentage of specimens 5 mm. or smaller declines in sediments finer than 50 microns and coarser than 90 microns. A peculiar interruption of the curve is shown in the middle of the graph at the 61-70 micron data class where the percentage of 5 mm. specimens declines. All of the data were examined for seasonal variations that would explain this drop in small specimens but no relationship was found. We believe that this decline represents inefficiency of the grab when sampling extraordinarily compact sediments of these median diameters.

## Distribution by Communities

More than 20 macrobenthic faunal communities have been recognized on the shelf and a number of these have been described (Barnard and Hartman, 1959; Barnard and Ziesenhenne, 1961; Hartman, 1955, 1956, 1960). The most extensively distributed association is dominated by the "smooth red ophiuroid" *Amphiodia urtica* and occurs generally along the deeper edge of the shelf. In the Santa Barbara area this association is modified by a co-dominant pelecypod, *Cardita ventricosa*. In areas of

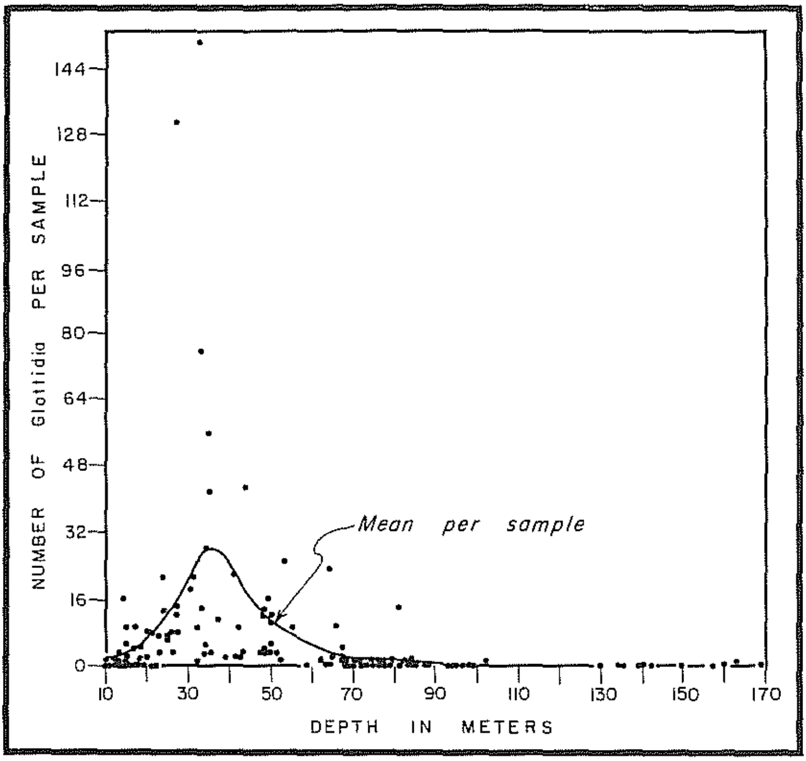


Fig. 7. Abundance of *Glottidia albida* per sample on sediments with median diameters ranging from 40 to 64 microns in relation to bottom depth in meters. The curve shown is the mean number of specimens per sample.

increasing sand content, the *Amphiodia urtica* association is altered by the addition of the subdominant polychaete *Onuphis nebulosa*. Large areas of the San Pedro Shelf are dominated by the ophiuroid *Amphioplus hexacanthus*, accompanied by *Amphiodia urtica* as a subdominant. Shoreward from the *Amphiodia-Cardita* association, in a large silt bed near Santa Barbara, is a unique community formed by the echiuroid *Listriolobus pelodes*.

Shallow bottoms of silty sand and of sand support the clam *Tellina buttoni* and the polychaete *Nothria elegans*, and where these flats merge with the sands just seaward of the surf zone the tiny polychaete *Prionospio* becomes dominant. On coarse sand bottoms near headlands the large tube-dwelling polychaete *Diopatra* often dominates; small but well developed beds of another polychaete, *Chaetopterus variopedatus*, occur on coarse black sand bottoms off the Palos Verdes headland. On the coarse sand bottoms of the San Diego shelf two other polychaetes, *Nothria stigmatis* and *Spiophanes bombyx*, prevail.

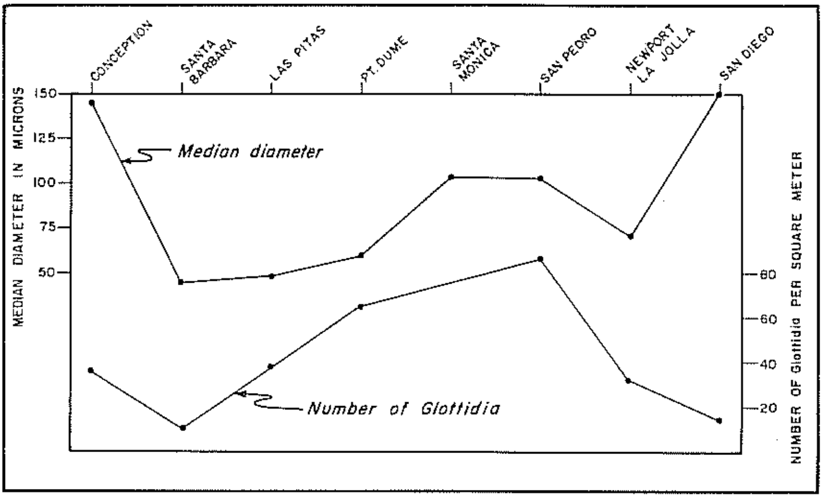


Fig. 8. Linear distribution of median diameter of sediments and mean number of *Glottidia* per square meter on the 8 coastal segments of southern California, from Point Conception on the northwest to San Diego on the southeast, in depths of 29 to 73 meters.

In deep water seaward of the *Amphiodia* and *Amphiodia-Cardita* communities the shelf and slope bottoms are dominated by the polychaetes *Chloeia pinnata* and *Pectinaria californiensis*.

The distribution of the principal benthic communities on the mainland shelf of southern California, in relation to depth and median diameter of the sediments, is illustrated as "community blots" in Figure 11.

*Glottidia albida* occurs at the highest density, 132 per square meter, in the *Amphioplus* community. The composition of this association is pictorially illustrated in Figure 12. In the *Tellina-Nothria* and the *Amphiodia urtica* communities *Glottidia* is only about a fourth as abundant as in the *Amphioplus* community. The first association is particularly prominent on the eastern half of the Santa Barbara shelf and in other fine to medium gray-sand bottoms. The second community is similar in structure to the *Amphioplus* aggregation and is extensively distributed along the outer edge of the shelf along its entire length.

*Glottidia* averages 21 per square meter in the *Diopatra* community, 18 per square meter in the *Listriolobus* community, 5 per square meter in the *Nothria-Spiophanes* community (also known as the red-sand community), and 2 per square meter in the *Amphiodia-Cardita* community.

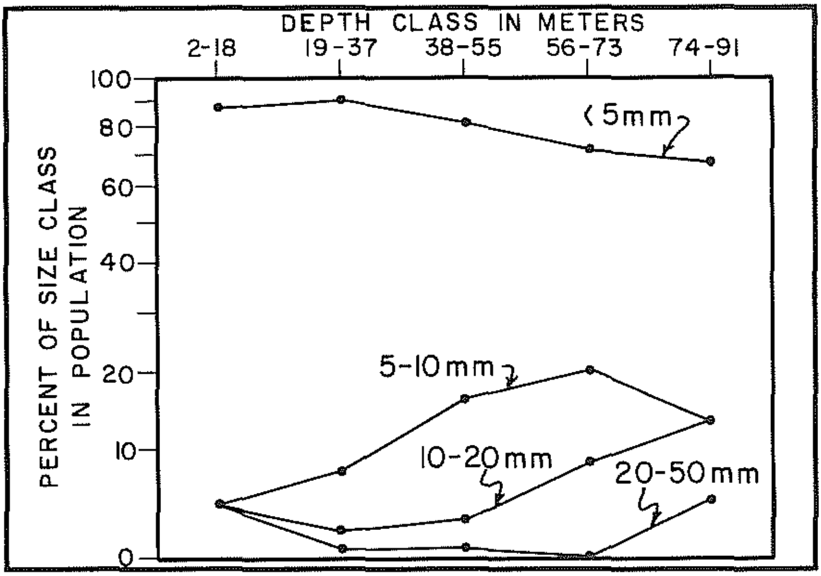


Fig. 9. Percentage of size classes of *Glottidia albida* in relation to depth of bottom.

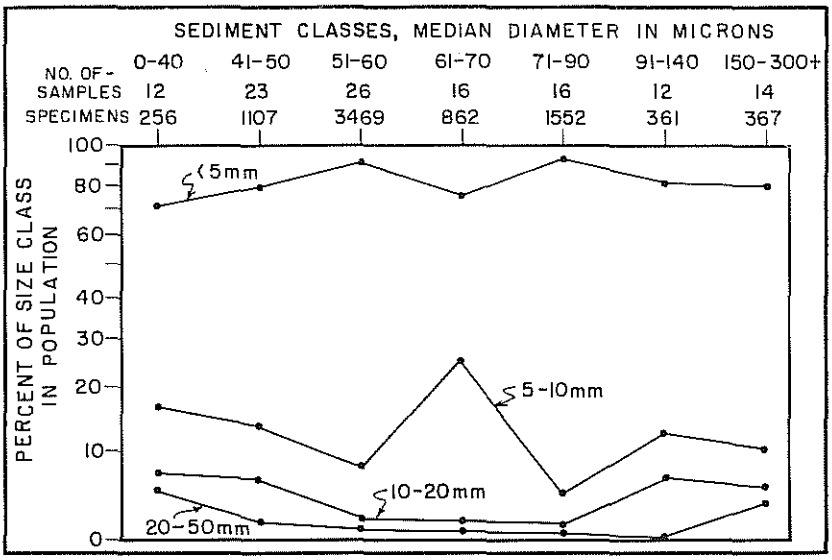


Fig. 10. Percentage of size classes of *Glottidia albida* in relation to sediment classes. See text for discussion of peculiar drops and peaks in the 61-70 micron class.

## THE ASSOCIATES OF GLOTTIDIA

Mollusks, polychaetes, amphipods and echinoderms have been identified by several specialists from 176 samples forming a proportionate half of the grid pattern assessing the benthos of the mainland shelf of southern California. Twenty-one of these samples, each with 12 or more *Glottidia*, were selected for a survey of the organisms associated with *Glottidia*. *Amphioplus hexacanthus* dominates eight of these samples. Nearly all of the remaining 13 samples have subdominant numbers of *Amphioplus*. In the eight samples dominated by *Amphioplus* the mean density of *Glottidia* is 265 specimens per square meter and in the 13 samples not dominated by *Amphioplus* the density of *Glottidia* is 130 specimens per square meter. In the 155 samples where *Glottidia* occurs at less than 12 specimens per sample it has a mean density of 10 specimens per square meter.

*Glottidia* is twice as abundant on the mainland shelf as *Amphioplus*, averaging 5.6 specimens per sample in contrast to 2.8 in the 176 samples. *Glottidia* occurred in 80 and *Amphioplus* in 54 of the 176 samples. Both species occurred together in 42 of the samples, so that *Glottidia* was associated with 78% of the positive *Amphioplus* samples but *Amphioplus* occurred in only 53% of the positive *Glottidia* samples. Based on these data the amount of association was tested by the method of Dice (1945); the resulting chi-square value of 44.5 is far above that for the one-percent level of significance (6.635, 1 d.f.) indicating that the observed association of these two species is not due to random sampling errors. The association of *Glottidia* and *Amphioplus* is also striking when reckoning total number of specimens, for the 42 samples in which both were collected contained 82% of the *Glottidia* and 89% of the *Amphioplus* specimens. Hence, only 18% of the *Glottidia* and 11% of the *Amphioplus* specimens were collected outside the areas of common occurrence.

*Nothria elegans* and *Tellina buttoni* dominate 5 of 21 samples having more than 12 specimens of *Glottidia*. *Amphiodia urtica* dominated 4 samples, *Diopatra* dominated 2 samples, *Onuphis* dominated one and *Ophiothrix* dominated one. The *Amphioplus* community has intergradation to the *Nothria-Tellina* community in shallower water and a somewhat weaker penetration to the *Amphiodia urtica* community in deeper water. Because *Glottidia* is a secondary dominant in the *Amphioplus* community, the high densities of *Glottidia* penetrating these other communities demonstrate their relationship to the *Amphioplus* community in terms of similarity in environment. Additional evidence is seen in that *Amphioplus* occurred in subdominant numbers in 9 of the 13 samples not classified as *Amphioplus*-dominated. Hence the 21 samples of high density of *Glottidia* include the optimal center of the *Amphioplus* community, as well as its fringes and ecotonal overlaps into neighboring communities.

Other associates of *Glottidia* in the 21 samples are shown in Tables 3 and 4, and important shelf species largely excluded from the *Glottidia*

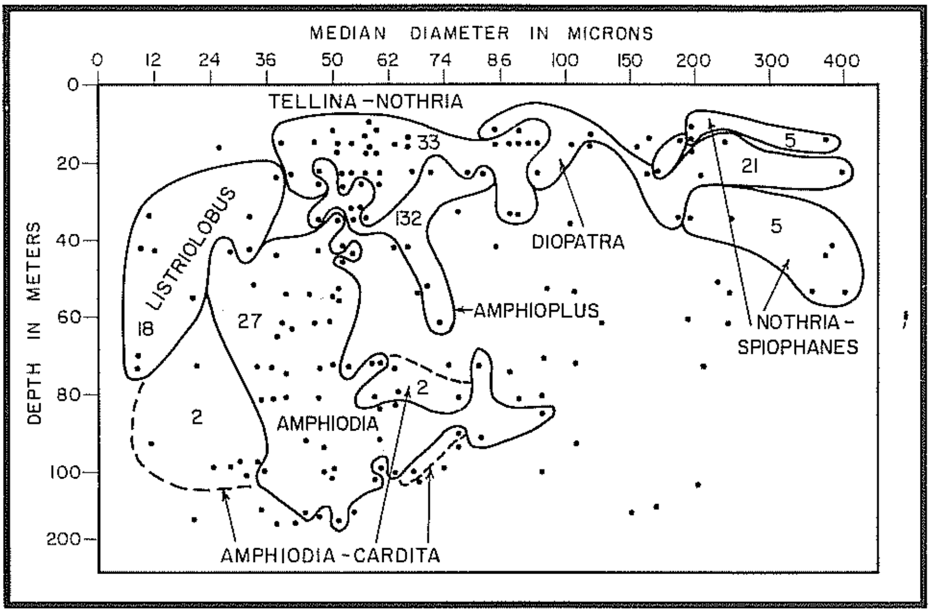


Fig. 11. Distribution of principal benthic communities on the mainland shelf of California, in relation to depth and median diameter of sediments. Community blots are outlined and named. Samples are represented by dots and include only a proportionate half of the 348 samples analyzed in the shelf survey. Dots outside community blots denote minor associations. Numerals inside each community blot represent the number of *Glottidia* per square meter.

beds are shown in Table 5. We have occasionally taken certain liberties with the careful identification of species by other systematists in combining species into generic groups or in removing trivial names where we believed the data could be simplified. As yet these samples have not been analyzed for many benthic groups, but the species mentioned are nevertheless among those most important on the mainland shelf in terms of numbers or standing crop. In Tables 3-5, there are letters to designate major classificatory assignments of the species: P=Polychaeta, O=Ophiuroidea, A=Amphipoda, M=Mollusca, D=Decapoda, B=Brachiopoda and H=Holothuroidea. In Table 3 a number of ranked species are omitted after no. 41 and only those important standing-crop species or mollusks which might be fossil indicators are given beyond that rank. Table 4 simply summarizes the important associates from Table 3.

The ophiuroid *Amphiodia urtica* is the most abundant species in *Glottidia* beds. It forms a community of its own in deeper waters but penetrates into almost all other communities. However, in the presence of peak densities of the major dominant, *Amphioplus hexacanthus*, its numbers

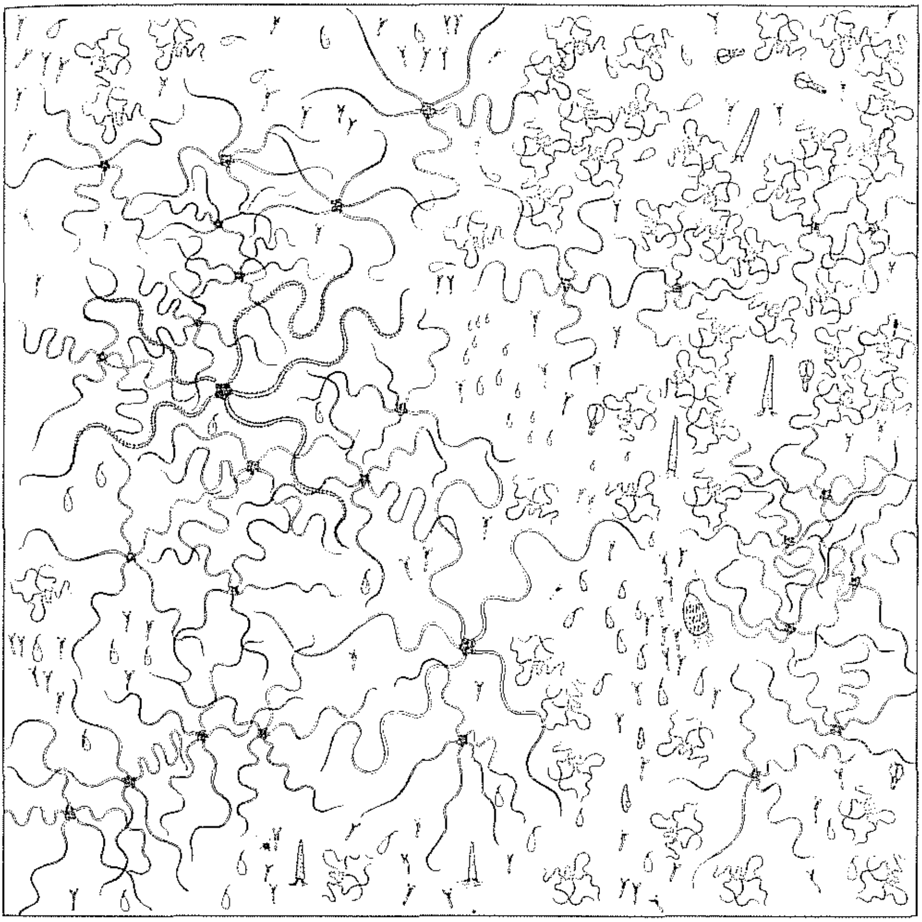

Fig. 12. Pictorial representation of the *Amphioplus hexacanthus* community in which *Glottidia albida* reaches its maximum concentration on the coastal shelf of southern California (After Barnard and Ziesenhenne, 1961).

and standing-crop dominance fall sharply (see Barnard and Ziesenhenne, 1961); but in the 13 samples of *Glottidia* it has a much higher density than in the 8 *Amphioplus-Glottidia* samples. A number of obviously unusual mixtures occur between *Glottidia* and other organisms. For instance, *Glottidia* and *Listriolobus* (Barnard and Hartman, 1959), the echiurid spoon worm, occur together in sufficient frequency that *Listriolobus* cannot be listed in table 6 as a strongly excluded species. Apparently some marginal or ecotonal samples of intermediate sedimentary composition can support the burrowing of subadult silt-oriented *Listriolobus* as well as individuals of the sand-oriented *Glottidia*.

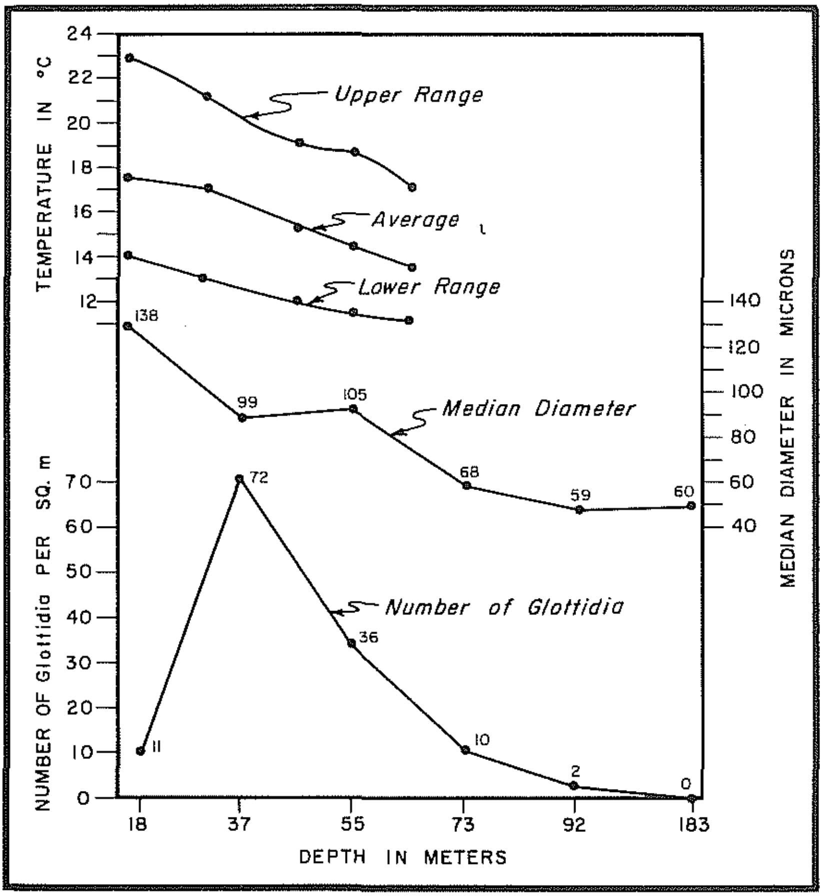


Fig. 13. Profiles of temperature ranges, median diameter of sediments and mean number of *Glottidia albida* per square meter in relationship to depth of the mainland shelf of southern California.

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Table 3

The important organisms occuring with *Glottidia*, listed in rank by specimens per square meter. Those forming important segments of the standing crop are marked with asterisks. See text for classificatory symbols.

Density in specimens per square meter.

| Rank | Name of species | *Glottidia* area 21 samples | Non-*Glottidia* area 155 samples | Total Mainland shelf 176 samples |
|---|---|---|---|---|
| 1* | *Amphiodia urtica* O | 322 | 458 | 428 |
| 2* | *Glottidia albida* B | 182 | 10.0 | 31 |
| 3* | *Tellina* spp. M | 162 | 55 | 68 |
| 4 | *Prionospio pinnata* P | 157 | 41 | 55 |
| 5 | *Prionospio* nr. *malmgreni* P | 135 | 108 | 112 |
| 6 | *Aricidea* spp. P. | 135 | 44 | 55 |
| 7 | *Ampelisca brevisimulata* A | 112 | 38 | 47 |
| 8 | *Tharyx* spp. P | 90 | 85 | 89 |
| 9* | *Nephtys* spp. P. | 79 | 42 | 46 |
| 10* | *Amphioplus hexacanthus* O | 75 | 5.0 | 13.3 |
| 11 | *Chaetozone spp.* P. | 74 | 37 | 41 |
| 12 | *Axinopsis serricatus* M | 70 | 65 | 65 |
| 13 | *Pholoe spp.* P | 66 | 38 | 41 |
| 14 | *Haploscoloplos elongatus* P | 60 | 39 | 41 |
| 15 | *Magelona* spp. P. | 57 | 28 | 32 |
| 16 | *Aoroides columbiae* A | 56 | 20 | 24 |
| 17 | *Paraphoxus epistomus* A | 56 | 16.9 | 22 |
| 18* | *Mysella* spp. M. | 55 | 26 | 30 |
| 19 | *Paraphoxus stenodes* A | 55 | 10.3 | 15.6 |
| 20 | *Paraphoxus obtusidens* A | 53 | 11.5 | 16.5 |
| 21 | *Ampelisca cristata* A | 52 | 29 | 32 |
| 22 | *Parapluestes pugettensis* A | 50 | 4.6 | 5.5 |
| 23 | *Amphideutopus oculatus* A | 50 | 15.0 | 19.2 |
| 24 | *Paraonis gracilis* P | 50 | 32 | 34 |
| 25* | *Pectinaria californiensis* P | 44 | 53 | 52 |
| 26 | *Amphipholis squamata* O | 39 | 44 | 44 |
| 27 | *Lumbrineris cruzensis* P | 36 | 39 | 39 |
| 28* | *Nuculana* spp. M. | 36 | 9.0 | 12.2 |
| 29 | *Paraphoxis bicuspidatus* A | 36 | 59 | 56 |
| 30 | *Photis brevipes* A | 34 | 33 | 33 |
| 31 | *Sthenelanella uniformis* P | 33 | 12.9 | 15.3 |
| 32* | *Sternaspis fossor* P | 33 | 15.4 | 17.5 |
| 33 | *Cossura spp.* P | 33 | 27 | 27 |
| 34 | *Paraphoxus fatigans* A | 32 | 6.2 | 9.5 |
| 35 | *Goniada* spp. P | 32 | 26 | 27 |
| 36 | *Metaphoxus frequens* A | 31 | 21 | 22 |
| 37 | *Paraphoxus abronius* A | 29 | 35 | 34 |
| 38 | *Axiothella rubrocincta* P | 29 | 15.8 | 17.3 |
| 39* | *Onuphis* sp. P | 28 | 20 | 21 |
| 40* | *Spiophanes missionensis* P | 27 | 24 | 24 |
| 41* | *Nothria elegans* P | 27 | 10.0 | 12.2 |
| 44* | *Pinnixa* spp. D | 24 | 10.8 | 12.4 |
| 47* | *Diopatra* sp. P | 23 | 14.2 | 15.4 |
| 52 | *Balcis* spp. M | 17 | 2.9 | 4.6 |
| 53 | *Cylichnella* spp. M | 16.7 | 5.7 | 7.0 |
| 54 | *Turbonilla* spp. M | 16.2 | 6.8 | 7.9 |
| 63 | *Macoma yoldiformis* M | 11.2 | 6.7 | 7.2 |
| 74 | *Cadulus* spp. M | 9.8 | 6.7 | 7.1 |
| 76 | *Solen* spp. M | 9.8 | 1.9 | 2.9 |

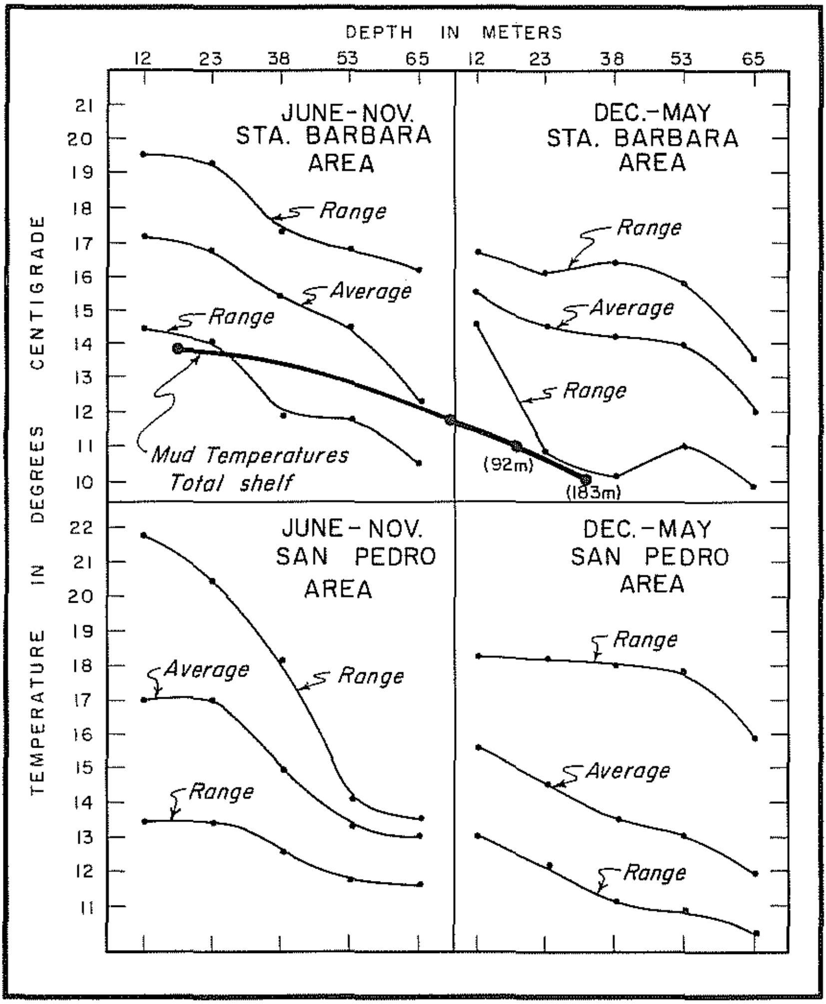


Fig. 14. Temperature profiles of bottom water of southern California, Nov. 1956 to April 1960 arranged into northern and southern groups. Santa Barbara Area = bottom water from Pt. Conception to Pt. Mugu; San Pedro Area = bottom water from Pt. Mugu to Mexican Border. Ranges and means are shown for Winter and Summer. Winter (colder six months) is defined to include December to May; Summer (warmer six months) from June to November. On the upper left hand quadrant is entered the indirect in-situ mud temperatures taken from 130 samples in all seasons of 1957-1958, the curve extending to the right to include depths of 92 and 183 meters. Note that the average mud temperatures approach the colder extremes of the bottom water.

Table 4
Organisms strongly associated with *Glottidia*.
Density in specimens per square meter.

| Rank | Name of species | *Glottidia* area 21 samples | Non-*Glottidia* area 155 samples | Total Mainland shelf 176 samples |
|---|---|---|---|---|
| 1 | *Glottidia albida* B | 182 | 10.0 | 31 |
| 2 | *Tellina* spp. M | 162 | 55 | 68 |
| 3 | *Prionospio pinnata* P | 157 | 41 | 55 |
| 4 | *Aricidea* spp. P | 135 | 44 | 55 |
| 5 | *Ampelisca brevisimulata* A | 112 | 38 | 47 |
| 6 | *Amphioplus hexacanthus* O | 75 | 13.3 | 5.0 |
| 7 | *Chaetozone* spp. P | 74 | 37 | 41 |
| 8 | *Aoroides columbiae* A | 56 | 24 | 20 |
| 9 | *Paraphoxus epistomus* A | 56 | 16.9 | 22 |
| 10 | *Mysella* spp. M | 55 | 26 | 30 |
| 11 | *Paraphoxus stenodes* A | 55 | 10.3 | 15.6 |
| 12 | *Paraphoxus obtusidens* A | 53 | 11.5 | 16.5 |
| 13 | *Parapleustus pugettensis* A | 50 | 4.6 | 5.5 |
| 14 | *Amphideutopus oculatus* A | 50 | 15.0 | 19.2 |
| 15 | *Nuculana* spp. M | 36 | 9.0 | 12.2 |
| 16 | *Paraphoxus fatigans* A | 32 | 6.2 | 9.5 |
| 17 | *Nothria elegans* P | 27 | 10 | 12.2 |

Table 5
Important mainland shelf species of southern California that are primarily restricted from the *Glottidia* beds. Those marked with "d" are species of the deep shelf province; those marked with "s" live on different sediments.
Density in specimens per square meter.

| Rank | Name of species | *Glottidia* area, 21 samples | Non-*Glottidia* area, 155 samples | Total mainland shelf, 176 samples |
|---|---|---|---|---|
| 1d | *Aruga* spp. A | 9.0 | 52 | 47 |
| 2d | *Bittium* spp. M | 7.9 | 37 | 32 |
| 3d | *Heterophoxus oculatus* A | 6.2 | 32 | 29 |
| 4 | *Dorvillia articulata* P | 1.9 | 31 | 27 |
| 5d | *Cardita ventricosa* M | 0.0 | 24 | 21 |
| 6d | *Ampelisca macrocephala* A | 1.0 | 22 | 19 |
| 7 | *Nucula* spp. M | 2.1 | 18.7 | 16.7 |
| 8d | *Ampelisca romigi* A | 0.0 | 13.2 | 11.7 |
| 9d | *Acila castrensis* M | 0.5 | 12.7 | 11.2 |
| 10d | *Byblis veleronis* A | 0.7 | 11.5 | 10.2 |
| 11d | *Urothoe varvarini* A | 0.0 | 11.5 | 10.1 |
| 12s | *Ceratocephala* sp. P | 0.0 | 8.2 | 7.2 |
| 13s | *Lima dehiscens* M | 0.0 | 6.0 | 5.2 |
| 14 | *Microdeutopus schmitti* A | 0.0 | 5.0 | 4.4 |
| 15s | *Molpadia intermedia* H | 0.0 | 1.1 | 1.0 |

## CONCLUSIONS

*Glottidia albida* occurs most densely on the San Pedro, Santa Monica, Mugu and Ventura shelves (Figures 3A, 3B; 8) but is scattered throughout southern California in depths from shoal water to about 165 meters. It is rare in depths shallower than 12 meters and deeper than 64 meters, reaching its peak of abundance at about 34 meters (Figure 4), where the approximate average temperature of the bottom was 13.5°C (read from Figure 14, interpreting bottom water from the southern profiles).

The dense concentration of *Glottidia* in median diameters of 48-64 microns is shown in the density diagram of Figure 5 and the scatter diagram of Figure 6. These sediments have particle sizes near the break between classified silts and sands.

Maximum abundance of *Glottidia* occurs in the *Amphioplus* community (Figures 11, 12) of the San Pedro shelf, lying on a substrate of especially compact fine sand (Barnard and Ziesenhenne, 1961). These sands mixed with coarse silt range from about 48 to 64 microns median diameter but are so well sorted as to be very compact. The community is comprised largely of non-burrowing, poorly-burrowing, and surface-dwelling organisms, such as ophiuroids and various small crustaceans and polychaetes.

With decreasing temperatures and increasing depth the density of *Glottidia* declines rapidly (Figure 13), although sediments at depths of 55 meters are approximately similar to those in 37 meters. Median diameters are calculated in Figure 13 on the basis of all samples, not just those bearing *Glottidia*, so that the shelf averages are higher. Nevertheless, in greater depths and at lower temperatures, similar sediments are available for *Glottidia* as in shallower depths, but the frequency of *Glottidia* declines rapidly with depth. On the other hand, in depths of 18 meters, temperatures are higher but the sediments are considerably coarser on the average, as reflected in the greatly declining populations of *Glottidia*. Thermal and sedimentary relationships are shown more directly in Figures 6 and 7, by plotting densities of *Glottidia*: (1) in supposedly optimum sediments against depth changes and (2) in supposedly optimum depths against sediment changes.

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