

DISTRIBUTION OF THE MIDWATER FISHES
OF THE GULF OF CALIFORNIA

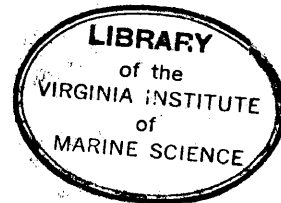
A Thesis

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of
Master of Arts



By

Bruce Hammond Robison

1968

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Arts

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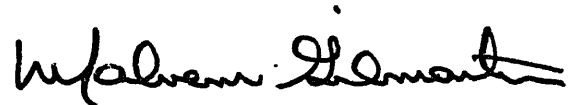
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of Master of Arts.

A handwritten signature in black ink, appearing to read "Malvern Gilmartin". The signature is fluid and cursive, with a prominent dot above the letter 'i' in "Gilmartin".

27 June 1968

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TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS	iv
LIST OF TABLES	vi
LIST OF FIGURES.	vii
ABSTRACT	ix
INTRODUCTION	2
METHODS.	12
THE ENVIRONMENT Oceanography of the Gulf of California . . .	22
RESULTS Distributional outline	33
DISCUSSION Distributional analysis.	62
SUMMARY AND CONCLUSIONS.	83
BIBLIOGRAPHY	86

LIST OF TABLES

Table		Page
1.	List of midwater collecting stations. .	16
2.	List of data sources. .	21
3.	List of midwater fishes collected .	47
4.	Comparison of meristic and morphometric characters between two forms of <u>Benthoosema panamense</u>	61

LIST OF FIGURES

Figure	Page
1. Cruise track of Stanford Oceanographic Expedition 16	10
2. Pelagic zonation in tropical regions. . .	11
3. Tucker trawl.	19
4. Collection sites.	20
5. Basins in the Gulf of California.	27
6. Bathymetry of the Gulf of California. . . .	28
7. Bottom profile of the Gulf of California. .	29
8. Parameter profiles; central Gulf.	30
9. Parameter profiles; southern Gulf	31
10. Parameter profiles; northern Gulf	32
11. Day-night vertical distribution of <u>Bathylagus stilbius</u>	48
12. Horizontal distribution of <u>Cyclothone acclinidens</u>	49
13. Day-night vertical distribution of <u>Cyclothone acclinidens</u>	50
14. Horizontal distribution of <u>Vinceguerria lucetia</u>	51
15. Daytime vertical distribution of <u>Vinceguerria lucetia</u>	52
16. Nighttime vertical distribution of <u>Vinceguerria lucetia</u>	53
17. Horizontal distribution of <u>Triphoturus mexicanus</u>	54
18. Daytime vertical distribution of <u>Triphoturus mexicanus</u>	55
19. Nighttime vertical distribution of <u>Triphoturus mexicanus</u>	56
20. Horizontal distribution of <u>Diogenichthys laternatus</u>	57

Figure	Page
21. Daytime vertical distribution of <u>Diogenichthys laternatus</u>	58
22. Nighttime vertical distribution of <u>Diogenichthys laternatus</u>	59
23. Day-night vertical distribution of <u>Benthoosema panamense</u>	60
24. Pelagic zonation in the Gulf of California.	79
25. Hypothetical representation of the factors excluding <u>Diogenichthys laternatus</u> from the northern Gulf.	80
26. <u>Benthoosema panamense</u> from the northern Gulf.	81
27. Eastern North Pacific water masses.	82
28. Diagrammatic outline of midwater fish penetration	85

ABSTRACT

This thesis represents the first attempt to assess systematically the midwater fish community of the Gulf of California using collection data from an opening-closing pelagic trawl.

The Gulf of California is an extension of the tropical zone containing Equatorial Pacific water in the chain of deep water basins which line the bottom in its central and southern portions. The northern basins contain water of local origin, and support a unique fish community.

A definition of the Gulf's pelagic zones is presented and distribution of the midwater fishes is correlated with the definition. Three groups of midwater fishes exist in the Gulf. Epi-mesopelagic migrators, meso-bathypelagic migrators and epi-bathypelagic migrators. Each of the groups exhibits a distinct horizontal and vertical range.

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INTRODUCTION

From September through November of 1967, Stanford Oceanographic Expedition 16 was conducted in the Gulf of California aboard the R/V TE VEGA (Figure 1). One of the research projects conducted during this Expedition was a study of the distribution of the midwater fishes in this region. This study is the basis of the following thesis.

The Gulf of California has been the object of much scientific interest since the end of the last century. Despite the attention given this region by marine scientists, it remains a relatively unknown area. Knowledge of the Gulf's midwater organisms has suffered from a lack of sampling programs designed to survey their populations accurately. Prior to Expedition 16, eight expeditions had conducted midwater trawling in the Gulf. Only two of these had sampled the northern portion. Too often, the sampling consisted of indiscriminate trawling. The samples produced yielded many new species and new distribution records for eastern Pacific fishes, but no information on the overall midwater fish community within the Gulf. A notable exception was the trawling survey conducted by the California Department of Fish and Game, reported by Lavenberg and Fitch (1966). This cruise sampled nearly the full length of the Gulf with a series of stations designed to examine the fauna of the shelf regions. Twenty-five midwater collection stations were made; unfortunately all

were made at night, in relatively shallow water, and with a continuously open net.

This study represents the first attempt to systematically determine the Gulf's midwater fish distribution with an opening-closing pelagic trawl combined with extensive measurements of the physical, chemical and biological environmental factors. It too, suffers from incompleteness and a lack of information on factors such as sampler bias and seasonal variation. Nonetheless, it is the most thorough and precise sampling effort to date. The distributional analysis of fishes presented herein is a working hypothesis. It attempts to unite the previous collection records with TE VEGA's collection data to provide a preliminary outline and analysis of the Gulf's midwater fish distribution.

The distribution of midwater fishes is dependent upon a variety of physical, chemical and biological limiting factors in the waters beyond the continental shelf. The geographic shape of the environment determines the potential living space, while light, temperature, salinity, currents, competition, and other factors define actual vertical and horizontal ranges.

Within an environment, zones are established by physical and chemical parameters. Many authors have attempted to offer general definitions of pelagic zones, with only limited success. Bruun (1957) produced the most reasonable outline. His concepts are diagrammed in Figure 2.

The lower limit of the epipelagic zone is defined by the farthest penetration of sunlight suitable for photosynthesis although light may be visible to certain fishes below the compensation depth. The mesopelagic zone extends from the epipelagic to the approximate depth of the 10° C isotherm. The bathypelagic zone lies between the 10° C isotherm and the depth of the 4° C isotherm, where it merges into the abyssopelagic zone.

The term "midwater" is herein applied to fishes which spend at least a portion of the diel cycle in either the mesopelagic or bathypelagic zones. Thus, by definition, midwater fishes inhabit a range containing a variety of potential limiting factors.

Diel migration is the most striking aspect of midwater fish distribution. Adult fishes move up to the surface at night from the dark waters they inhabit during daylight. Presumably the fishes obtain the bulk of their food in the more superficial layers, feeding on the multitude of planktonic forms which abound in the epipelagic zone.

The trophic structure of the pelagic population has six levels: the permanent phytoplankton component of the epipelagic zone, detrital feeders, herbivorous and carnivorous zooplankters which migrate vertically (perhaps to maintain a constant level of illumination), herbivorous fishes which feed on the phytoplankton, predatory fishes which feed on the smaller herbivores, and predators which

eat the herbivores and smaller predators. In this scheme larval and pre-adult fishes, while feeding on even smaller forms, may be a major food source for adults of the same or other species.

Several alternative hypotheses have been offered to explain aspects of the vertical migration. The fishes may feed in the upper layers at night so that darkness can continually shield them from predators, and the daytime descent may provide a metabolic advantage which outweighs the energy expenditure involved in the vertical migrations. Paxton (1967) indicates that surface feeding may not provide a primary selective advantage. He states that it is possible that certain species migrate because they are following a shallower bioluminescent layer through its vertical movements. The scheme requires a high light sensitivity by which each group selects a depth relative to the light intensity of the layer above.

Light as a limiting factor is of prime importance in affecting vertical migrations, at least in the upper layers. Light has been the only non-biological factor whose variations in intensity have been observed to correspond directly with the timing of the migrations. As evidence of this correlation, Barham (1957) reports fish populations to

be higher in the water column when phytoplankton blooms, fog and overcast skies, reduce light penetration. Clarke (1966) concludes that myctophids associate with a particular level of light intensity, although the intensities are extremely low. Paxton (1967) estimates that myctophids may be able to distinguish between light intensities at depths as great as 400 to 600 m.

In the course of their vertical migrations, the fishes pass through a range of limiting factor gradients. Temperature is probably the most important factor affecting distribution. In the epipelagic layer, temperature is most important in influencing distribution in a horizontal plane. In this mixed layer, immediately below the surface, significant temperature changes occur, mainly due to climatic conditions. Below the epipelagic zone, stratification of water structures and the decrease of temperature with depth affect distribution in the vertical plane. Bruun (1957) has described the 10° C isotherm as "the most useful ecological boundary." Similarly, the 4° C isotherm is important as the lower limit of the bathypelagic region.

Temperature as a limiting factor can act in one of two ways; to inhibit reproduction, or to prevent survival. Seldom does a single temperature regime encompass the entire life cycle of a midwater fish. Most often, the different stages in a life cycle appear to require quite different temperatures. The larvae are found epipelagically and

succeeding growth stages are found at ever increasing depths. The phenomenon appears as decreasing stenothermality with the vertical range becoming greater with age. Adults are found to exhibit a wider thermal tolerance. During diurnal migrations they often cover the entire temperature range occupied by all of the pre-adult stages.

Salinity varies little in an oceanic water column, and below the mixed layer seldom acts alone as a limiting factor. In the epipelagic zone, evaporation, rainfall and river effluence can cause salinity changes which may limit horizontal distribution and thus vertical distribution within localized areas.

Most midwater fishes are physiologically adapted to wide variations in oxygen tension. Respiratory consumption is generally independent of oxygen tension down to the lower limits of oxygen concentration. An oxygen minimum layer is prevalent in the eastern Pacific and in the Gulf of California it characteristically shows concentrations of less than 0.2 ml/liter. The minimum does not appear to influence most fish distribution directly. It may however have an indirect effect on fish distribution by excluding zooplankton, which cannot tolerate the low tensions at depths above and below the minimum layer.

The effect of physical and chemical factors in the sea is not as great individually as it is when they are combined. The concept of water masses, defined by density and

characterized by varying temperatures and salinities, is well established as a distributional factor. Certain fishes are preferentially restricted to an environment delimited by temperature and salinity controlled density. Populations of fishes within the water masses tend to be most dense where the characteristic water qualities are most distinct. In areas of transition between water masses, the populations often dwindle and intermingle with populations having different affinities.

Competition for living space within a marginal sea such as the Gulf of California can be intense. Those fishes best adapted to feed and reproduce within a given region will persist. At any one depth in the water column, relatively few species live together and competition is thus partitioned in the vertical plane. Records of deep scattering layers suggest that some components of the midwater fauna are sharply stratified. Marshall (1963) comments that the hydrographic differences between deeper water inside and outside a basin with a shallow sill may be correlated with genetic divergences between immigrant stocks of midwater fishes and the parent populations that live outside the basin. The greater the physical divergence, the more pronounced the genetic divergence.

In the sea, few boundaries are static. The sea is a moving, changing medium in which daily, seasonal, annual and random variations occur to move and alter the factors

within a geographical area. Often, distributional studies are hampered by terminology which describes a collection of fishes from the "bathypelagic" or "mesopelagic" zones, when no real effort has been made to define these regions. The practice of choosing zonal names for collections has been as arbitrary as drawing lines in the sea. Faunal zones should be described for specific areas in terms of environmental factors which have been empirically determined.

Fish population boundaries are unstable. As fishes live, they move and as communities persist, they shrink or grow. Thus, a definition of distribution must invoke the artificiality of described boundaries which themselves are not definite.

Figure 1. Cruise track of the R/V TE VEGA, during Stanford Oceanographic Expedition 16. September through November, 1967.

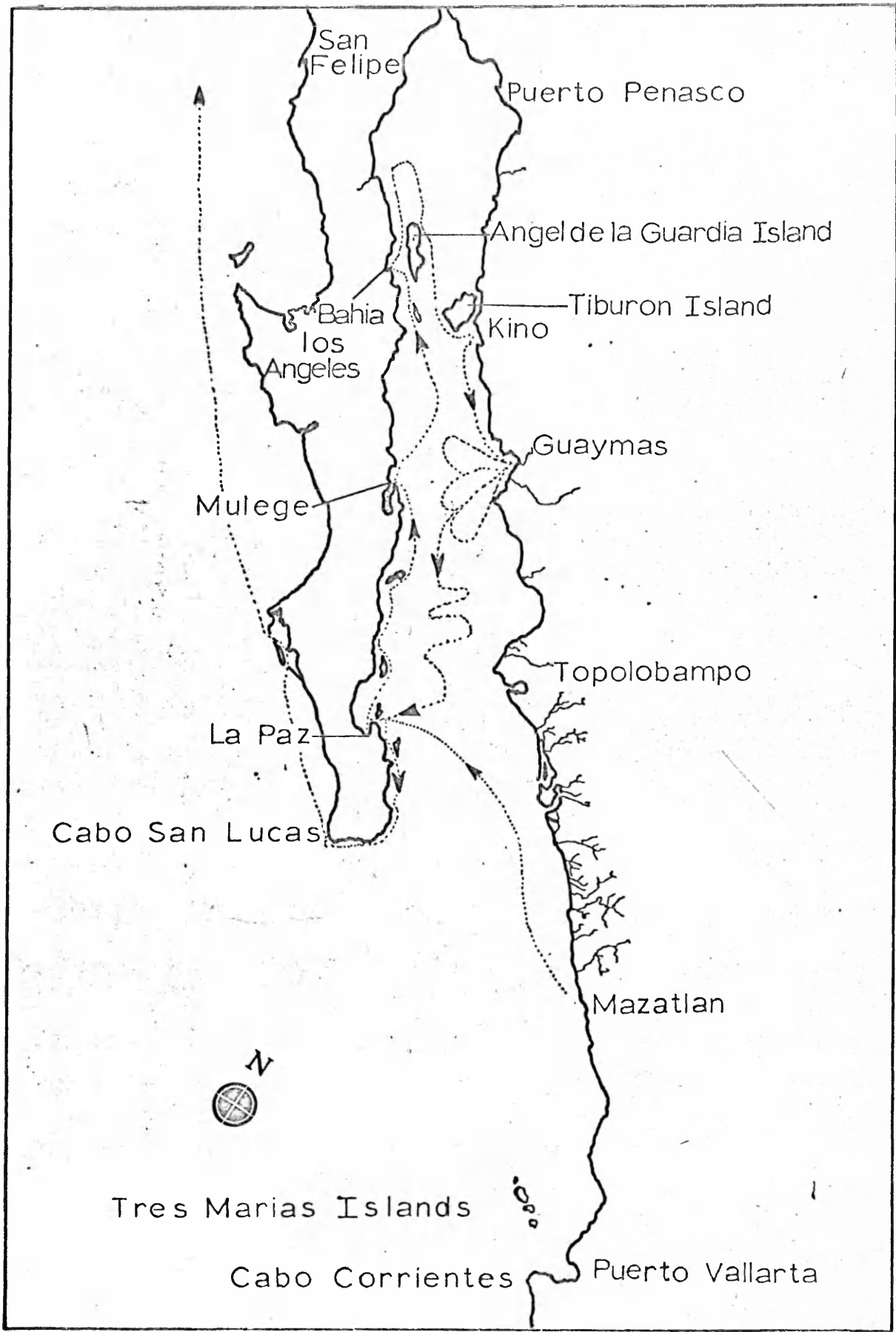
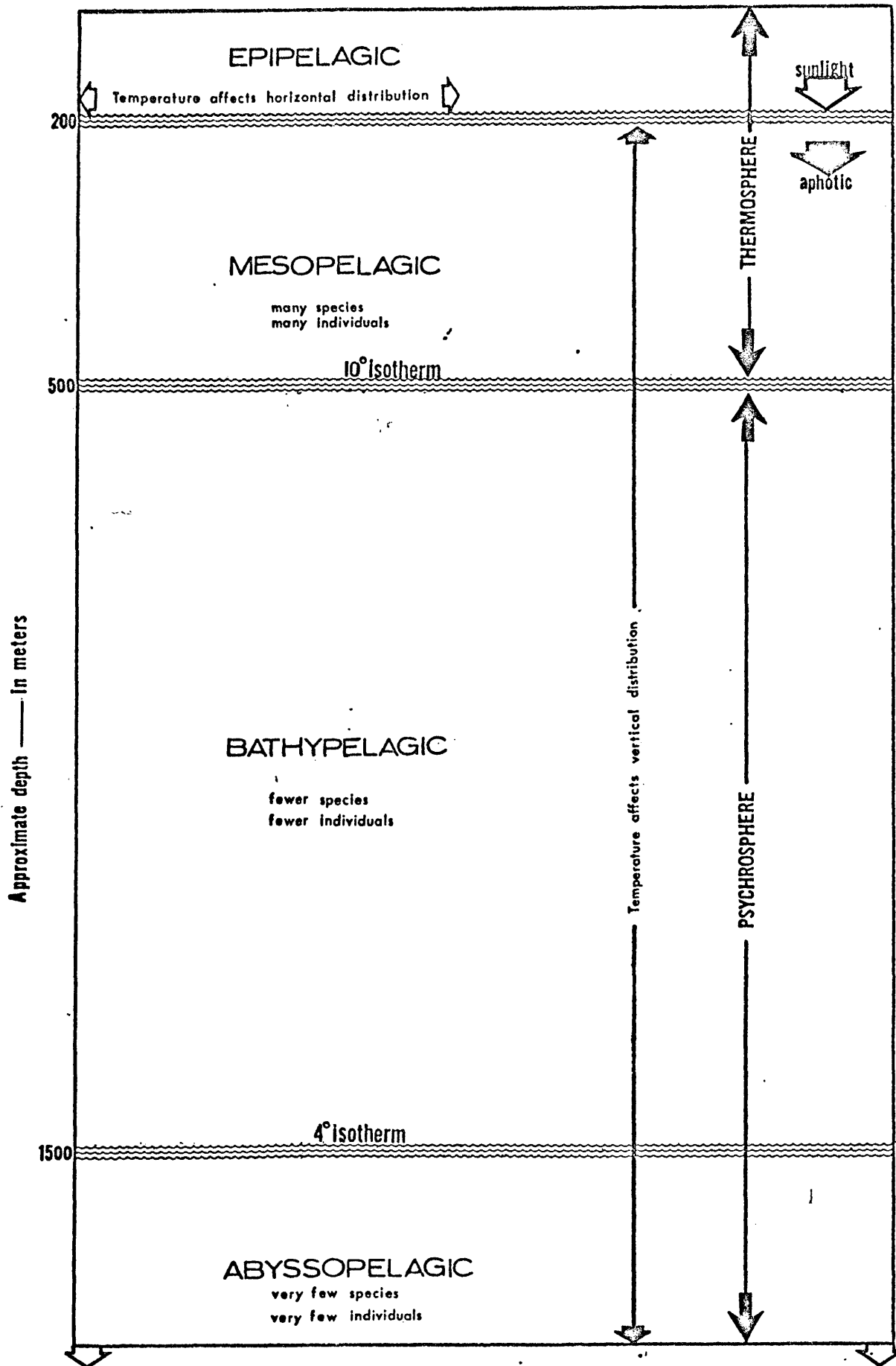


Figure 2. Pelagic zonation of the deep sea in a tropical or subtropical region. Modified after Bruun (1957).



METHODS

Seventy-one midwater collecting stations were made by the R/V TE VEGA from September through November of 1967, in the Gulf of California (Table 1). The collections were made with a modified 6-foot Tucker trawl (Tucker, 1951). The trawl had a mouth opening of 1.8 m by 1.8 m and an overall length of 9 m. The main scoop was constructed of 0.5 cm mesh. The cod end was a plastic cylinder, 15 cm in diameter, 50 cm long. It was preceded by a 0.1 cm-mesh section which tapered back from the main scoop (Figure 3).

A mechanical opening-closing device restricted fishing to predetermined depths. The trawl was opened at depth and towed for 1-2 hours at a speed of 2 knots.

The precise depth sampled was measured by a pressure-depth recorder attached to the gear. A standard meter net was placed from 1-10 m above the Tucker trawl on most hauls and fished continuously while in the water.

Before each station, the trawl was laid out on the fantail of the vessel and the timing mechanisms were set. The clockwork of the opening mechanism was set for a lag time sufficient to allow the net to reach the desired depth. The closing clock was set for the lag time plus 1 hour. The trawl was then lowered over the stern and the wire paid out. Wire-angle measurements were made to determine when the desired sample depth was reached.

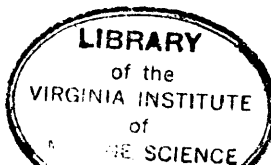
In operation, the net mouth had three positions. While lowering, the two bars connected to the top and bottom

portions of the net mouth were held together by bridles leading to the timers. When the lag period ended, the opening timer released the bridle connected to the bottom bar. This bar dropped downward along the wire of the net frame and opened the net. One hour later the second clock released the bridle to the upper bar, which dropped to the level of the first bar, closing the net.

An additional 10-15 minutes were allowed before the trawl was hauled back to the surface. On deck, the cod-end bucket was removed and the sample poured into pans of fresh seawater. The net was then placed back in the water to wash behind the moving vessel.

The effectiveness of the Tucker trawl as a midwater sampling device is generally undetermined. Certainly the larger and faster pelagic fishes can avoid the net's 3 m² opening at speeds of 2 knots. Meter nets are often used in combination with other midwater trawls and a comparison of collections from a meter net-Isaacs-Kidd combination is roughly the same as a comparison of the meter net-Tucker trawl combination, indicating a general equality of sampling ability. Other midwater nets used in the Gulf of California have yielded collections similar to those of the Tucker trawl.

Foxton, of the Plymouth Laboratory in England, has reported that the Tucker trawl is equal to or better than a similarly operated, equal-sized, Isaacs-Kidd midwater trawl, in number and variety of fishes collected (Weibe, personal



communication).

Twelve additional collections were made using meter nets in vertical hauls. At each of these stations a series of nets was brought to the surface, at a speed of 30 m/min, from staggered depths. The nets remained closed until they started their ascent. Sample differences between the nets were assigned to the depth differences between the nets.

Collections were made from latitude 29° 59' N to 22° 42' N, encompassing nearly the entire length of the Gulf (Figure 4). Stations were concentrated in the deeper water over basins but many were taken in the shallower waters between basins. On two occasions, 27 October 1967 and 29 October 1967, a series of trawls was made at various depths while the vessel cruised back and forth over the same track (stations 121-127 and stations 135-140).

Hydrographic data were gathered at stations which were usually within one mile of the biological stations. Deep Scattering Layer (DSL) information was obtained with a 30 KC Simrad echo sounder and an 11 KC Simrad fathometer.

Samples were initially preserved in 10% formalin. The adult fishes were later separated from the plankton and transferred to 70% ethanol. Preliminary identifications were made at sea. Final identifications were made with the aid of the most recently published revisions and the reference collections at Stanford University's Museum of Systematic Biology, The Los Angeles County Museum, and the University of Southern California's Allan Hancock Foundation.

Certain identifications were confirmed by Dr. Robert J. Lavenberg (L.A.C.M.), Dr. Basil Nafpaktitis (U.S.C.) and Dr. Alfred W. Ebeling (University of California, Santa Barbara).

Supplementary midwater fish collection data were obtained from the Scripps Institution of Oceanography (Dr. Carl L. Hubbs), the Allan Hancock Foundation and the Los Angeles County Museum. Supplementary information was also obtained from published reports of every previous expedition to the Gulf of California which sampled its midwater fishes (Table 2).

Table 1. Station list of midwater collecting stations from Stanford Oceanographic Expedition 16. TT represents Tucker trawl, MN the meter net and VPT vertical plankton tows.

STATION	SAMPLER	SAMPLE DEPTH (meters)	LATITUDE (north)	LONGITUDE (west)	TIME	DATE
19	TT	400-420	24° 26'	109° 9.5'	1651-1751	24 IX 67
21	TT+MN	15	24° 21'	109° 1.5'	2045-2145	24 IX 67
22	TT	50	24° 25'	109° 03'	2230-2330	24 IX 67
29	VPT	760	24° 53'	110° 29'	1630-1700	25 IX 67
33	TT+MN	60	25° 08'	110° 11'	0200-0300	29 IX 67
35	TT+MN	355	25° 36'	110° 42'	1102-1202	29 IX 67
39	TT+MN	50-55	25° 46.3'	110° 40.5'	2025-2125	29 IX 67
56	TT+MN	20	27° 04.2'	111° 50'	2141-2241	5 X 67
57	VPT		27° 07'	111° 48'	2230-2300	5 X 67
59	VPT		27° 25'	111° 51'	1600-1630	7 X 67
61	TT	45-65	27° 26'	111° 47.5'	2110-2210	7 X 67
62	TT+MN	325-365	27° 14.5'	111° 58'	1032-1132	8 X 67
63	TT+MN	425-445	28° 06'	112° 04'	1500-1600	8 X 67
64	TT+MN	180-190	28° 02'	112° 02'	1237-1337	8 X 67
66	VPT		28° 00'	112° 05'	1900-1930	8 X 67
67	TT+MN	35-45	28° 01'	112° 06'	2205-2305	8 X 67
74	TT	180	28° 36'	112° 54.5'	1610-1710	10 X 67
83	TT	70-100	29° 13.3'	113° 23'	2117-2217	12 X 67
84	TT	60	29° 13'	113° 29'	0347-0447	13 X 67
86	VPT		29° 09'	113° 26'	0820-0850	13 X 67
87	TT	255-305	29° 12'	113° 31'	1257-1357	13 X 67
88	TT+MN	270-295	29° 09'	113° 26'	1507-1607	13 X 67
90	TT+MN	60-65	29° 52'	113° 51'	0034-0134	14 X 67
91	TT+MN	225-235	29° 59'	113° 54'	0245-0345	14 X 67
94	TT+MN	25-30	29° 48'	113° 55'	1650-1750	14 X 67
95	TT+MN	60	29° 45'	113° 50'	2033-2133	14 X 67
102	TT	40-45	27° 50.5'	111° 24'	2342-0042	18 X 67
111	TT+MN	225-475	27° 09'	111° 15'	1102-1202	25 X 67

STATION	SAMPLER	SAMPLE DEPTH (meters)	LATITUDE (north)	LONGITUDE (west)	TIME	DATE
112	TT+MN	850	27° 07.5'	111° 01'	1335-1435	25 X 67
113	TT+MN	35	27° 05'	111° 00'	2127-2227	25 X 67
114	TT	65-90	27° 11'	111° 06'	2322-0022	25 X 67
116	VPT		27° 01'	111° 11'	1100-1130	26 X 67
118	TT+MN	275-290	26° 52'	111° 01'	1845-1945	26 X 67
119	TT+MN	55-65	26° 55'	111° 05'	2029-2129	26 X 67
120	VPT		26° 53'	111° 03'	2200-2300	26 X 67
121	TT+MN	175	26° 53'	111° 11'	0945-1045	27 X 67
122	TT+MN	235	26° 55'	111° 11.5'	1200-1300	27 X 67
123	TT+MN	540-650	26° 54'	111° 11.5'	1420-1520	27 X 67
124	TT+MN	65-70	26° 50'	111° 13'	1619-1719	27 X 67
125	TT+MN	260-265	26° 57.5'	111° 13'	1957-2057	27 X 67
126	TT+MN	55-60	26° 57.5'	111° 13'	2157-2257	27 X 67
127	TT+MN	30	26° 55.5'	111° 13'	2336-0036	27 X 67
130	VPT		27° 14'	111° 19'	1030-1100	28 X 67
131	TT+MN	50-65	27° 13.6'	111° 20.2'	1940-2040	28 X 67
132	TT+MN	90-100	27° 17'	111° 20.5'	2130-2230	28 X 67
133	VPT		27° 19'	111° 22'	2300-0250	28 X 67
135	TT+MN	290-345	27° 23'	111° 24'	1035-1135	29 X 67
136	TT+MN	320-360	27° 23'	111° 20.5'	1237-1337	29 X 67
137	TT+MN	165	27° 24.5'	111° 20.5'	1440-1540	29 X 67
138	TT+MN	90-95	27° 25'	111° 19.5'	1640-1740	29 X 67
139	TT	45-55	27° 21'	111° 17.8'	1837-1937	29 X 67
140	TT	25-30	27° 16'	111° 24.5'	2015-2115	29 X 67
143	VPT		26° 22'	111° 44'	1030-1100	1 XI 67
144	TT+MN	525-560	26° 27.5'	110° 45'	1029-1129	3 XI 67

STATION	SAMPLER	SAMPLE DEPTH (meters)	LATITUDE (north)	LONGITUDE (west)	TIME	DATE
145	TT+MN	390	26° 23'	110° 47'	1250-1350	3 XI 67
147	TT+MN	1170-1520	26° 14'	110° 46'	1830-2030	3 XI 67
148	TT+MN	165-220	26° 09.5'	110° 35.5'	2210-2310	3 XI 67
152	TT+MN	240-260	25° 29.5'	110° 37.5'	2218-2318	4 XI 67
156	TT+MN	125-135	25° 17'	110° 28.5'	2010-2210	5 XI 67
157	TT+MN	300-330	25° 17'	110° 23'	2209-2309	5 XI 67
158	TT+MN	580-595	25° 17'	110° 19.5'	0025-0125	6 XI 67
159	TT+MN	2250-2280	25° 17'	110° 15'	0345-0545	6 XI 67
160	TT+MN	325-400	25° 16'	110° 09.5'	0745-0845	6 XI 67
161	TT+MN	250-300	25° 16'	110° 04'	0950-1050	6 XI 67
162	TT+MN	355-380	25° 13'	109° 58'	1200-1300	6 XI 67
163	TT+MN	130-145	25° 12.5'	109° 56.5'	1405-1505	6 XI 67
165	TT+MN	445-490	25° 06.5'	109° 48.5'	2040-2140	6 XI 67
166	VPT		25° 03.2'	109° 44.5'	2303-0003	6 XI 67
168	TT+MN	775-1260	24° 52'	109° 33'	0520-0650	7 XI 67
169	TT+MN	60	24° 49'	109° 30'	0805-0905	7 XI 67
170	VPT		24° 51'	109° 25'	0945-1045	7 XI 67
172	VPT		24° 52'	109° 15'	1900-2230	7 XI 67
178	TT+MN	160-175	23° 38'	109° 20'	2258-2358	11 XI 67
179	TT+MN	610-625	23° 34'	109° 15.5'	0120-0220	12 XI 67
180	TT+MN	375-395	23° 31'	109° 11.7'	0355-0455	12 XI 67
184	TT	360-390	22° 45.5'	109° 54'	1520-1620	13 XI 67
186	TT+MN	645-665	22° 47'	110° 04'	1939-2039	13 XI 67
188	TT	70-75	22° 44.5'	110° 12.5'	2222-2322	13 XI 67
189	TT+MN	400-490	22° 42'	110° 51'	0050-0250	14 XI 67
190	TT+MN	30	22° 46'	110° 23'	0352-0452	14 XI 67
191	TT+MN	170-175	22° 47.5'	110° 28.5'	0604-0704	14 XI 67
192	TT+MN	770-830	22° 48'	110° 37'	0845-1045	14 XI 67
193	TT+MN	275	22° 51'	110° 46'	1235-1335	14 XI 67

Figure 3. Modified 6-foot Tucker trawl used by the R/V
TE VEGA at midwater collection stations in
the Gulf of California.

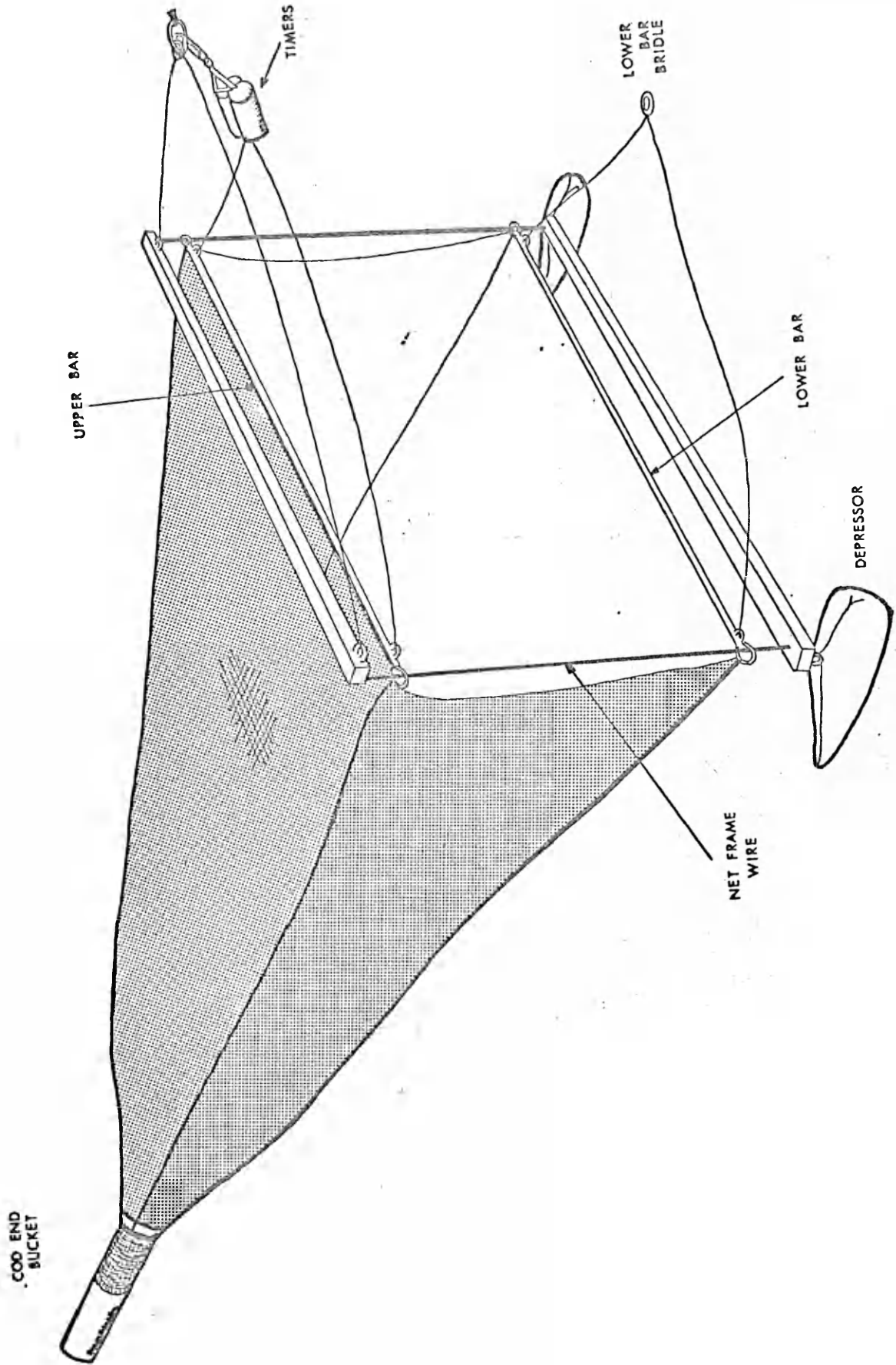


Figure 4. Midwater collection sites of Stanford Oceanographic Expedition 16.

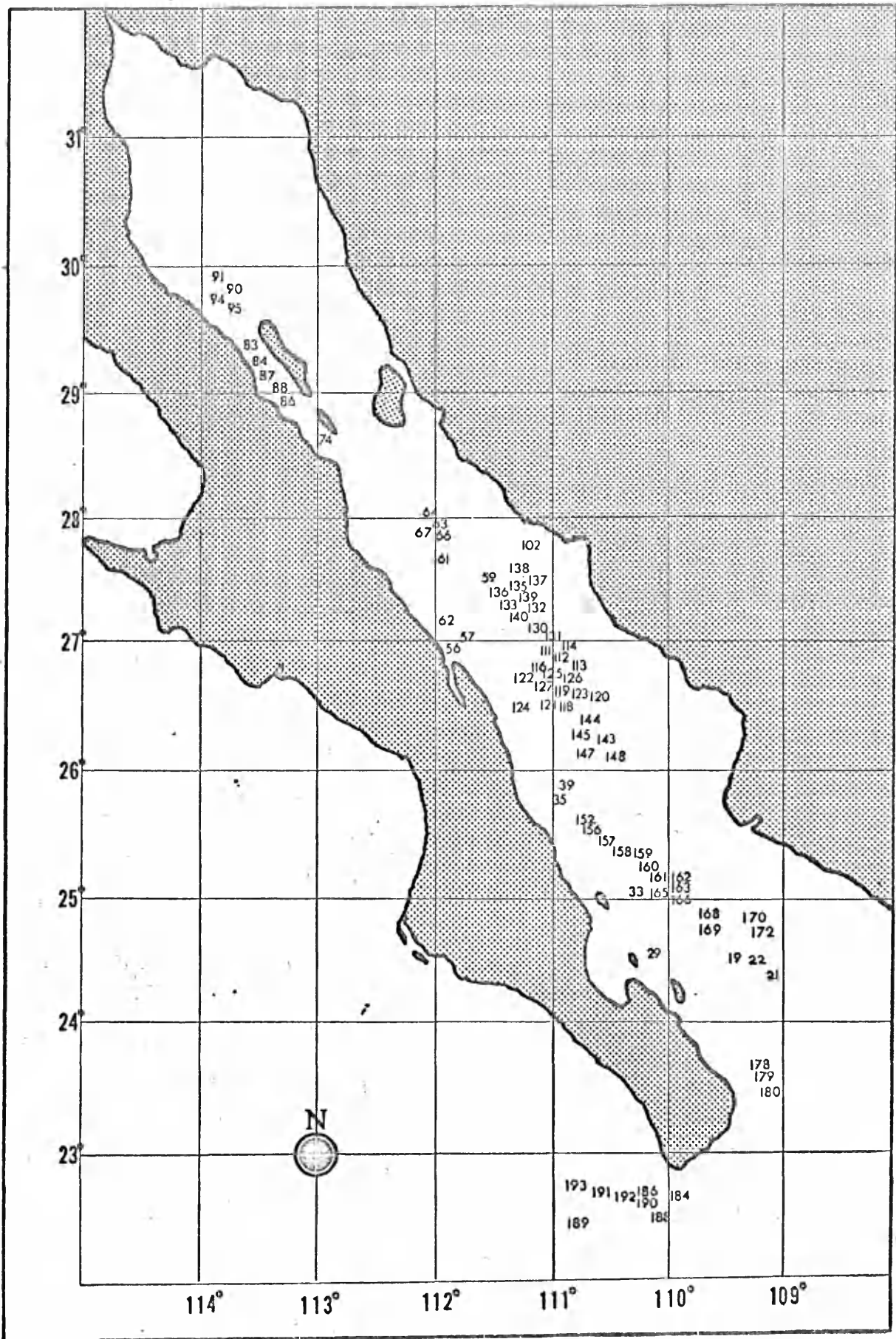


Table 2. List of expeditions from which data used in this study were obtained.

NAME	SHIP	DATES	SOURCE
American Museum of Natural History	ALBATROSS	Mar.-Apr., 1911	Townsend and Nichols (1925)
Yale University Bingham Foundation	PAWNEE	1929	Parr (1931)
Templeton Crocker Expedition	ZACA	Mar.-May, 1936	Beebe (1937)
California Department of Fish and Game - Tuna cruises	various vessels	1952 - 1959	Clemens and Nowell (1963)
California Department of Fish and Game - cruise 64-A2	ALASKA	Mar.-Apr., 1964	Lavenberg and Fitch (1966)
Stanford Oceanographic Expedition 14	TE VEGA	Mar.-June, 1967	Stanford Oceanographic Expeditions
Stanford Oceanographic Expedition 15	TE VEGA	June-Sept., 1967	Stanford Oceanographic Expeditions
Stanford Oceanographic Expedition 16	TE VEGA	Sept.-Nov., 1967	Stanford Oceanographic Expeditions
Scripps Institution of Oceanography Cruise SIO68-I MVI-68-I	Thomas C. Washington	Jan., 1968	Dr. Carl Hubbs (personal communication)

THE ENVIRONMENT
OCEANOGRAPHY OF THE GULF OF CALIFORNIA

The Gulf of California is a marginal sea lying between the Baja California peninsula and the Mexican coastal plain. Roughly rectangular in shape, the Gulf averages 150 km in width and is 1400 km long. The southernmost portion opens directly to the Pacific Ocean at a latitude of 23° N. The Gulf was probably formed as the result of a split along the San Andreas fault during the Paleozoic era (Allison, 1964). The central axis runs from southeast to northwest.

With the exception of the Sal Si Puedes and Delfin Basins, the northern third of the Gulf is of continental-shelf depth. The central and southern thirds contain a chain of large, deep, central basins (Figure 5) which gradually increase in depth to the south (Figure 6). Transverse ridges separate each of the Gulf's basins, yet all but the northernmost two are in open communication with the ocean (Rusnack, Fisher and Shepard, 1964). See Figure 7.

Many small islands dot the western edge of the Gulf. Two major Islands, Angel de la Guardia and Tiburon, lie off opposite coasts in the northern third.

Standard hydrographic observations during Stanford Oceanographic Expedition 16 indicated that the water-mass structure during the cruise was similar to that identified by previous Gulf investigators (Sverdrup, 1941; Roden, 1958; Roden and Groves, 1959). The character of the water in the

Gulf is generally the same as that in the Equatorial Pacific, slightly altered at the surface by evaporation (Roden, 1958). The Gulf is an evaporation basin, resulting in characteristically warm, high-salinity surface water. The annual surface temperature range is 14 to 30° C in the south, 12 to 32° C in the north. Surface salinities range from 34.9 to 35.2 ‰ in the south and 35.4 to 36.0 ‰ in the north (Hubbs and Roden, 1964). Surface water is nearly saturated with oxygen. Wyrcki (1967) classifies this layer as Subtropical Water.

The physical and chemical properties between 20 and 40 m are generally uniform throughout the Gulf, due to wind mixing. At depths greater than 50 m, significant differences exist between the characteristic water columns to the south of and to the north of the Sal Si Puedes Basin sill (200-250 m) (Sverdrup, 1941).

South of the sill, subsurface waters form three distinct vertical layers. Below the mixed layer is a discontinuity layer of rapid density increase (50 to 150 m) due to rapidly decreasing temperature. The oxygen concentration also decreases rapidly at comparable levels. Stratification induces a vertical stability which restricts the exchange of properties between the surface and underlying layers (Hubbs and Roden, 1964). At depths below 150 m, physical and chemical properties display a reduced and very gradual gradient toward the bottom.

In the central and southern portions of the Gulf, sills

fall far short of approaching the stable stratified layers. In these regions of the Gulf the gentle temperature and salinity gradients of the deep waters, which extend to a considerable distance above the sills, result in relatively uniform densities and vertical instability. As a consequence there is a ready exchange with the open ocean, and deep water (below the discontinuity layer) in these regions, represents an intrusion of the Equatorial Pacific Subsurface Water Mass. This mass can be divided into Subtropical Subsurface Water (250 to 400 m with a temperature range of 14-18° C and a salinity range of 34.8-35.1 ‰) and Equatorial Intermediate Water (from 400 m down with a temperature range of 4-8° C and a salinity range of 34.5 to 35.0 ‰). Associated with the upper limits of the Equatorial Intermediate Water Mass are the 10° isotherm (300 to 400 m) and an isohaline of 34.7 ‰ (400 to 800 m; Hubbs and Roden, 1964). A distinct oxygen minimum layer (concentrations of less than 0.2 ml/liter) ranges from 200 to 800 m (Hubbs and Roden, 1964). Below 800 m both salinity and oxygen increase slightly with depth (Figures 8 and 9).

North of the Sal Si Puedes Basin sill, the water is mostly of local origin (Sverdrup, 1941). In the area between Baja California and Angel de la Guardia Island, strong tidal mixing results in unstable surface layers.

The northern basins differ significantly from their central and southern counterparts because Equatorial Pacific

Subsurface Water does not extend beyond the Sal Si Puedes Basin sill. The isolated nature of the basins results in high temperatures, salinities and oxygen concentrations at great depths (Blackburn, 1962). The 10° isotherm is depressed to a depth of from 600 to 1000 m. The salinity minimum is about 34.9 ‰ at 800 m. An oxygen minimum layer does not occur (Figure 10).

The strong tidal currents through the Ballenas Channel (over the Sal Si Puedes Basin) are not matched in the rest of the Gulf. Elsewhere, there is a general surface outflow of water in the winter and spring, and an inflow during summer and fall. Below the surface, an outward flowing current runs along the west coast and an inflow along the east. The subsurface circulation is generally counterclockwise (Sverdrup, 1941).

At Cabo San Lucas there are pronounced temperature and salinity gradients at the boundary between the cold and low-salinity California Current and the warmer, high-salinity Gulf Water. Similar, but weaker, shallow gradients occur at Cabo Corrientes, with a confrontation between Gulf Water and Eastern Tropical Pacific Surface Water (Blackburn, 1962). These particular fronts are shallow (no deeper than 80 m), but at greater depths they merge into even stronger gradients. To depths of 150 m, the California Current Water encounters the North Equatorial Current which transports warm, high-salinity, low-oxygen water from the tropics (Hubbs and Roden, 1964). The line of fronts between Cabo

San Lucas and Cabo Corrientes marks the southern boundary of Gulf Water.

Changing wind directions result in variable surface current patterns throughout the year. Strong northwesterly winds in the winter and spring cause upwelling along the mainland margin of the Gulf. The pattern is reversed during the summer and fall months. The southwesterly winds are of less magnitude than their seasonal counterparts and the corresponding upwellings along the coast of Baja California are of lesser volume. The Gulf is well known for the rich plankton blooms that occur whenever upwelling brings cold nutrient-rich water to the surface (Van Andel, 1964); red blooms are particularly common around Angel de la Guardia and Tiburon Islands (Hubbs and Roden, 1964).

Hurricane ("Chubasco") season in the Gulf lasts from May to December with its peak in September. The storms travel in a general northwesterly direction and are related to hydrographic conditions (Hubbs and Roden, 1964). Surface currents are dominated by these occasional winds and they may be responsible for abnormal patterns of water transport.

Figure 5. Deep water basins of the Gulf of California.
Modified after Van Andel (1964), Rusnack,
Fisher and Shepard (1964).

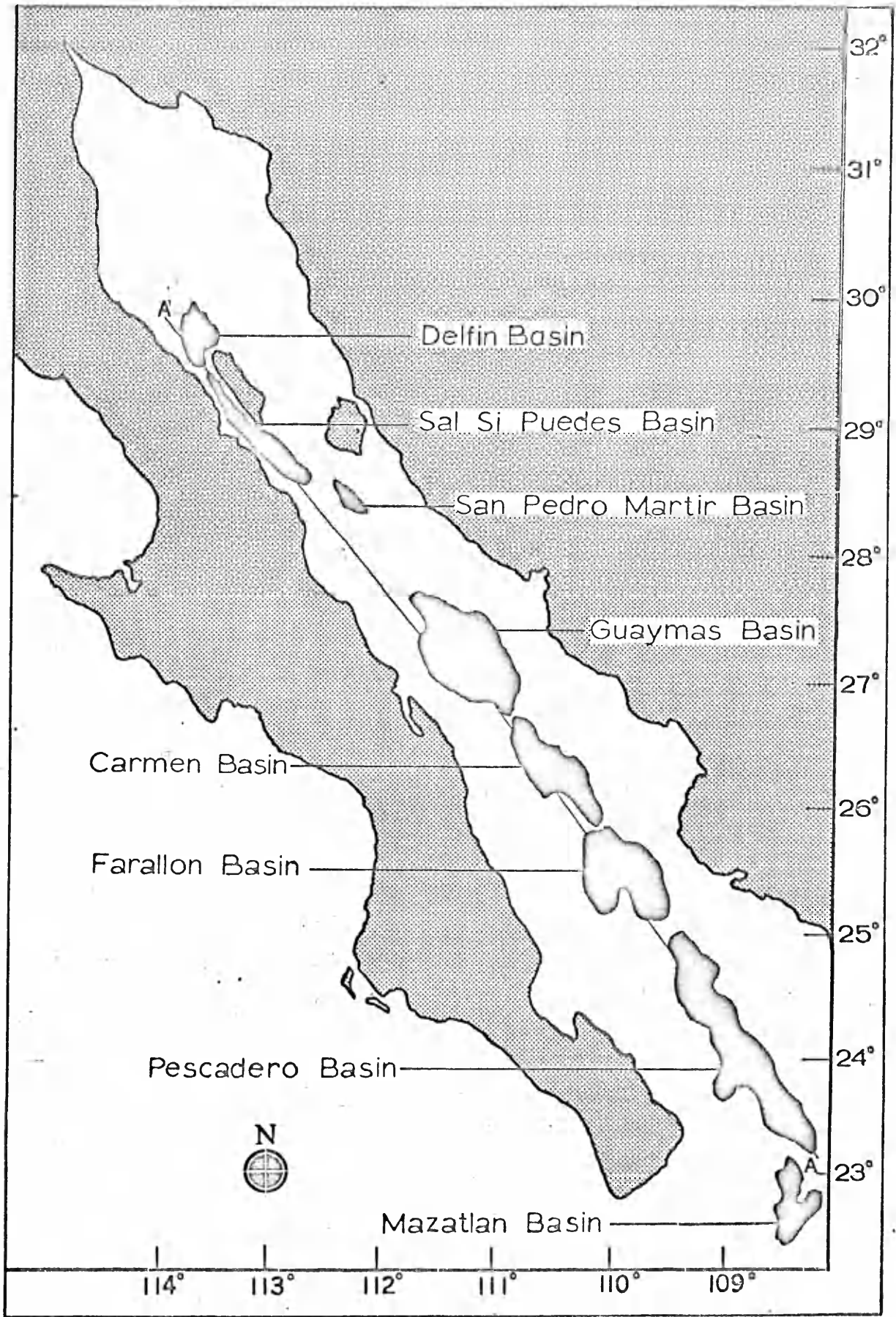


Figure 6. Bathymetry of the Gulf of California.
Modified after Roden (1958), Rusnack,
Fisher and Shepard (1964), and Curray
and Moore (1964). Depths are in meters.

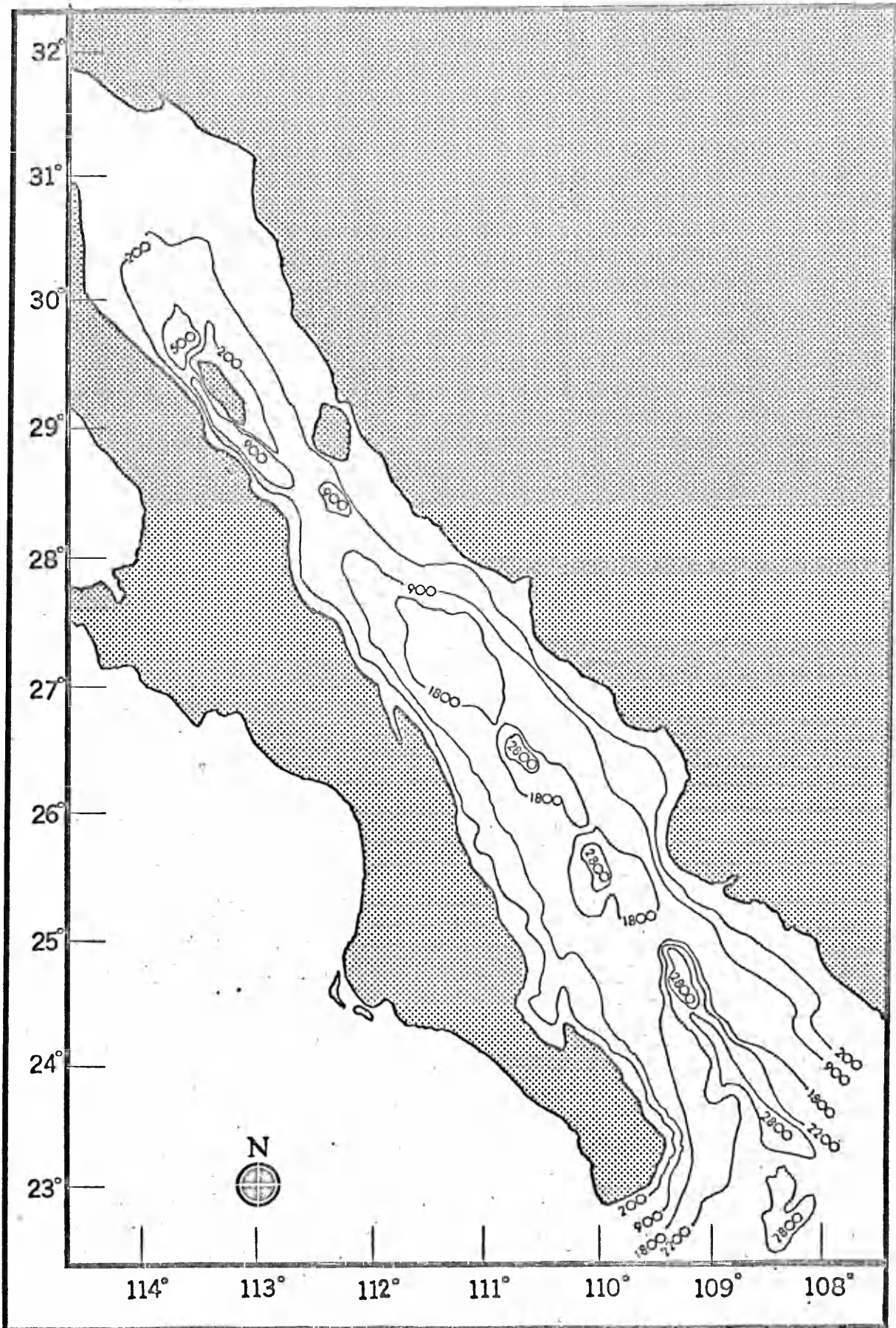


Figure 7. Bottom profile of the Gulf of California.

Line A-A' is shown in Figure 5.

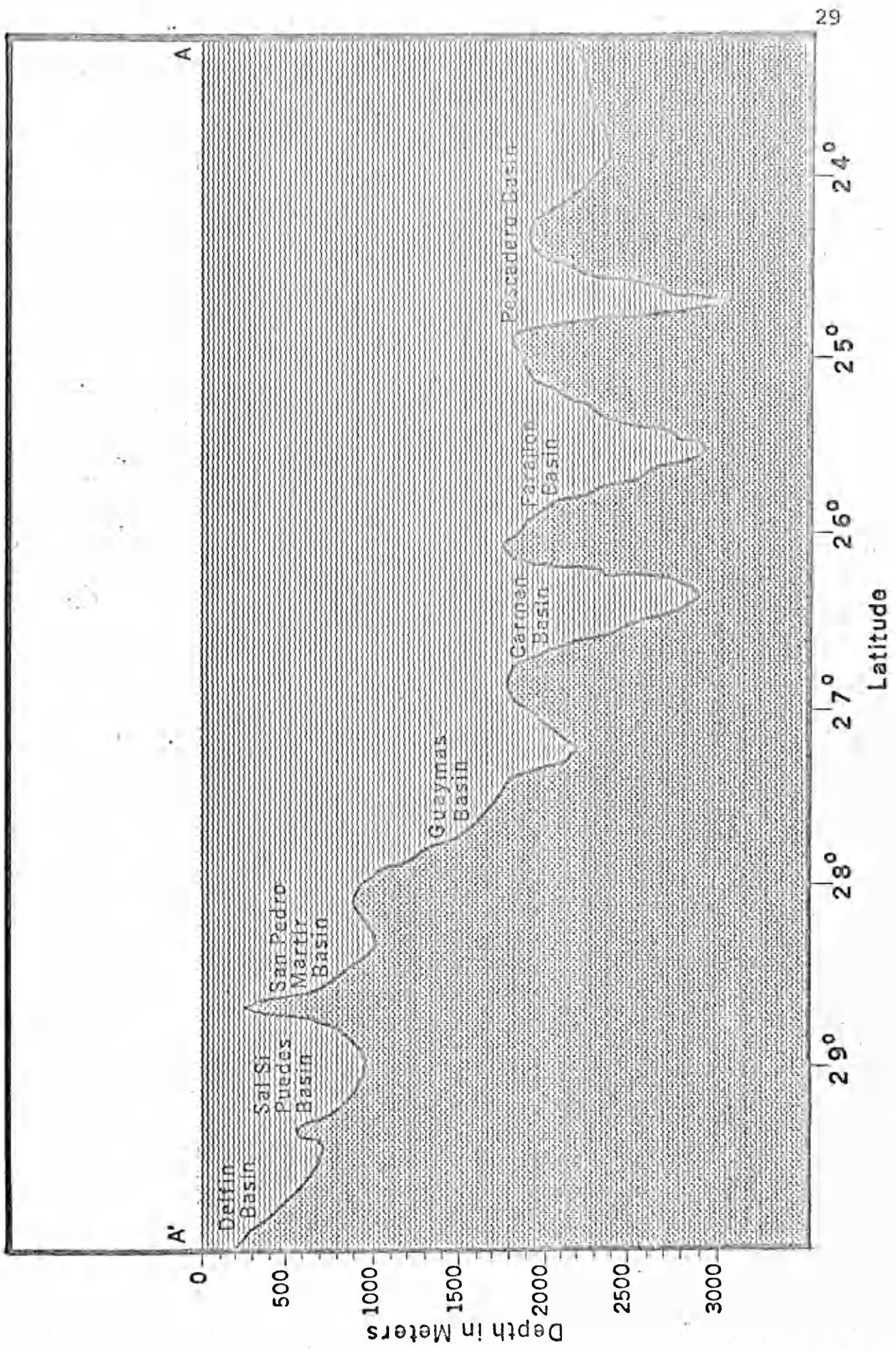


Figure 8. Temperature, salinity and oxygen concentration profiles across a generalized central Gulf cross section. Modified after Roden (1958 and 1964).

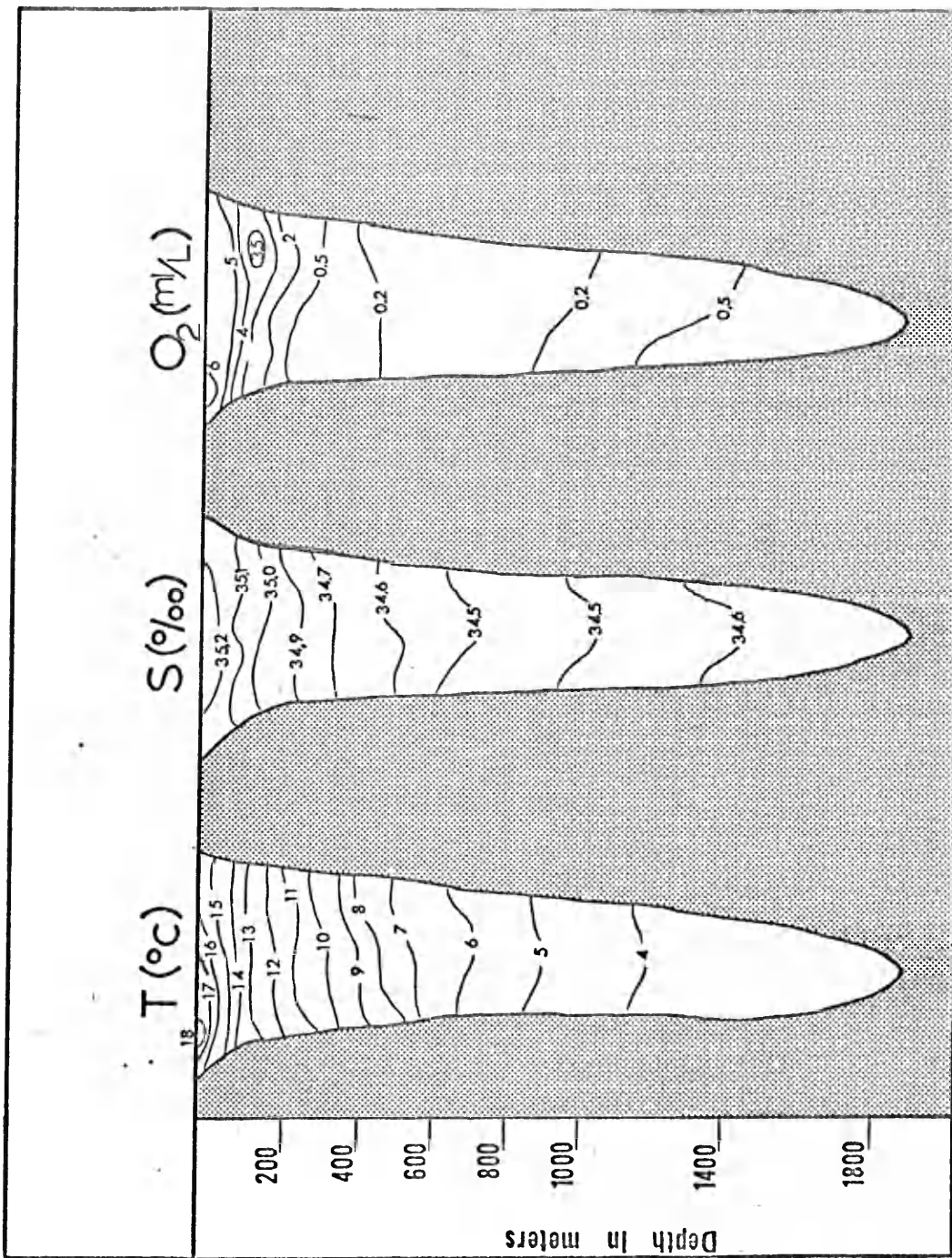


Figure 9. Temperature, salinity and oxygen concentration profiles across a generalized southern Gulf cross section. Modified after Roden (1958 and 1964).

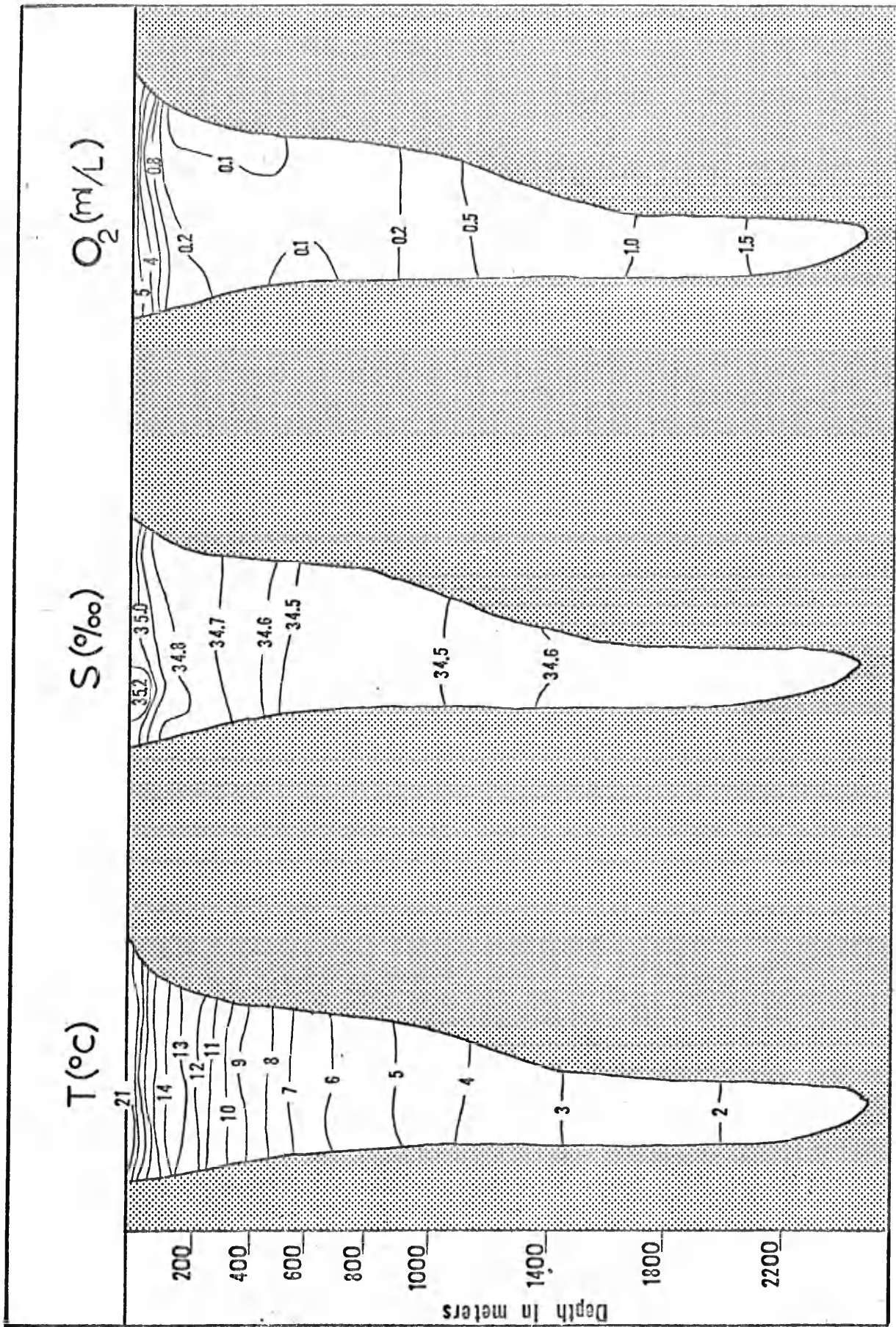
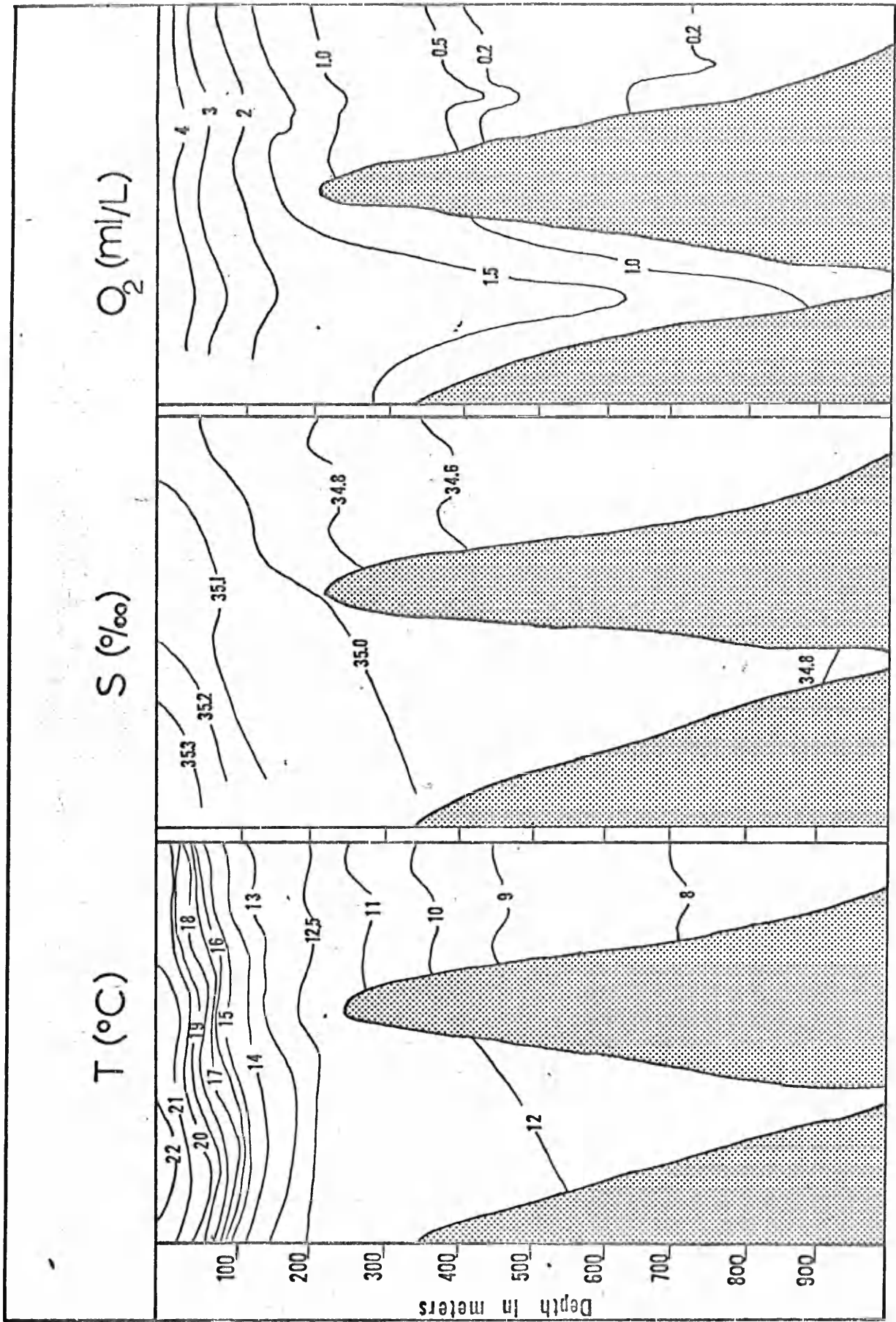


Figure 10. Temperature, salinity and oxygen concentration profiles across a generalized northern Gulf cross section. Modified after Roden (1958 and 1964).



RESULTS - Distributional Outline

A total of 10,466 midwater fishes, representing 11 families, 22 genera and 26 species were collected by the R/V TE VEGA at 83 midwater sampling stations during Stanford Oceanographic Expedition 16 to the Gulf of California (Table 3).

The family Myctophidae yielded the most species (seven) and the greatest number of individuals. Triphoturus mexicanus represented about 60% of the total midwater fish catch. The family Gonostomatidae yielded three representative species and was the second most numerous in numbers of individuals. The second most numerous species of midwater fish was the gonostomatid Cyclothone acclinidens, representing 6% of the total catch. These two families comprise the bulk of the Gulf's midwater fish population.

Two species of the family Bathylagidae were collected, one of which (Bathylagus stilbius) was common throughout the Gulf. The family Melamphaidae was represented by six species, however, few individuals were collected. Of the remaining seven families from which representatives were captured, no more than ten individuals of each were collected.

The greatest number of fishes in a single haul was 1629 (station 145). Four hauls (138, 158, 193, 190) collected no fishes, although the Tucker trawl appeared to be functioning normally. The greatest number of species

collected at a single station was 8 (station 145). The average number of species per haul was 3.

Annotated Collection List

The collection of midwater fishes is listed below, phylogenetically by family. Station numbers are presented in a north to south progression. The station number of each catch is followed by parentheses containing the number of fish collected by each type of sampler: 88 (5/2) indicates that 5 fish of a certain species were collected by the Tucker trawl and 2 by the meter net which accompanied the trawl at station 88. Numbers presented without the diagonal represent fish taken in a vertical meter-net haul. An outline of the distribution of each species follows the numerical data.

ALEPOCEPHALIDAE

Bajacalifornia burragei (Norman):

147 (1/).

A single specimen was taken at 1325 m during a nocturnal haul in the Carmen Basin.

BATHYLAGIDAE

Bathylagus stilbius (Gilbert):

84 (1/); 88 (1/1); 63 (/1); 62 (1/); 111 (3/); 125 (7/); 126 (2/); 123 (1/3); 118 (6/); 124 (6/); 144 (7/5); 148 (12/1); 152 (1/1); 157 (2/); 19 (/1); 192 (/1).

Total catch - 64 fish at 16 stations.

Although captures were made along the entire length of the Gulf, Bathylagus stilbius was caught primarily over the deep water in its middle portion. Specimens were taken at depths from the mixed layer to 600 m. Diurnal migration is indicated by TE VEGA's collections (Figure 11) but the data are not numerous enough for any detailed analysis.

Bathylagus nigrigenys (Parr):

152 (1/).

A single adult specimen of this species was collected in a nighttime haul at 250 m in the Guaymas Basin.

STERNOPTYCHIDAE

Argyropelecus lychnus (Garman):

145 (1/); 161 (1/); 162 (1/); 166 (/1); 184 (1/).

Total catch - 5 fish at 5 stations.

Argyropelécus lychnus was collected in four nighttime hauls between 320 and 390 m. A single specimen came up from 375 m during the day. All were taken from deep water over the Gulf's southern basins.

GONOSTOMATIDAE

Cyclothone acclinidens (Garman):

82 (2); 135 (2/1); 139 (1/); 133 (1); 140 (3/); 111 (2/1);
112 (23/3); 57 (1); 116 (1); 123 (1/); 120 (1); 145 (17/7);
143 (1); 147 (31/21); 148 (1/); 35 (3/); 157 (3/); 158 (/1);
159 (1/8); 160 (25/16); 161 (4/); 162 (142/33); 163 (4/);
165 (/2); 166 (7/1); 168 (35/22); 172 (3); 170 (1); 19 (2/1);

21 (/4); 178 (1/); 179 (47/4); 180 (8/1); 192 (4/52); 186 (27/17); 184 (19/); 188 (1/); 189 (42/17).

Total catch - 679 fish at 38 stations.

The most abundant gonostomatid collected in the Gulf was Cyclothone acclinidens; it was the second most numerous midwater fish. Numbers captured increased toward the south with highest concentrations over the deep water of the Gulf's basins. No decrease in abundance was observed at the mouth of the Gulf (Figure 12).

Vertical range was wide, with individuals collected from the mixed layer down to depths of 2250 m. Diurnal migrations were not apparent although captures were more common near the surface at night (Figure 13). No association with the DSL was observed. The depths between 200 and 400 m yielded the greatest numbers of specimens.

Vinceguerria lucetia (Garman):

84 (2/); 88 (4/2); 67 (3/3); 102 (35/); 61 (5/); 135 (2/); 136 (3/7); 139 (23/); 133 (1); 132 (9/); 140 (3/); 131 (32/8); 114 (10/); 111 (12/1); 112 (/4); 57 (1); 56 (/37); 116 (1); 126 (76/); 127 (9/); 119 (1/12); 124 (/1); 145 (19/14); 147 (/1); 148 (1/); 39 (37/27); 35 (31/41); 152 (2/); 156 (2/1); 160 (1/6); 161 (12/46); 162 (1/); 163 (2/); 33 (49/); 165 (/1); 168 (/2); 19 (/2); 22 (11/); 21 (/1); 179 (/5); 193 (/4); 191 (/2); 190 (/3); 188 (/1).

Total catch - 623 fish at 44 stations.

• Vinceguerria lucetia was found to range the entire length of the Gulf. The center of its distribution, as

measured by TE VEGA's midwater sampling, was between 26° N and 25° N, with numbers collected decreasing toward the north and south (Figure 14). Horizontally, the population appeared to be concentrated in the deeper, central waters over basins and decreased toward the coasts until depths shallower than 200 m served to exclude the species entirely.

Vinceguerria lucetia occupied depths from 100 to 400 m during daylight hours with the greatest concentration between 300 and 400 m (Figure 15). At night, the depth range was from the surface to 250 m with the majority of the captures between the mixed layer and 100 m (Figure 16). Association with the DSL was strong.

Diplophos proximus (Parr):

145 (1/1); 162 (/2); 21 (/1); 192 (/1).

Total catch - 6 fish at 4 stations.

All captures of Diplophos proximus were made over the deepest water in the southern third of the Gulf. The single nocturnal capture was made at 15 m. Of the daylight captures, only one was made by the Tucker trawl and can thus be assigned with certainty to a specific depth (390 m). The three daytime meter net captures were made with the sampler fishing for an hour at a single depth; 390 m, 320 m, and 800 m respectively.

STOMIATIDAE

Stomias atriventer (Garman):

132 (1/); 125 (1/); 119 (1/); 148 (1/); 156 (1/); 165 (/1);

179 (1/); 189 (1/).

Total catch - 8 fish at 8 stations.

Eight specimens of Stomias atriventer were captured in the waters over the Guaymas, Carmen, Farallon and Pescadero Basins. One specimen was taken in deep water just south of Cabo San Lucas. All captures were made at night, at a variety of depths ranging from 60 to 625 m.

NEOSCOPELIDAE

Scopelengys tristis (Alcock):

192 (/2).

Two specimens were taken by the meter net in a two-hour haul during the day at 800 m off Cabo San Lucas.

MYCTOPHIDAE

Triphoturus mexicanus (Gilbert):

91 (1/3); 90 (4/4); 94 (2/); 83 (3/); 87 (/1); 88 (5/2); 86 (1); 74 (3/); 64 (33/35); 63 (3/8); 67 (135/31); 66 (4); 61 (111/); 59 (5); 137 (11/); 135 (65/23); 136 (146/110); 139 (146/); 133 (5); 132 (39/2); 140 (18/); 62 (1132/83); 130 (27); 131 (96/25); 114 (112/); 111 (122/); 112 (4/3); 113 (1/); 116 (9); 125 (75/4); 126 (145/3); 127 (26/); 122 (1/1); 119 (31/5); 123 (6/1); 120 (1); 118 (104/12); 144 (123/24); 145 (1542/70); 143 (2); 147 (1/8); 148 (176/9); 39 (86/13); 35 (109/93); 152 (13/11); 156 (85/12); 157 (36/15); 158 (/8); 159 (/4); 160 (119/42); 161 (169/31); 162 (281/34); 163 (4/); 33 (275/1); 165 (/9); 166 (4/13); 29 (4); 168 (2/6); 172 (1);

170 (4); 19 (/5); 22 (16/); 21 (/2); 178 (1/); 180 (2/);
186 (/2); 184 (21/); 189 (/1).

Total catch - 6477 fish at 68 stations.

The dominant midwater fish in TE VEGA's Gulf of California collections was the myctophid Triphoturus mexicanus. Its population density was greatest in the central Gulf with abundance decreasing toward the northern and southern extremes. The horizontal distribution extended to all regions of the Gulf that were sampled (Figure 17), where the water depth was greater than 300 m. North of the Sal Si Puedes Basin sill (28° 30'N), abundance decreased so significantly that another myctophid (Benthoosema panamense) became the dominant midwater fish. South of latitude 23° N, the decrease in relative abundance was less pronounced. Instead of being replaced by a single species, a number of other myctophids appeared as the T. mexicanus population dwindled numerically.

During daylight hours, Triphoturus mexicanus was captured over a depth range of from 25 to 1200 m. Individuals were concentrated in the 300 to 400 m range (Figure 18). At night the bulk of the population was found between the mixed layer and 200 m (Figure 19). Although there is clear evidence of a diurnal migration of some 200 to 300 m, a relatively large number, 7% of the sampled population, were found at the 200 to 400 m depth of heavy daytime concentration even at night.

Observations of Triphoturus mexicanus suggest that the

standard length of the individuals increased with the depth of capture. Catches in the northern Gulf yielded very few of the large individuals (6-7 cm standard length) that were abundant in the central and southern Gulf.

The diel migration appeared to be directly correlated with the vertical movements of the DSL. Day or night, when the sampler was at the depth of the DSL, catches of Triphoturus mexicanus were noticeably greater than similar hauls which did not sample in the DSL. The average catch of T. mexicanus in the 16 daylight hauls which hit the DSL was 223 fish per haul (range, 0-1542), average catch in the 17 daytime hauls when the sampler was above or below the DSL was 25 fish (range, 0-123).

Diogenichthys laternatus (Garman):

67 (6/6); 102 (5/); 61 (9/); 59 (2); 135 (1/1); 136 (4/6);
 139 (13/); 133 (1); 140 (4/); 62 (7/); 130 (1); 131 (10/8);
 114 (17/); 111 (3/); 57 (1); 113 (3/); 56 (8/9); 116 (1);
 126 (33/2); 127 (3/2); 122 (/1); 119 (/1); 123 (/1); 121
 (/1); 118 (1/1); 144 (/2); 145 (36/6); 143 (1); 147 (1/3);
 148 (1/); 39 (16/10); 35 (4/5); 157 (/1); 158 (/1); 159 (/1);
 160 (24/6); 162 (29/3); 163 (/1); 33 (8/2); 165 (1/); 168
 (/2); 170 (2); 19 (7/11); 22 (2/); 21 (/6); 178 (5/5); 179
 (/2); 180 (/1); 192 (/6); 191 (/1); 190 (/3); 184 (6/); 188
 (1/); 189 (/2).

Total catch - 396 fish at 54 stations.

The second most numerous myctophid collected was Diogenichthys laternatus. The center of its abundance was

in the central portion of the Gulf, with the numbers decreasing to the north and south (Figure 20). None were captured north of the Guaymas Basin's northern slope, and the proportional decrease in numbers toward the south was far less abrupt than in the case of Triphoturus mexicanus. Unlike T. mexicanus, individuals were often collected at stations where the water depth was less than 300 m.

Vertical distribution was sharply limited to a depth range of 300 to 400 m during hours of daylight (Figure 21). Darkness found them between the surface and 200 m with the large majority concentrated above 100 m and only a very few at depths greater than 400 m (Figure 22). As was the case with Triphoturus mexicanus, catches of Diogenichthys laternatus seem to be correlated with the movements of the DSL. When the Tucker trawl sampled the depths occupied by the daytime DSL (12 hauls), the average number of D. laternatus per haul was 8.9 (range, 0-36); the average for trawls away from the DSL (16 hauls), was 2.5 (range, 0-24).

Observations of the daytime samples of Diogenichthys laternatus indicated a gradation of size according to depth. Post-larval, pre-adult fish were found well above the adult population range, at 200-300 m. Larval forms were present between 200 m and the surface.

Benthoosema panamense (Tåning):

91 (5/1); 90 (1/4); 94 (9/); 95 (27/); 83 (7/); 84 (14/);
87 (2/); 88 (2/8); 74 (6/); 63 (1); 102 (4/); 61 (10/1);

136 (1/2); 139 (7/); 140 (4/); 62 (1/); 131 (2/1); 114 (1/);
111 (1/); 113 (13/1); 56 (12/2); 126 (1/); 127 (7/); 122
(31/6); 123 (1/1); 145 (9/2); 39 (10/); 35 (1/).

Total catch - 220 fish at 28 stations.

North of the Sal Si Puedes Basin sill, the dominant midwater fish was Benthoosema panamense. At TE VEGA's 10 stations in the basin's waters, B. panamense outnumbered the only other myctophid collected (Triphoturus mexicanus), 87 individuals to 29. South of the basin, B. panamense was captured primarily in shallow hauls or in shallow waters along the Gulf's coasts. Frequency of capture decreased toward the south and none were taken south of 25° N.

Vertical distribution varied with location. Over the Sal Si Puedes Basin, Benthoosema panamense was captured from the surface to 300 m in both day and night hauls. In the rest of the Gulf, nighttime catches were made between the surface and 100 m. Specimens taken in daytime hauls ranged from depths of 185 to 595 m (Figure 23).

Specimens from the Gulf of California differ in certain meristic and morphometric characters from material taken in the Gulf of Panama as originally described by Tåning (1932). They have larger eyes, a smaller number of lateral line pores, an additional VO photophore, and differ in the relative positions of the dorsal and anal fins. The significance of these differences is treated in the general discussion.

Diaphus pacificus (Parr):

102 (1/); 131 (/1); 126 (4/); 145 (4/1); 39 (3/); 160 (2/);
162 (1/); 33 (33/); 178 (6/); 186 (/1); 188 (1/).

Total catch - 58 fish at 11 stations.

Diaphus pacificus was collected sparsely in the central and southern Gulf. The northernmost occurrence was at the northeastern slope of the Guaymas Basin. Trawls in deep water yielded more individuals than those along the coasts. Vertical distribution appeared to be keyed to the movements of the DSL. All nighttime captures were between the surface and 200 m. Daytime captures were between 300 and 400 m.

Lampanyctus idostigma (Parr):

160 (/3); 178 (16/1); 186 (/1); 188 (1/); 189 (1/1).

Total catch - 24 fish at 5 stations.

All specimens of Lampanyctus idostigma were collected over relatively deep water in the southern portion of the Gulf. The single daytime capture of 3 specimens was made by the meter net at 360 m. Nocturnal collections ranged from 75 to 445 m.

Hygophum atratum (Garman):

144 (5/); 112 (/1); 160 (/1).

Total catch - 7 fish at 3 stations.

Hygophum atratum was collected in the southern Gulf at only three stations. Both of the daytime captures were made at relatively great depths (500-850 m), the single nighttime

capture was made near the surface.

Gonichthys tenuiculus (Garman):

178 (1/).

A single specimen, representing the first recorded capture of this species in the Gulf of California, was taken at night between 160 and 175 m in the southern portion.

SCOPELARCHIDAE

Scopelarchus nicholsi (Parr):

166 (1/); 180 (1/); 189 (1/).

Three specimens, each collected at night by the Tucker trawl, were captured at depths ranging from 320 to 445 m. All were taken in the southern Gulf.

NEMICHTHYIDAE

Nemichthys scolopaceus (Richardson):

125 (/1); 157 (/1); 159 (1/); 166 (/1); 189 (1/).

Total catch - 5 fish at 5 stations.

Four specimens of Nemichthys scolopaceus were collected over deep water in the central and southern Gulf. A fifth was captured just south of Cabo San Lucas. All captures were made at night. The two specimens taken in the Tucker trawl were caught at 445 m and 2265 m. Meter-net collections were made with the net fishing for an hour at 265 m, 315 m, and 320 m respectively.

The specimen from station 125 measured 108 cm from beak to tip of tail; I believe this to be the largest

specimen on record.

Borodinula bowersi (Garman):

152 (/1).

A single specimen was collected in a nighttime meter-net haul of one hour at 250 m over the Farallon Basin.

BREGMACEROTIDAE

Bregmaceros bathymaster (Jordan and Bollman):

125 (1/); 144 (/1).

One specimen was taken from 560 m by the meter net in a daytime haul over the Carmen Basin. A nighttime Tucker-trawl sample yielded a single specimen from 265 m in the Guaymas Basin.

MELAMPHAIDAE

Scopelogadus mizolepis bispinosus (Gilbert):

166 (1/); 19 (/1).

Two specimens were taken, a nighttime Tucker-trawl capture from 320 m in the Farallon Basin and a daytime meter-net specimen from 410 m in the Pescadero Basin.

Melamphaes macrocephalus (Parr):

157 (1/); 179 (1/).

Two specimens were taken at night by the Tucker trawl; one from the Farralon Basin at 315 m and one from the Pescadero Basin at 625 m.

Melamphaes acanthomus (Ebeling):

192 (/1).

A single specimen was taken by the meter net fishing during the day for two hours at 800 m, off Cabo San Lucas.

Melamphaes spinifer (Ebeling):

180 (1/).

One specimen was collected by the Tucker trawl at 395 m during a nighttime trawl over the Pescadero Basin.

Melamphaes laeviceps (Ebeling):

189 (1/).

A single specimen was collected by the Tucker trawl in a nighttime trawl to 445 m off Cabo San Lucas.

Scopeloberyx robustus (Gunther):

147 (1/); 168 (/1).

Two specimens were captured. One, the northernmost capture of a melamphaid, by the Tucker trawl was taken at night from 1350 m in the Carmen Basin; another, by the meter net during a daytime haul to 1000 m in the Pescadero Basin.

Table 3. Midwater fishes collected by the R/V TE VEGA
during Stanford Oceanographic Expedition 16.

<p>ALEPOCEPHALIDAE:</p> <p><u>Bajacalifornia burragei</u> (Norman)</p> <p>BATHYLAGIDAE:</p> <p><u>Bathylagus stilbius</u> (Gilbert)</p> <p><u>Bathylagus nigrigenys</u> (Parr)</p> <p>STERNOPTYCHIDAE:</p> <p><u>Argyropelecus lychnus</u> (Garman)</p> <p>GONOSTOMIDAE:</p> <p><u>Cyclothone acclinidens</u> (Garman)</p> <p><u>Vinceguerra lucetia</u> (Garman)</p> <p><u>Diplophos proximus</u> (Parr)</p> <p>STOMIATIDAE:</p> <p><u>Stomias atriventer</u> (Garman)</p> <p>NEOSCOPELIDAE:</p> <p><u>Scopelogadus tristis</u> (Alcock)</p> <p>MYCTOPHIDAE:</p> <p><u>Triphoturus mexicanus</u> (Gilbert)</p> <p><u>Diogenichthys laternatus</u> (Garman)</p> <p><u>Bentosema panamense</u> (Tåning)</p>	<p><u>Diaphus pacificus</u> (Parr)</p> <p><u>Lampanyctus idostigma</u> (Parr)</p> <p><u>Hygophum atratum</u> (Garman)</p> <p><u>Gonichthys tenuiculus</u> (Garman)</p> <p>SCOPELARCHIDAE:</p> <p><u>Scopelarchus nicholsi</u> (Parr)</p> <p>NEMICHTHYIDAE:</p> <p><u>Nemichthys scolopaceus</u> (Richardson)</p> <p><u>Borodinula bowersi</u> (Garman)</p> <p>BREGMACEROTIDAE:</p> <p><u>Bregmaceros bathymaster</u> (Jordan & Bollman)</p> <p>MELAMPHAIDAE:</p> <p><u>Scopelogadus mizolepis bispinosus</u> (Gilbert)</p> <p><u>Melamphaes macrocephalus</u> (Parr)</p> <p><u>Melamphaes acanthomus</u> (Ebeling)</p> <p><u>Melamphaes spinifer</u> (Ebeling)</p> <p><u>Melamphaes laeviceps</u> (Ebeling)</p> <p><u>Scopeloberyx robustus</u> (Günther)</p>
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Figure 11. Day-night distribution of Bathylagus
stilbius in the Gulf of California.

Figure 12. Horizontal distribution of Cyclothone acclinidens
in the Gulf of California.

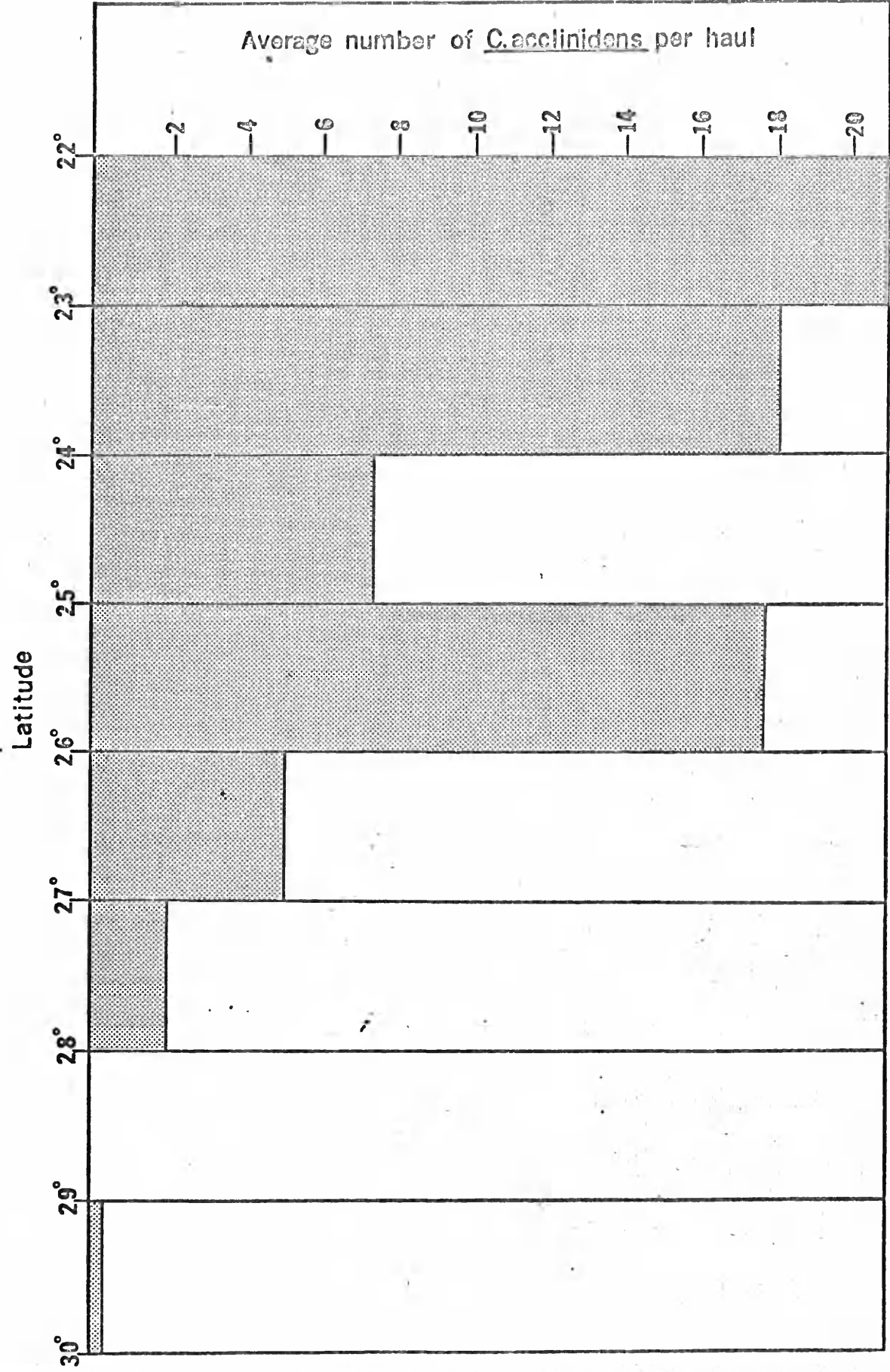


Figure 13. Day-night vertical distribution of Cyclothone
acclinidens in the Gulf of California.

Numbers of C. acclinidens

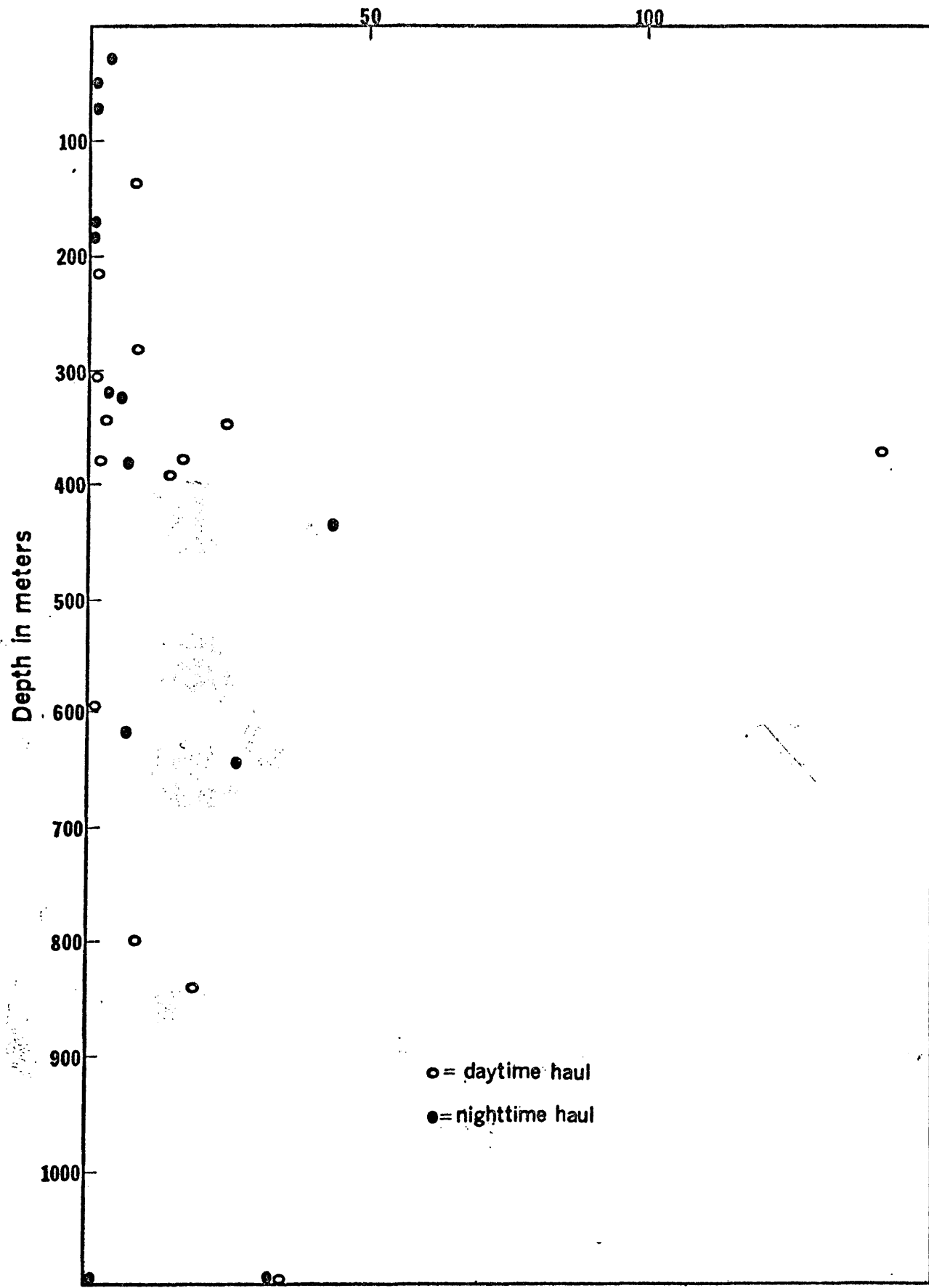


Figure 14. Horizontal distribution of Vinceguerria
lucetia in the Gulf of California.

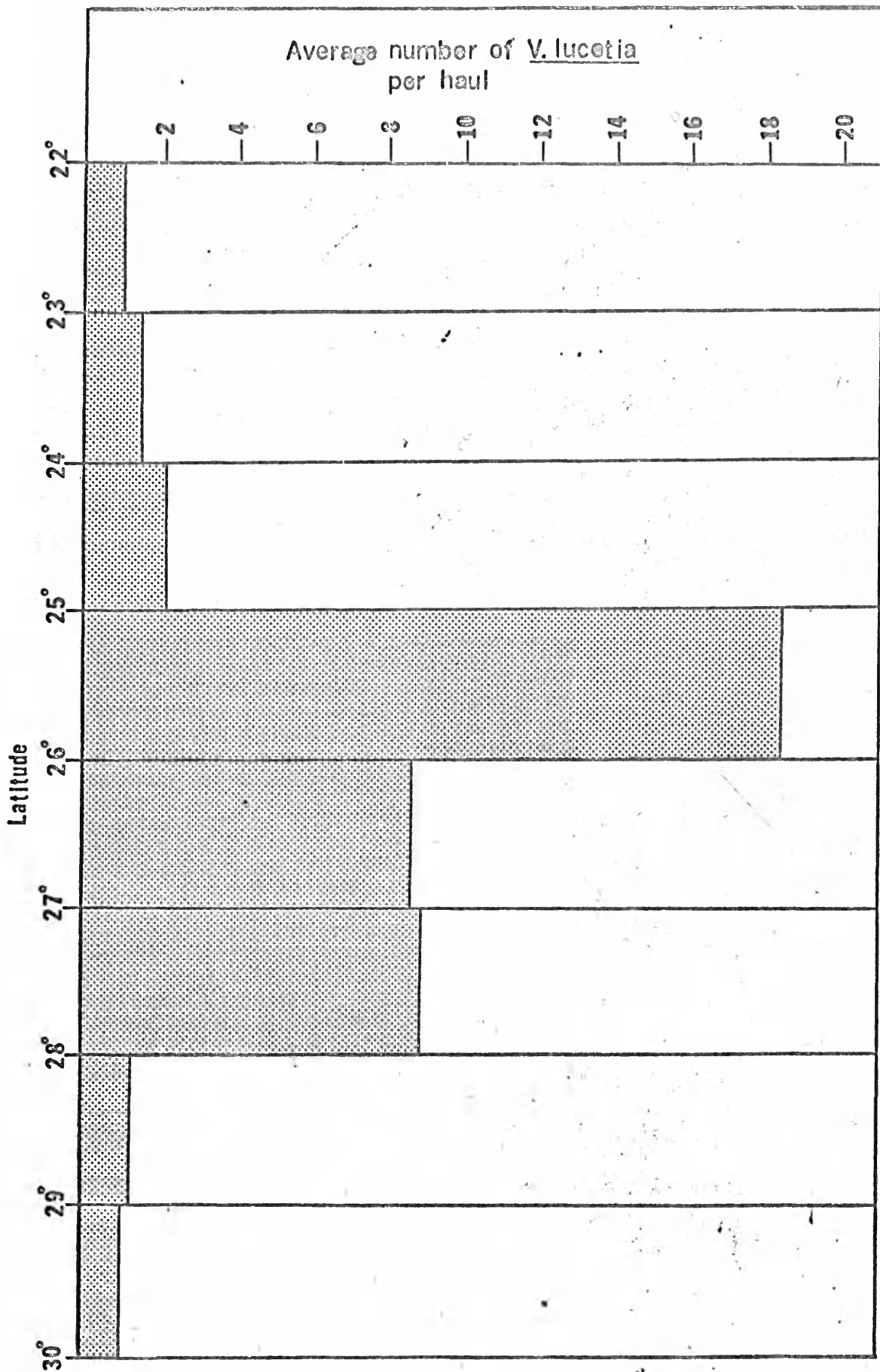


Figure 15. Vertical distribution of Vinceguerria
lucetia during daytime hauls.

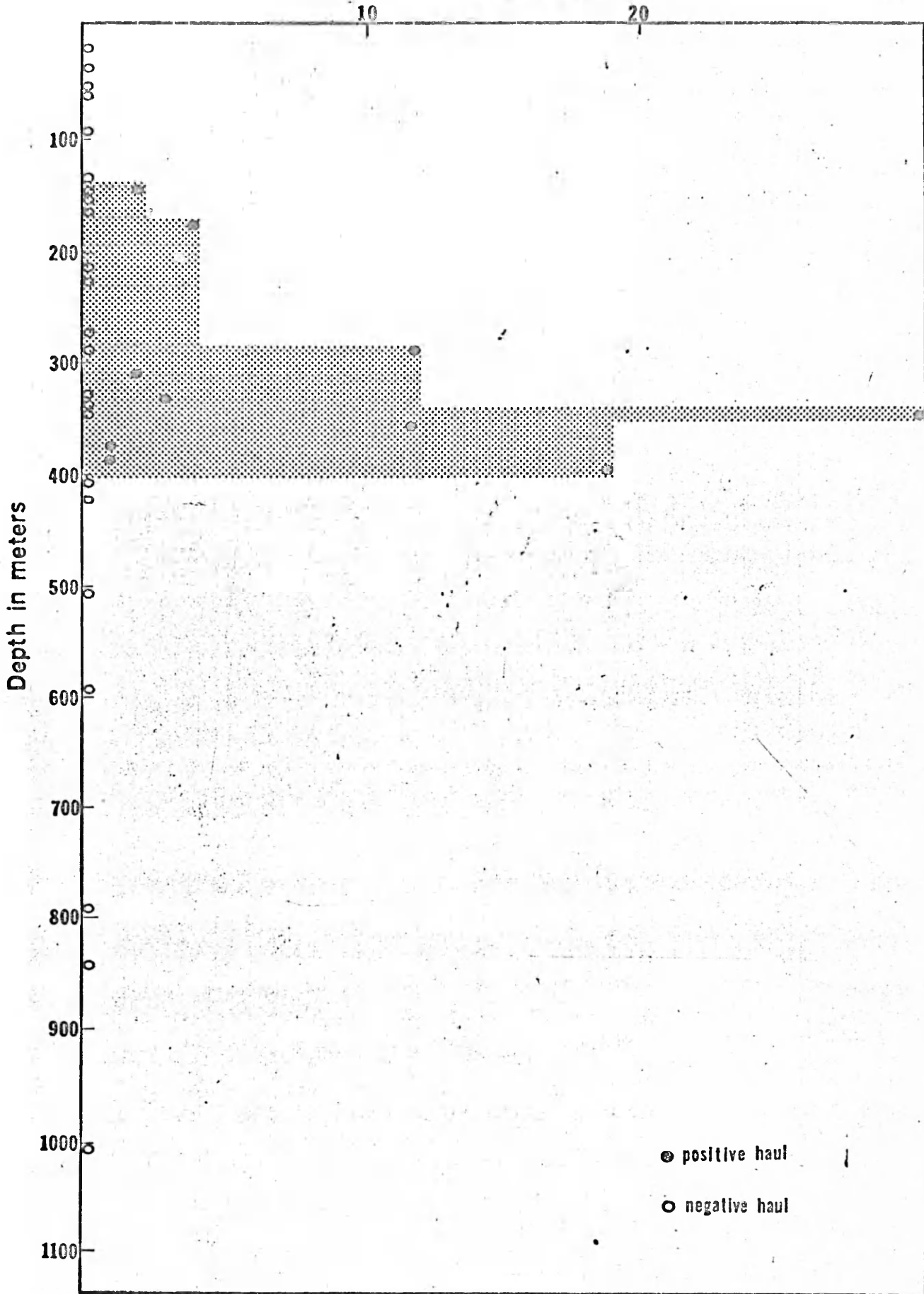


Figure 16. Vertical distribution of Vinceguerria
lucetia during nighttime hauls.

Figure 17. Horizontal distribution of Triphoturus
mexicanus in the Gulf of California.

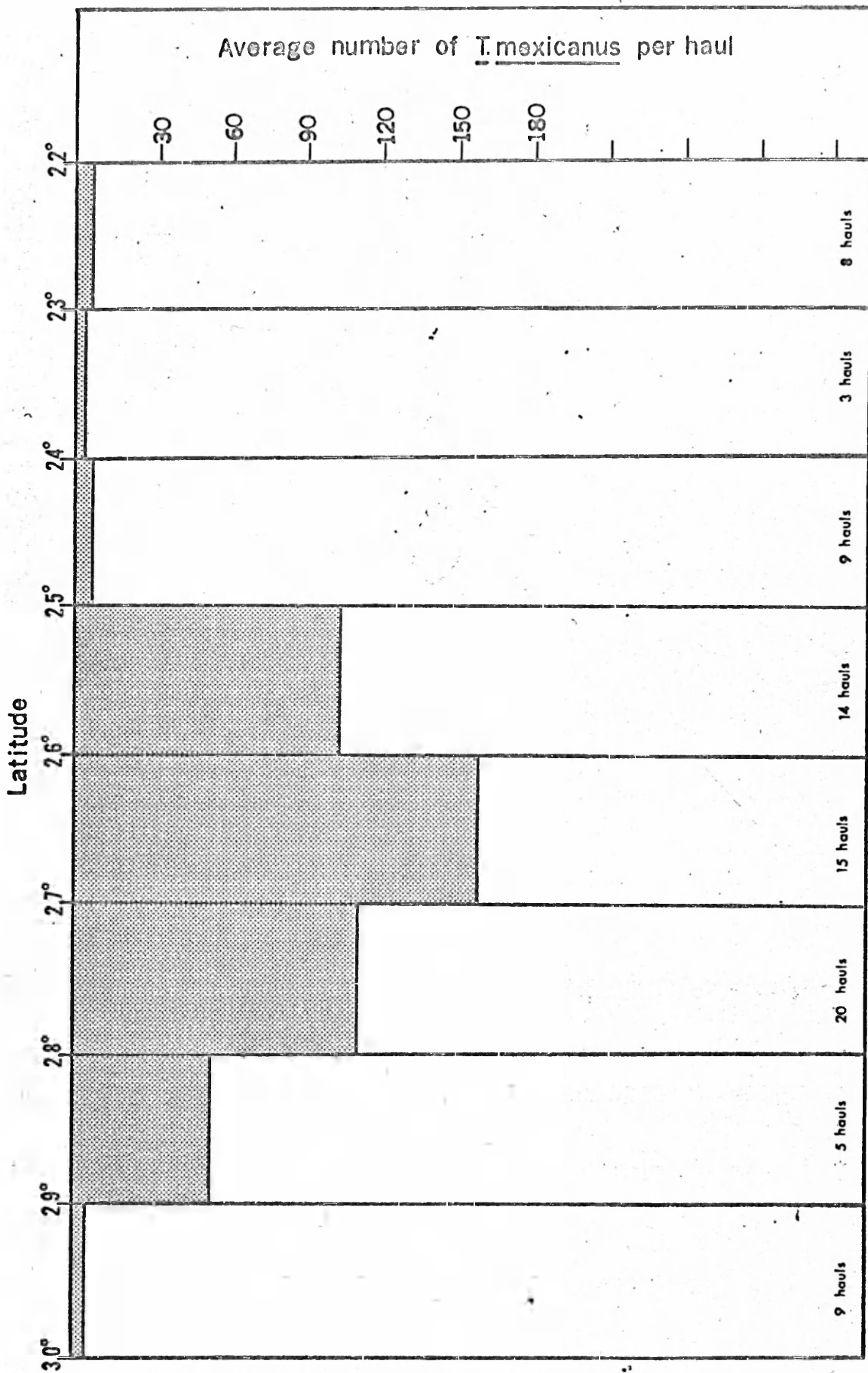


Figure 18. Vertical distribution of Triphoturus mexicanus in Gulf of California during daytime hauls.

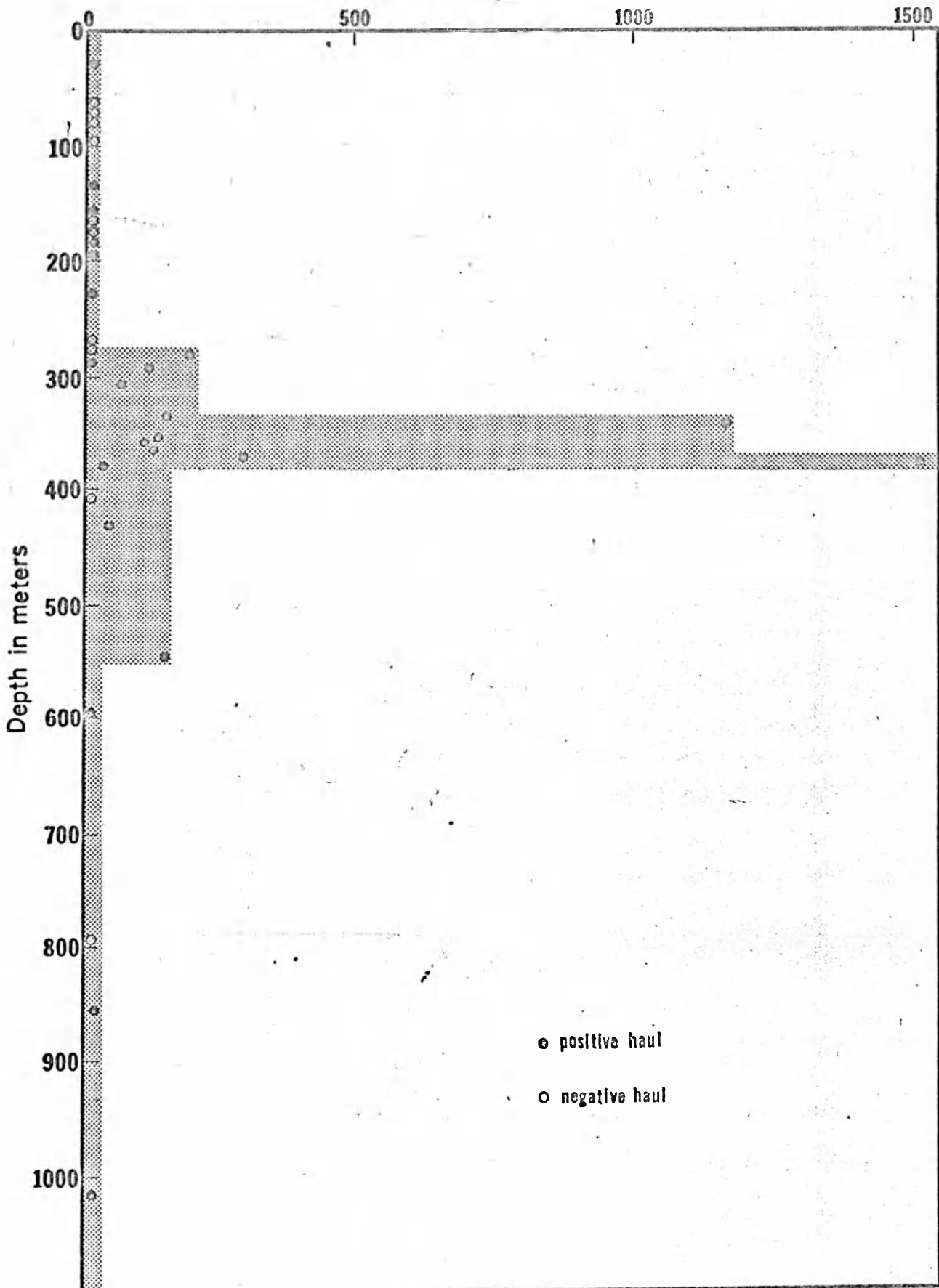


Figure 19. Vertical distribution of Triphoturus mexicanus
in the Gulf of California during nighttime hauls.

Numbers of *T. mexicanus*

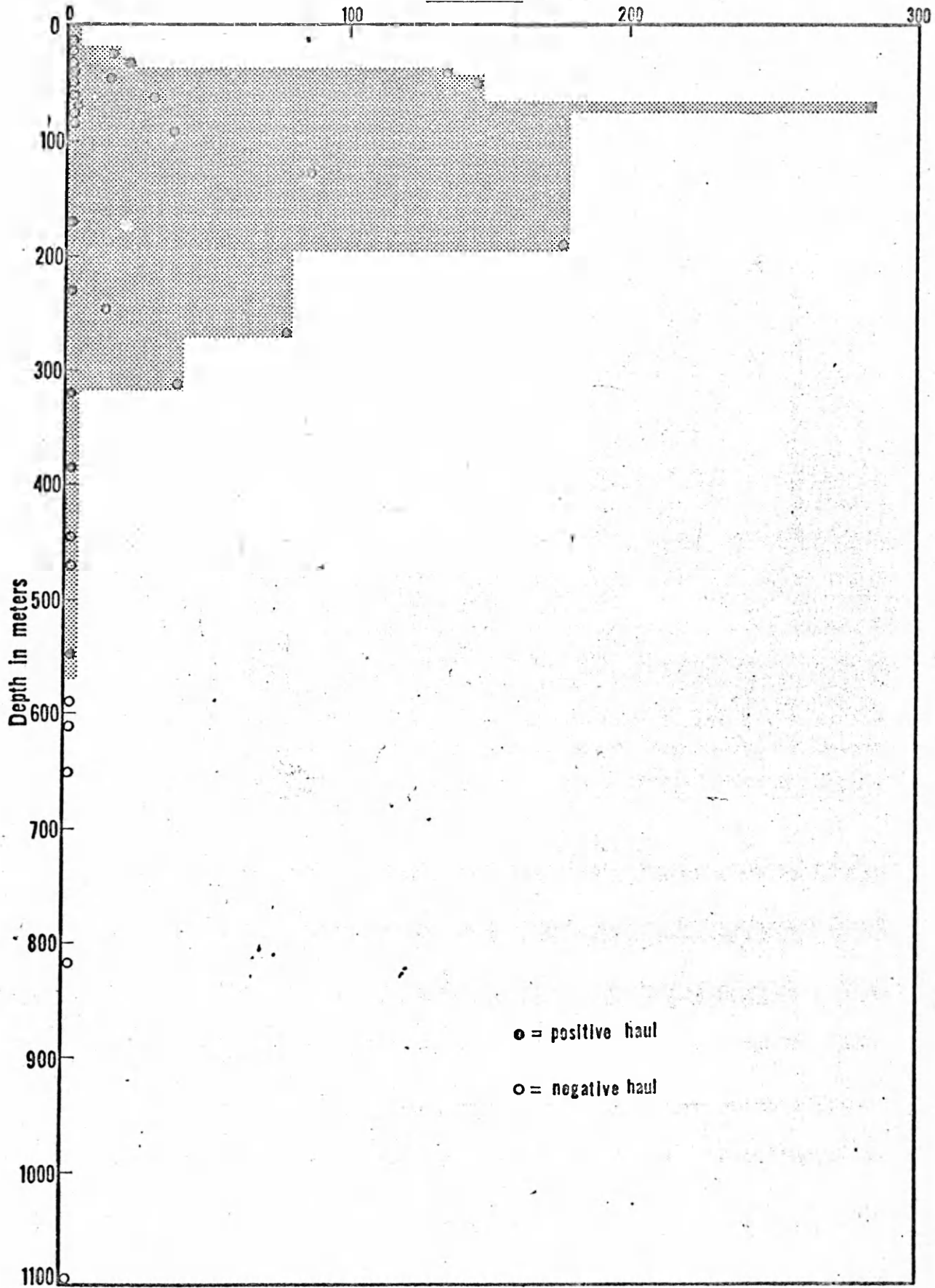


Figure 20. Horizontal distribution of Diogenichthys
laternatus in the Gulf of California.

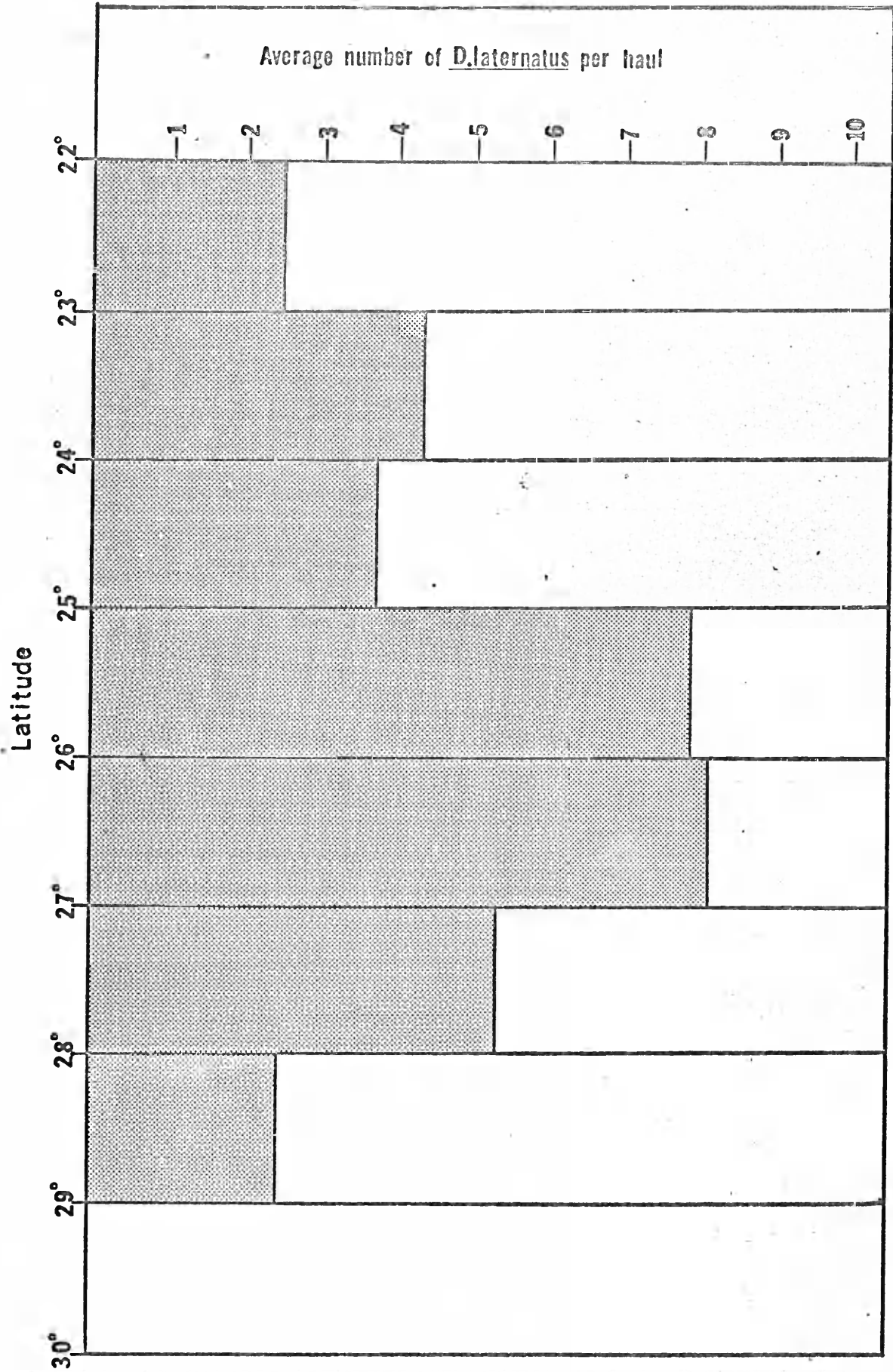


Figure 21. Vertical distribution of Diogenichthys laternatus
in the Gulf of California during daytime hauls.

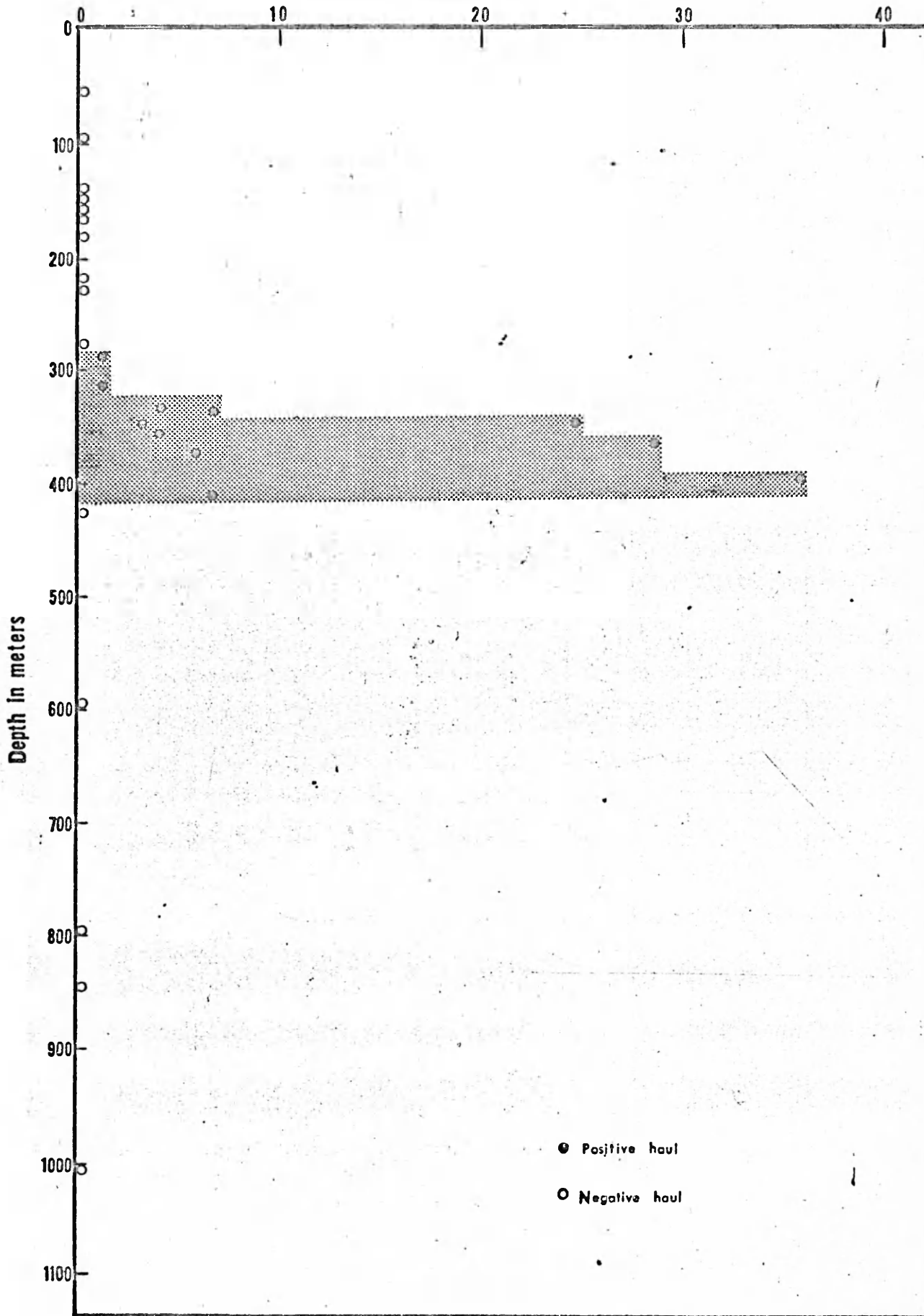


Figure 22. Vertical distribution of Diogenichthys laternatus
in the Gulf of California during nighttime hauls.

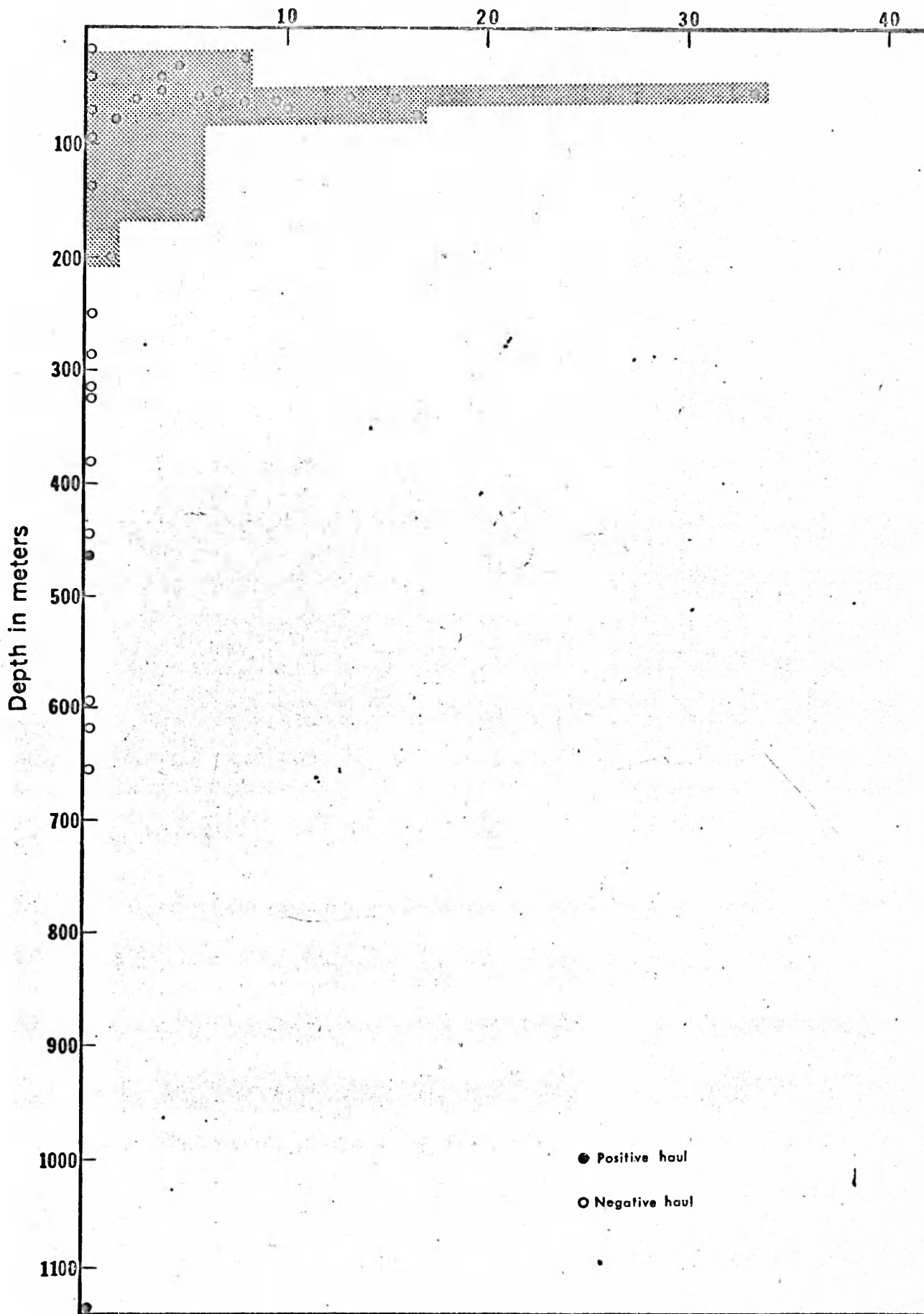


Figure 23. Day-night vertical distribution of Benthoosema
panamense to the north of and to the south of
the Sal Si Puedes Basin sill.

Table 4. Comparative list of the meristic and morphometric characters of specimens of Benthoosema panamense from the northern Gulf of California and the Gulf of Panama (Tåning, 1932).

Character	Specimens from the Gulf of Panama	Specimens from the Gulf of California
number of times eye diameter is contained in head length	much more than three	no more than three
origin of anal fin	immediately below dorsal-base end	behind dorsal-base end
anal fin rays	20-22	21-22
lateral line pores	about 33	29
gill rakers on first arch	8-10 (1) 10-12 + 6-7	8-10 (1) 10-12 + 6-7
VO photophores	4	5

DISCUSSION - Distributional Analysis

The specific composition of the trawl catches varied according to the location of each station, probably as a function of a variety of physical, chemical and biological factors. The fishes appear to fall into three distinct distributional groups, based on their habitat preferences and the range of their vertical migrations. I term these: epi-mesopelagic migrators, meso-bathypelagic migrators and epi-bathypelagic migrators. These categories relate to a definition of the pelagic zones of the central and southern Gulf as shown in Figure 24. The zonation is based on Bruun's (1957) zonal classification (Figure 2).

In the central and southern portions of the Gulf, the epipelagic zone extends from below the mixed layer (surface to 40 m) to approximately 200 m depending on water clarity. The epipelagic merges into the mesopelagic at the upper limits of the Equatorial Pacific Subsurface Water Mass. The mesopelagic extends from this level to the 10° C isotherm, between 300 and 400 m, then merges into the bathypelagic zone in the region of the transition from Subtropical Subsurface water to Equatorial Intermediate water at about 400 m. The bathypelagic reaches down to the 4° isotherm at 1000-1200 m.

In the northern Gulf, (north of the Sal Si Puedes Basin sill) the zonation of pelagic waters is much different. The epipelagic zone is in a constant state of flux due to the extremes of tidal current flow. The mesopelagic zone is

extremely wide, in a vertical plane, as the 10° isotherm is depressed to a depth of from 600-900 m. Consequently, the bathypelagic zone is extremely narrow, vertically, and at times may not exist at all.

EPI-MESOPELAGIC MIGRATORS

The fishes comprising this group are by far the most numerous in the Gulf, in both numbers of species and numbers of individuals. The movements of the group appear to be correlated with the migrations of the DSL, where they feed. During the day they inhabit the mesopelagic zone above the region of the 10° isotherm (200-400 m). At night, they migrate upward to the epipelagic zone. Most are found below the mixed layer although some rise to the surface.

Their habitat preferences are generally for slope or basin waters and their numbers appear to increase as the water below them increases in depth. In the Gulf of California this group is made up of the myctophids and the gonastomatid Vinceguerria lucetia.

Triphoturus mexicanus

Collection data on Triphoturus mexicanus is extensive due to this species' great abundance and wide distribution. It is undoubtedly the most abundant midwater fish in the Gulf of California.

The horizontal range, as indicated by TE VEGA's collections, extends throughout the entire Gulf wherever the water depth is greater than 300 m. The center of distribution

appears to be the waters of the Carmen Basin. The presence of the species T. mexicanus is significantly reduced in the Sal Si Puedes Basin, probably due to the changes in hydrographic conditions. The water in this basin is warmer and more saline (Figure 10), conditions which are apparently less suitable for the species.

The center of distribution may move seasonally as much as several degrees of latitude to the north and south. As determined from TE VEGA's data, the center is between 26° and 27° N. The center indicated by similarly treated data from Scripps Institution of Oceanography and the California Department of Fish and Game, is between 23° and 24° N. (in the Pescadero Basin). An analysis of the three collections with reference to general surface current patterns, show the probable reason for this variation. The TE VEGA collections coincided with the autumn inflow of surface water, while the other two collections were made during the winter and spring outflow.

The vertical distribution of T. mexicanus is relatively broad. The daytime concentration is in the 100 m above the 10° isotherm. At night, the fish are concentrated between the mixed layer and 200 m. This suggested a correlation with the vertical migrations of the DSL. Lavenberg and Fitch (1966) report that their collections of T. mexicanus were always associated with the natant decapod Sergestes, a recognized DSL component. Beebe and Vander Pyl (1944) noted strong evidence of schooling in their eastern

Pacific samples of the species. Paxton (1967) also stated that their capture indicates a non-random aggregation which approaches schooling. Both of these studies describe a depth of concentration significantly deeper than that found in the Gulf. Two possible explanations exist for this difference. Most likely, the Gulf's mesopelagic zone does not extend as deep as that in the open ocean (the 10° isotherm in the Gulf is generally found 100 m closer to the surface than in the open ocean) and the fish are probably following a DSL which does not range as widely. Sampling error may also have played a role in this difference. The Tucker trawl allows discrete depth sampling whereas the trawls used in the other studies did not close and the captures could have passed through dense schools of T. mexicanus while being retrieved, making the concentrations appear deeper than they were. Another factor which contributes to sampling error is the use of wire-angle measurements to determine trawling depths. Depth estimates based on wire-angle measurements aboard TE VEGA were often erroneous when compared with the more accurate data from the pressure-depth recorder attached to the trawl.

The 7% of the population captured at 300-400 m during the nighttime migration may indicate that the migratory rhythm is not endogenous. Myctophids are generally considered to be opportunistic feeders (which feed wherever and whenever food is present). This also serves to negate the idea of an endogenous rhythm. Individuals from the

remnant group were examined and found to be large adults of both sexes. No gravid females were present and stomachs were generally empty. It may be that adults of the species remain at depth for breeding.

The Gulf of California, between latitudes 23° N and 28° N appears to be an ideal environment for T. mexicanus. It reaches a dominant position in the midwater community that is not matched anywhere else in its eastern Pacific range. Apparently there is a general migration of northern individuals southward (to the central part of the Gulf) with advancing age to regions where water is not restricted to small basins, but is readily available for daytime retreat over wide areas. At the mouth of the Gulf, a variety of other myctophids increase in abundance to the point where the population of T. mexicanus is only one of a number of important species present. Yet none of these potential competitors has penetrated the Gulf and proliferated there as has T. mexicanus.

Diogenichthys laternatus

The horizontal distribution of D. laternatus was generally similar to that of T. mexicanus. The center was in the Farallon and Carmen Basins (25° N to 27° N), with abundance decreasing toward the mouth of the Gulf. To the north, distribution stopped abruptly at the northern slope of the Guaymas Basin. A possible explanation of this distribution follows.

Except for the San Pedro Martir Basin (which has

never been sampled) the only avenue of deep water to the north runs along the western coast of the Gulf (see Figure 6). This is along the path of the outward flowing subsurface current. Below the current, at 200-250 m, lies the sill of the Sal Si Puedes Basin. Assuming that the effective depth of the subsurface current reaches to 200 m, a 50 m "slot" can be described through which fish movement would be uninhibited either by the current or the sill. This slot would be sufficient space for the passage of a species whose vertical range included the depth of the slot. Such a range is exhibited T. mexicanus (see Figures 18 and 19). The 200-250 m depth is constantly occupied by a significant portion of the population. The slot is probably the means by which T. mexicanus has penetrated into the basin.

In the past, Diogenichthys laternatus has been described as a species with no preferred depths. Beebe and Vander Pyl (1944) described it as being peculiar in their hauls in that there was no sharp demarcation of vertical limits, no special emphasis on certain depths. They found that on the whole, however, evidence for schooling was positive, because the fishes were seldom captured singly. Paxton (1967) mentions an emphasis on certain depths in the San Pedro Basin off the California coast.

TE VEGA's finite depth sampling shows a strict adherence to definite diurnal depth limits in the Gulf. Figures 20 and 21 show that the population of D. laternatus, at night, is limited to a range between 20 and 200 m. The

daytime range is restricted to depths between 290 and 410 m. This leaves the 50 m slot range unoccupied except during times of vertical migration. D. laternatus is such a strongly schooling species that it seems improbable for a significant portion of the population to penetrate into the basin during vertical migration. Individuals are rigidly following the movements of the mass and not those of a few fish which might stray.

Thus, the combined effects of sill depth, currents and a strict adherence to certain depths may prohibit the passage of this species into the Sal Si Puedes and Delfin Basins (Figure 25).

Another factor affecting the northern limits of this species may be the different character of the environment north of 28° N. The large Gulf population of T. mexicanus is only weakly represented to the north; D. laternatus has similar deep-water affinities and its smaller population would find an extension into the northern basins even more difficult. No other expedition has collected D. laternatus north of the Guaymas Basin.

Collection records from Scripps Institution of Oceanography and the California Department of Fish and Game cruises indicate a seasonal shift of the population center like that observed in T. mexicanus. It is assumed that the surface current pattern is responsible. With the subsurface current pattern that exists in the Gulf, D. laternatus has probably been swept into the San Pedro Martir Basin and

further collection will find it there.

The vertical migration of D. laternatus appears to be strongly correlated with the movements of the DSL. Representative subsamples showed that those few individuals collected away from the DSL had empty stomachs while those associated with the layer had been feeding.

Benthoosema panamense

The dominant midwater fish found in the Sal Si Puedes and Delfin Basins was Benthoosema panamense. Its range in TE VEGA's collections extended south to 25° 30' N. Its dominance to the north indicates a preference for the warm, high salinity waters found in the northern Gulf. North of the Sal Si Puedes sill, the vertical range is such that B. panamense cannot be considered an epi-mesopelagic migrator. The turbulent currents north of the sill probably overpower any efforts by individuals of the species to perform a patterned migration. South of the sill however, the migratory pattern of B. panamense is similar to that displayed by other members of the family. Captures to the south were most often made in shallower levels at night.

The California Department of Fish and Game, and Scripps Institution of Oceanography collections suggest a greater abundance further south than is indicated by TE VEGA's collections. This is most likely due to circumstances similar to those which cause other epi-mesopelagic migrators to move to the south at different seasons.

The meristic differences noted above may be an

indication of reproductive isolation. The genetic link between the "colonizing" population in the northern Gulf and the "parent" population to the south is probably weak. The semi-isolated population in the Delfin and Sal Si Puedes Basins is the northernmost collection of the species on record. The Gulf population may be undergoing an evolutionary change and may be presently at the subspecific level (Figure 26).

Diaphus pacificus

The last myctophid collected in sufficient numbers to be described separately as an epi-mesopelagic migrator is D. pacificus. The Gulf is the northernmost extent of its range and the species was first reported from this body of water by Lavenberg and Fitch (1966). TE VEGA's collections place it even farther north in the Gulf than the earlier record, extending the known limit of distribution about 95 miles from 26° 16.3' N to 27° 50.5' N. The Gulf of California population appears to be relatively weak; 58 individuals were collected by TE VEGA and 37 were reported by Lavenberg and Fitch.

The population appears to be centered over deep water in the central Gulf. Vertical migration is indicated with a nighttime range from 50 to 200 m and daytime limits between 300 and 400 m.

Other myctophids which probably belong in the group termed epi-mesopelagic are Lampanyctus idostigma, Hygophum atratum, and Gonichthys teniculus. In the southern Gulf

these species appear to occupy some of the environment vacated by the diminishing population of T. mexicanus. Lavenberg and Fitch (1966) also reported Hygophum reinhardti, Lampanyctus parvicauda, Lepidophanes pyrsobilus and Myctophum aurolaternatum aurolaternatum in small numbers from the southern Gulf.

Vinceguerria lucetia

The gonostomatid Vinceguerria lucetia has a horizontal range in the Gulf from the northern basins to the mouth. The Gulf population appeared to be centered over the Farallon Basin and its density decreased toward the north and south.

Ahlstrom and Counts (1958) reported an abundant population of the species distributed from 20° N to 14° S. The concentration was less dense in the eastern Pacific from 20° N to 35° N although the species is still present. They further commented that Cabo San Lucas is a particularly rich area.

Vertical migration ranged from nighttime depths of 20-250 m to daytime levels of 300-400 m in the Gulf.

Argyropelecus lychnus is collected abundantly outside the Gulf from the mesopelagic zone. Very few however, have been taken in the Gulf. Those collected, were at depths between 300 and 400 m. Conditions within the Gulf must not be favorable for a large population. The position of a limiting factor such as the oxygen minimum layer may be such that required conditions are found at a depth where only a

few individuals can persist.

In summary, the populations of epi-mesopelagic migrators inhabiting the Gulf of California exhibit similar ranges of depth preferences. None penetrate significantly below the 10° isotherm into the bathypelagic zone. All of them concentrate in the 100 m above the isotherm during daylight hours. At night they rise, following the zooplankton layers to the surface. There is strong evidence of separate stratification at subsurface levels during the hours of darkness. Nonetheless, all are contained in the epipelagic zone.

The Gulf of California is a northern extension of the tropical zone (Figure 27), and as such it provides a more suitable environment for southern than for northern species. All of the abundant epi-mesopelagic forms in the Gulf stem from groups with tropical affinities. The few representatives from western groups are not prominent in the Gulf and do not penetrate beyond the Gulf's midsection.

The line of fronts between Cabo San Lucas and Cabo Corrientes have been described as the southern limit of characteristic Gulf water. The changing character of the water across this transitional area is probably matched by a change in the character of the resident fishes. The Gulf's epi-mesopelagic migrators will probably not be found in the same proportions to the south of this line. TE VEGA's collections showed that the relative numbers of species which characterize this group diminish in the transition

area north of the line (at the mouth of the Gulf) and further sampling should reveal a different population to the south.

MESO-BATHYPELAGIC MIGRATORS

The fishes termed meso-bathypelagic migrators comprise a smaller group than the epi-mesopelagic migrators in the Gulf of California. These fishes feed irregularly in the lower levels of the DSL. Their daytime living space is below the 10° isotherm in the bathypelagic zone. At night they migrate upward and are found in the mesopelagic zone. Their habitat affinities are for deep water; the fishes are found only over basins and not in slope or in shelf regions. The Gulf of California fishes which have been assigned to this designation are the melamphids and the nemichthyids.

The migrations performed by this group are not of the same character as those of the previous group. They are not correlated with the movements of the DSL and probably undergo the reverse of the upper layer diel rhythm in some instances. At least some members of the group may move upward during daylight hours, to feed on the forms driven downward by increasing light. No clear picture of their vertical movements is apparent, but they do inhabit two of the described pelagic zones, the mesopelagic and the bathypelagic. Hence the justification for their inclusion in an outline of this type. It may be that the proper name for this group should not include the term "migrators" and

that they are more fittingly "meso-bathypelagic fishes."

The vertical movements of this group may be further clarified by identifying the lower range as being within the Equatorial Intermediate Water Mass and the upper levels as within the Subtropical Subsurface Water Mass. All are contained in the Equatorial Pacific Subsurface Water Mass (see Figure 24). The collection of representatives is small enough to warrant their treatment by family.

Melamphaidae

This family of deep-sea fishes is only sparsely represented in TE VEGA's Gulf of California collections. Data from other expeditions indicate that Scopelogadus mizolepis bispinosus is the most abundant melamphaid in the Gulf. Ebeling and Weed (1963) described the genus as the only one in the family to be closely adapted to the bathypelagic environment, the others being oriented toward even deeper water (abyssopelagic, in the scheme presented here). The Carmen Basin was the northernmost collection site in the Gulf and the population appeared to increase in density toward the mouth as the water depth increased.

The range of vertical distribution in the Gulf was 315 m to 1350 m for the entire family. Ebeling and Weed (1963) state that diurnal vertical migrations, although possible, are not probable. The larvae and young stages, however, are found in the upper layers. They believed that oxygen concentration is the limiting factor for the upper range of the adults and this is borne out by TE VEGA's

collection data, as none of the specimens were taken above the oxygen minimum layer.

The sparse population of melamphaidids in the southern Gulf may be analogous to the depauperate fauna of the Gulf's northern basins. Both groups extend into an area just barely suitable for persistence in terms of temperature and light penetration, because of relative shallowness.

According to Ebeling (1962) the Genus Melamphaes is distributed throughout the major oceans of the world (except the Arctic and Mediterranean) and are usually found in tropical waters. Melamphaes acanthomus is a near coastal species, not taken more than 130 miles from shore. It ranges from the Gulf of Panama to southern California. Melamphaes laeviceps and Melamphaes spinifer are limited to the Equatorial Pacific Water Mass.

Nemichthyidae

Individuals of this family were taken at six stations from the Guaymas Basin to the mouth of the Gulf. Lavenberg and Fitch (1966) report that nemichthyids have been captured in surface tows on the Pacific side of the Baja California Peninsula. On the Gulf side however, despite extensive surface trawling, representatives have only been taken below 300 m.

Migration is more apparent than in the melamphaidids. The daytime range is from the lowest levels of the bathypelagic zone. At night they are seldom found above the 10° isotherm.

It is difficult to classify the family on the basis of migration pattern due to the lack of sufficient data. Based on what is available, and the limited information on their life histories, they are here termed meso-bathypelagic.

Scopelengys tristis is reportedly restricted to depths below 700 m, with a lower limit around 2000 m. The Gulf probably does not provide the appropriate vertical range necessary for the persistence of a strong population of this species.

EPI-BATHYPELAGIC MIGRATORS

The group of fishes with the widest range of vertical movement has been termed epi-bathypelagic. Its members usually reside in the bathypelagic region of the Equatorial Pacific Water Mass (the Equatorial Intermediate layer), perhaps being fed upon by the meso-bathypelagic group. There is little evidence of mass movements toward the surface at night for the group. Their range is best described as being upper bathypelagic during the day and epi-mesopelagic at night, for many of them move upward, following upper layers, at night. Numbers increase over deep water and they are more abundant near the mouth of the Gulf than in its upper reaches. Numerically, this is the second most important of the three distributional groups.

Cyclothone acclinidens

The widest ranging member of this group is the

gonostomatid, Cyclothone acclinidens. Abundance increased from north to south with no decrease at the mouth. The pattern appears to be that of a direct intrusion from the open Pacific, the vertical range tending to be narrower and shallower as the Gulf floor rises. Highest concentrations were found over the deep-water basins.

Cyclothone acclinidens feeds on zooplankton, yet in its vertical movements it does not appear to be directly correlated with the DSL. The chance of capture, however, is greatest in the epipelagic zone at night and in the bathypelagic zone during the day. The center of vertical distribution is the transition area between the mesopelagic and bathypelagic layers. Grey (1956) mentions that they have often been taken abyssopelagically in the open sea. Their presence in the northern basins can be explained as was done with Triphoturus mexicanus.

Bathylagus stilbius

The Gulf population of Bathylagus stilbius extends from the northern basins to the mouth. The population is small, and concentrated over deep water. The vertical range is from 600 m (bathypelagic) to just below the surface. Diurnal migration is apparent.

Stomias atriventer, Diplophos proximus

The small population of S. atriventer is to be found over deep water in the Gulf's basins from Guaymas south. No diurnal migration is apparent although they are known to feed

on myctophids and thus may be expected to follow them. Collections were from all three of the pelagic zones.

Diplophos proximus inhabits a similar range but feeds on invertebrate zooplankton. Both species are most likely to be found in the epipelagic layer at night and in the bathypelagic layer during the day, although very little is known of their habits and preferences.

The series of trawls taken on 27 October 1967 best indicates the general picture of vertical distribution in the Gulf. Two daytime hauls at 65 m and 175 m yielded larval fish and juvenile myctophids respectively. Another daytime haul at 235 m brought up 60 myctophids while another, to 600 m, took three myctophids, two Bathylagus stilbius, three Cyclothone acclinidens and one Argyropelecus lynchus. At night, a surface haul produced 56 myctophids and nine Vinceguerria lucetia. A nighttime haul to 60 m took 179 myctophids, two Bathylagus stilbius, and 76 Vinceguerria lucetia. A third, to 265 m, brought up 75 myctophids, seven Bathylagus stilbius and one Stomias atriventer. This series of trawls, taken in one spot, indicate not only the vertical movements of the three groups of midwater fishes in terms of succeeding levels, but their relative numbers as well.

Figure 24. Pelagic zonation in the Gulf of California
south of the Sal Si Puedes Basin sill.

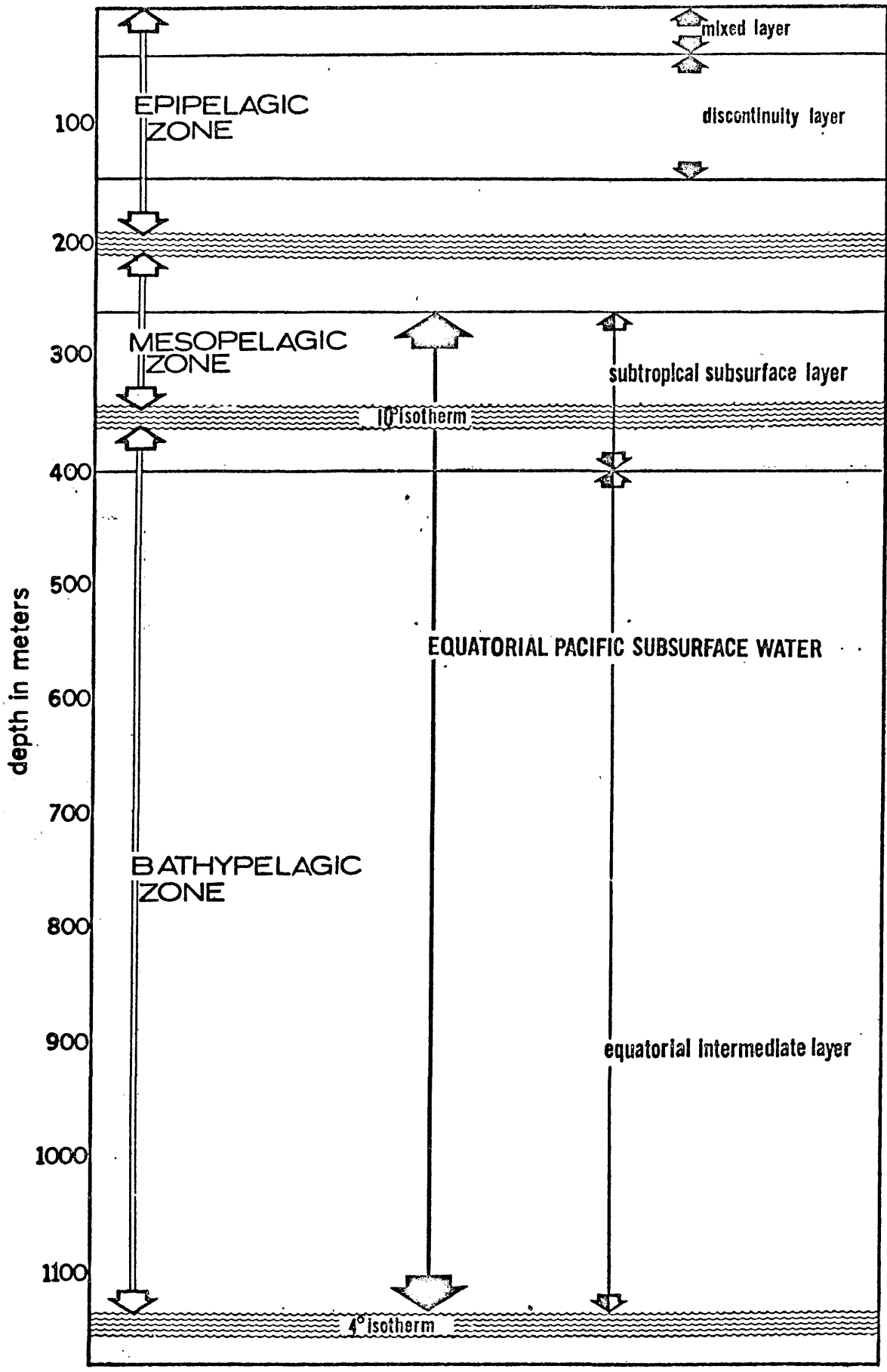
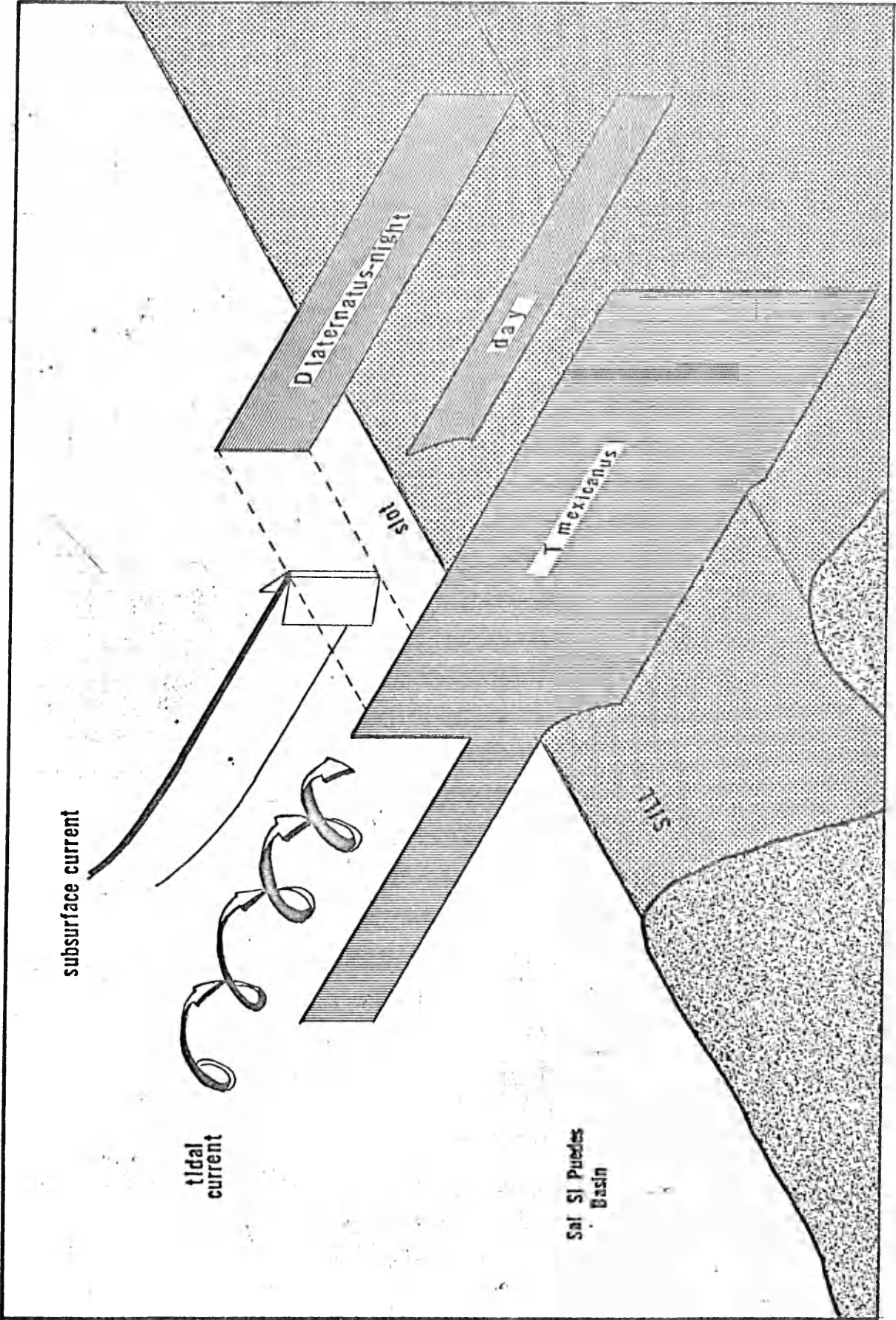


Figure 25. Hypothetical representation of the factors which may prevent the penetration of Diogenichthys laternatus into the Sal Si Puedes Basin.



subsurface current

tidal current

D. laternatus-night

day

T. mexicanus

slot

slot

Sal Si Puedes
Basin

Figure 26. An adult Benthoosema panamense from the northern Gulf of California. A possible new subspecies. Standard length is 60 mm.

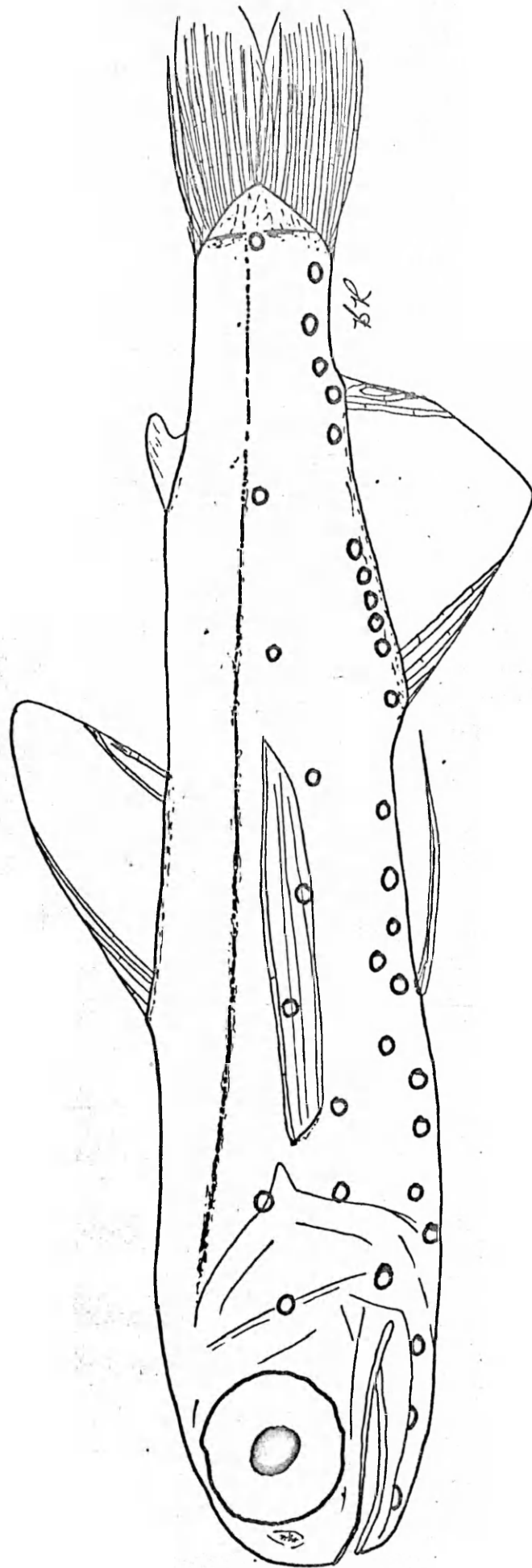
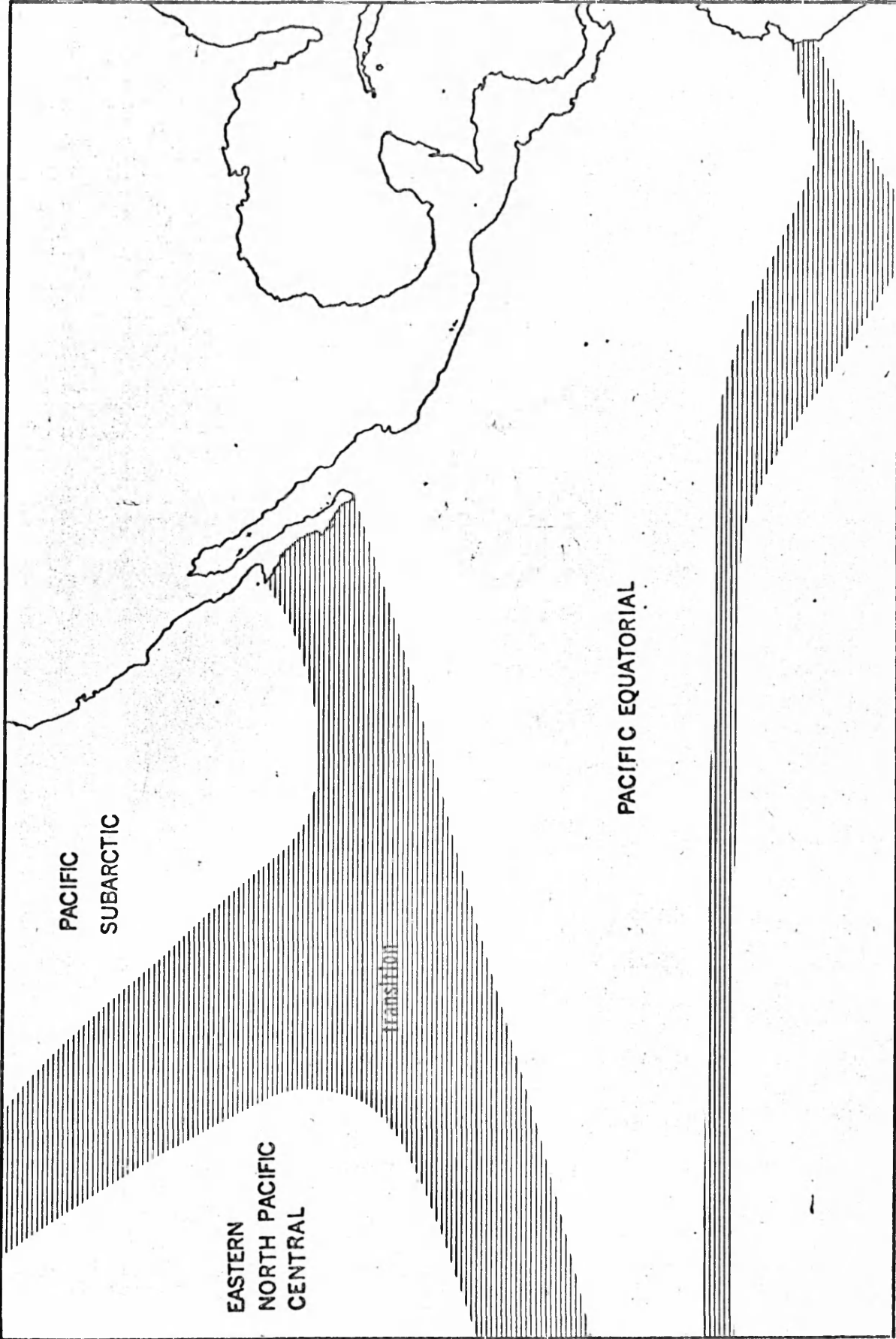


Figure 27. Eastern North Pacific water masses.



SUMMARY AND CONCLUSIONS

The Gulf of California is a unique oceanic environment supporting an equally unique and characteristic community of midwater fishes. The Gulf floor is marked by a chain of deep-water basins over which most of the midwater fishes live. All but the northern two are in direct communication with the open Pacific (at levels well below the 10° C isotherm). The northernmost two differ from those to the south in that the water within them is warmer and more saline than water of corresponding depth to the south.

The subsurface current pattern in the Gulf is counterclockwise and there is a seasonal variation in the surface current patterns. A generalized system of pelagic zonation is presented in Figure 24, which relates the types of living spaces present in a typical Gulf water column.

The midwater fishes of the Gulf of California appear to fall into three distinct distributional groups, each with a particular horizontal and vertical range. When viewed as a whole, they take the form of an inverted wedge (Figure 28), those types occupying successively deeper layers being progressively restricted in their penetration of the Gulf by the shoaling of the water toward the north. The group occupying the uppermost layers is composed of epi-mesopelagic migrators, primarily the myctophids and the gonostomatid Vinceguerria lucetia.

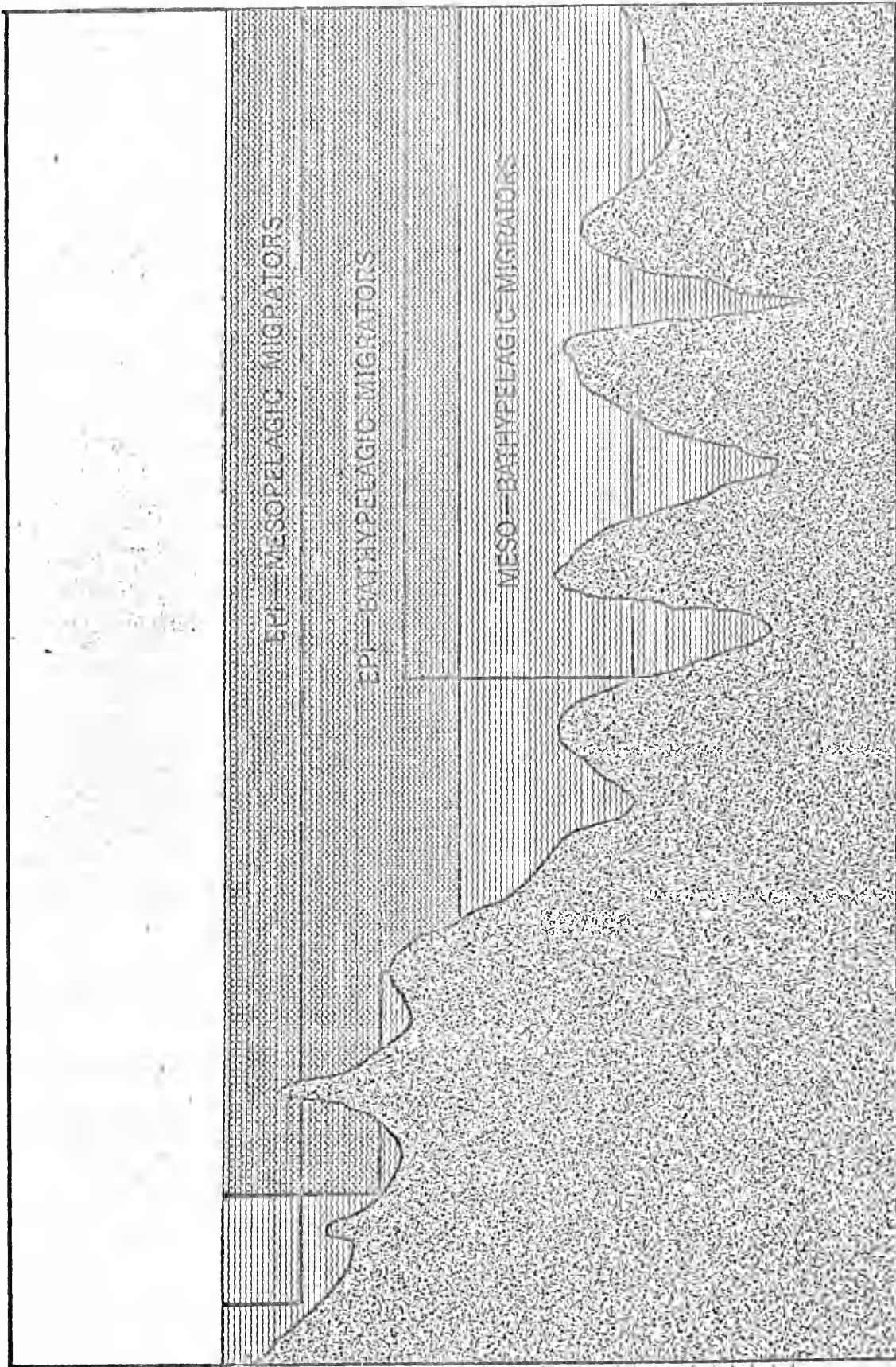
Representatives of this group extend the full length of the Gulf and are the most numerous of the three.

Epi-bathypelagic migrators are the median group, in terms of both their numbers and the center of their depth range. The gonostomatids Cyclothone acclinidens and Diplophos proximus, the bathylagid Bathylagus stilbius and the stomiatid Stomia atriventer comprise this group in the Gulf. Least numerous and having the greatest and deepest vertical range are the meso-bathypelagic migrators. Representatives of this group extend only midway into the Gulf. The families Melamphaidae, Nemichthyidae and Scopelarchidae are typical of this group.

The Gulf's midwater fish population is derived mainly from southern groups with tropical affinities. A line between Cabo San Lucas and Cabo Corrientes probably designates the transition area in which the midwater fish population changes from that typical of the Gulf, to one characteristic of the open tropical Pacific.

The fauna of the northern basins is depauperate, probably because of the sill depth of the Sal Si Puedes Basin, currents which inhibit horizontal migration, and the unusual hydrographic regime.

Figure 28. Diagrammatic outline of midwater fish penetration into the Gulf of California.



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