HYDROGRAPHY AND MIDWATER FISHES OF THREE CONTIGUOUS OCEANIC AREAS OFF SANTA BARBARA, CALIFORNIA[1]

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ABSTRACT: The continental shelf or borderland off southern California is characterized by a complex of basins varying in their depth and nearness to the coast. The biota of these basins are influenced by major water masses that converge and mix over the borderland, subarctic water from the north, central water from the west, and equatorial water from the south. Faunal studies were conducted in two basins and in an area over the continental shelf off Santa Barbara that constitute three contiguous but oceanographically distinct borderland environments. Midwater fish faunas were sampled with a six-foot Isaacs-Kidd midwater trawl during cruises of the General Motors Research Vessel SWAN, 1964-1967. The three areas sampled are separated from each other by an undersea ridge and island chain and are differentially affected by the land and by the prevailing oceanic currents. Intense upwelling occurred in the Santa Cruz and Santa Barbara basins, due to a seasonal redistribution of mass in the complex California Current system off southern California.

The midwater fish fauna of the inshore Santa Barbara Basin was the least diverse but the most abundant of the three. The comparative shallowness of this basin excluded most bathypelagic species. The intermediate-deep Santa Cruz Basin contained a typical bathypelagic fauna, including relatively many southern species. The fish fauna of the Rodriguez Dome area over the continental slope was most diverse, including many exotic central and northern species. The faunas of the two offshore areas resembled each other more than either resembled the fauna of the Santa Barbara Basin. The Santa Barbara Basin is physiographically and hydrographically isolated from the offshore areas and is enriched by coastal runoff from the land. This isolation and enrichment has produced a relatively eutrophic environment, containing a somewhat provincial fish fauna. The Santa Cruz Basin contains a fauna more typical of the greater borderland environment, while the Rodriguez Dome area, which is directly influenced by the California Current, contains a typically oceanic fauna.

INTRODUCTION

The oceanic environment off the west coast of North America is influenced by the interaction of three major water masses in the eastern north Pacific

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Ocean. Subarctic water of low salinity moves southward between the west coast of North America and the warmer, more saline central water mass offshore. This subarctic water is formed in high latitudes and is characterized by low salinity, high oxygen, and abundant nutrients. Eastern north Pacific central water occurs to the west and is associated with a clockwise gyre between Hawaii and the coast. This water is warm and has a high salinity (Sverdrup et al., 1942). Equatorial water, formed in the lower latitudes, is warmer, more saline, and denser than the subarctic water. Some of this relatively dense water flows inshore northward along the coast of southern California, usually under the mixed, southward flowing subarctic water. This circulation has been extensively studied by oceanographers associated with the California Cooperative Oceanic Fisheries Investigations (e.g., Reid et al., 1958; Wyllie, 1966).

Brinton (1962) recognized each of these three water masses as primary faunal regions and pointed out that a transitional or secondary faunal region is created off the west coast by their mixing. An area of oceanographic transition constitutes an ecotone of faunal mixing. This mixing has been documented in several zoogeographical studies: e.g., of euphausiids by Brinton (1962, 1967), of deep-sea fishes by Ebeling (1962), of chaetognaths by Alveriño (1965), of copepods by Fleminger (1964), of mesopelagic fishes and euphausiids by Pieper (1967). The transitional water also supports an endemic fauna (e.g., Brinton, 1962).

The California Current is the major eastern boundary current of the north Pacific Ocean. This current transports subarctic water southeastward along the coast of North America. When the California Current turns west at about 10°N to join the north Equatorial Current, the subarctic water has been modified by mixing and by increasing insolation and evaporation. In fact, only a small salinity minimum remains to indicate its origin (Reid et al., 1958).

The intensity of the California Current is greatest during the late spring when the northwesterly winds are strongest off Washington and Oregon. The long shore component of the wind stress and the earth's rotation cause extensive upwelling along the coast. This upwelling brings to the surface pockets of cool, nutrient-rich, and saline water, which mixes with the subarctic water. This upwelled water is derived partly from lower subarctic water and partly from the modified equatorial water of the submerged countercurrent (Reid et al., 1958). During fall and winter, the winds are less intense and shift to the west and southwest. Then, the California Current weakens, upwelling subsides, and the countercurrent develops at the surface between the California Current and the coast.

Point Conception has generally been recognized as a zoogeographical boundary between littoral biotas (Hedgpeth, 1957; Neushul et al., 1967). North of this boundary the subarctic component of the California Current dominates environmental conditions, while to the south and inshore, intrusions of southern water over the continental shelf predominate. This relatively narrow and basin-pitted continental shelf off southern California was designated continental borderland by Shepard and Emery (1941).

Vertically, the water column may be divided into three zones (Lavenberg and Ebeling, 1967). The lighted epipelagic zone of locally-warmed and wind-mixed surface water extends to some 50-100 m. Between 100 and 500-600 m subarctic water and, to a lesser extent, central water dominate the weakly-lighted mesopelagic zone of rapidly changing temperature with depth. Southern water occupies the aphotic bathypelagic zone. Over the borderland, this zone extends from 500-600 m to the bottom (Emery, 1960). This bathymetric zonation has its biological counterpart. Many mesopelagic fishes are relatively strong-bodied; have well-developed eyes, photophores and swimbladders; are countershaded; and undergo extensive diel vertical migrations. Bathypelagic fishes, on the other hand, are weak swimmers. They have reduced or no eyes, photophores, and/or swimbladders. Most are uniformly brown or black and undergo restricted or no diel migrations (Marshall, 1960).

The objective of the present study was to compare the midwater fish faunas off Santa Barbara relative to the hydrography and physiography (1) of the shallow inshore Santa Barbara Basin between the coast and the Channel Islands some 20 miles offshore, (2) of the intermediatedeep Santa Cruz Basin immediately seaward of these islands, and (3) of the slope area about the Rodriguez Dome seamount to the northwest. The faunas in these three areas

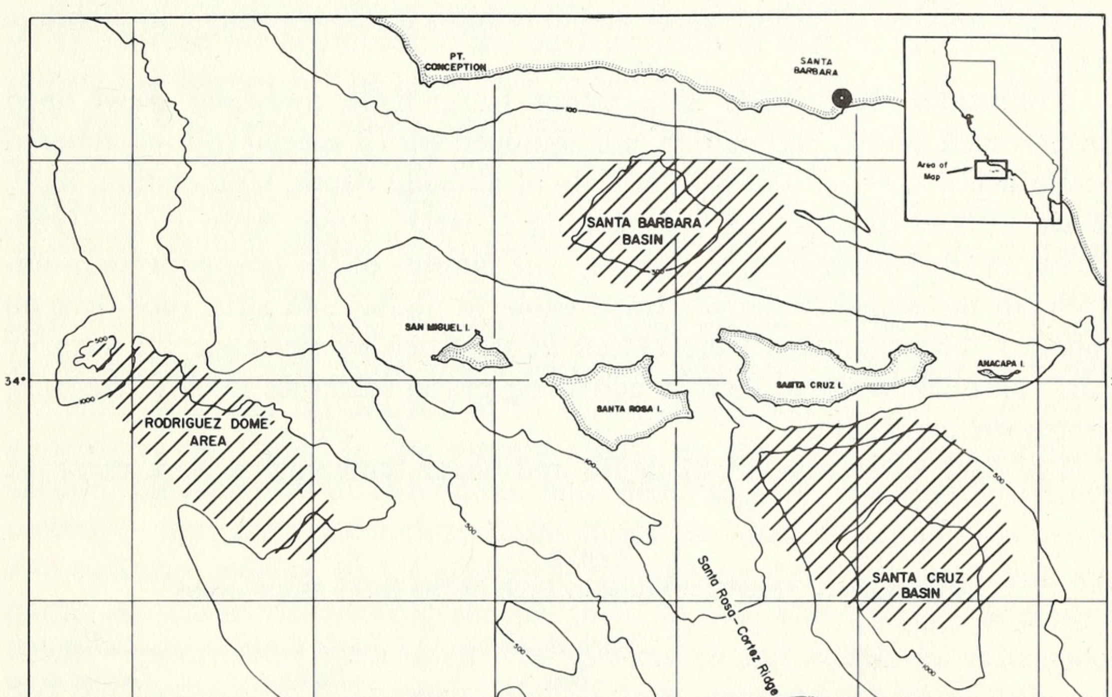

FIGURE 1. Deep water areas of the continental shelf off Santa Barbara, California. The three areas sampled are hatched.

were compared in terms of the abundance, diversity, composition, and distribution of their included species. Abundance reflects the productivity of the environment; diversity indicates its complexity; composition reflects the adaptations of its species; and distributions indicate its heterogeneity in space and time.

The Santa Barbara Basin is a relatively shallow, inshore basin with a maximum depth of 600 m and a still at 475 m opening to the west (Fig. 1). The Santa Cruz Basin has a maximum depth of 2000 m with a still at 1075 m opening on the borderland to the south.

MATERIALS AND METHODS

Sampling the midwater environment

To investigate the oceanography and midwater faunas off Santa Barbara, 28 cruises were made aboard the General Motors Research Vessel SWAN by personnel from the University of California at Santa Barbara Marine Laboratory. Only the Santa Barbara and Santa Cruz basins were sampled during the first 13 cruises, beginning in the fall of 1964. In July, 1966, a third area to the southeast of the Rodriguez Dome seamount was added to the study. This area is over the continental slope between the 1000 and 2500 m bottom contours. During the 28 cruises, 204 midwater trawl stations were occupied and 568 separate successful collections were made (Table 1). Less than three per cent of the total number of collections were rejected as unsuccessful because of presumed or actual failures in the trawling and monitoring gear.

Collections were made in a 6-foot Isaacs-Kidd midwater trawl lined with half-inch stretch bait netting and equipped with a special four-chambered discrete depth sampler and with sensors of ambient depth, temperature, light, and water flow through the net opening (Clarke, 1966; Aron et al., 1964; Bercaw, 1966; Bourbeau et al., 1969). The outputs of the sensors were multiplexed up the single-conductor trawl cable to digital and strip recorders on shipboard. The chambers were closed in sequence by reversing the polarity of the depth channel and thereby activating piston solenoids to close the gates between the chambers.

For each collection, trawl depth and water temperature were recorded

TABLE 1
Summary of trawl activities in each of the three study areas

	Santa Barbara Basin	*Santa Cruz Basin*	*Rodriguez Dome area*
Number of collections	210	267	91
Number of cruises	28	25	11
Total effort as km linear flow	520.7	826.8	316.8
Fish volume (ml)	24,675	10,891	3,859
Number of individuals (fish)	13,800	11,415	2,999

from the digital display that accompanied the strip recording. Surface water temperature was measured at each trawl station with a bucket thermometer, and a bathythermograph cast was made with each series of trawls in an area. Bottom depth and the depth of the Deep Scattering Layer were monitored by a Precision Depth Recorder.

Hydrographic casts were made near the centers of each of the three areas during the last 15 cruises, weather permitting (see hatched areas, Fig. 1). Water samples were collected in a vertical series of ten Nansen bottles with reversing thermometers. In the Santa Barbara Basin the bottles were usually placed on the hydrographic wire at 0, 25, 50, 75, 100, 150, 200, 300, 400, and 500 m. In the two offshore areas, the bottles were placed at 0, 30, 60, 100, 200, 350, 500, 650, 800, and 1,000 m. These intervals assured measurements from the three main bathymetric zones; epipelagic, mesopelagic, and bathypelagic.

Oxygen samples were drawn first, preserved within 15 minutes, and analyzed using the Winkler titration method as outlined by Strickland and Parsons (1965). Titration volumes were converted to ml/liter, and percent saturation at *in situ* temperatures and salinities was determined using the tables of Green and Carriet (1967). Salinities were analyzed later with a Hytech Portable Laboratory Salinometer. Temperatures were recorded as the average reading of two observers. Temperature, salinity, and oyxgen were contoured as vertical profiles for each month of 1967.

The three major depth zones were sampled. The trawl was set with all gates between the chambers in the open position so that no sample was taken during the lowering. The trawl was lowered to the first sampling depth, the first gate was closed, and a horizontal (discrete) collection was made. The second gate was then closed and an oblique collection was made while the trawl was retrieved to a shallower depth for the second horizontal sample. A fourth, oblique sample was made as the trawl was brought to the surface.

Each trawl haul usually provided four collections, which were sorted into groups of fishes and invertebrates. After measuring the liquid displacement volume of each group, it was preserved separately in 10 percent buffered formalin and later transferred to 55 percent isopropyl alcohol. Only the fish collections were used in the present study. As the fishes were identified to species, the numbers of individuals and their ranges in standard length were recorded for each collection. Individuals of *Stenobrachius leucopsarus, Leuroglossus stilbius,* and *Cyclothone acclinidens* were separated into categories of young (individuals shorter than 50, 50, and 25 mm in standard length, respectively) and adult. The number of individuals of each species and displacement volume per collection were standardized by dividing each value by the kilometers of linear effort for that collection, measured as the average distance between ticks on the depth trace recorded on shipboard from the trawl's flow meter. Each tick represented 1000 revolutions of the propeller in the flow meter. Obviously, this linear measurement is proportional to the volume of water filtered by the trawl net. A total of 28,214 individuals were captured, belonging to 81 species in 39 families (Table 1; Appendix). All station and collection records are on file at the Natural History Museum of Los Angeles County.

Faunal analyses

All environmental and collection data were punched on two sets, respectively, of computer cards for sorting and analysis at the Computer Center at UCSB.

There are two main sources of variation among the samples. Variation in the abundances of fishes may represent fluctuations in the actual densities of their populations or merely fluctuations in the sampling effectiveness of the trawl caused by distributional patchiness, net avoidance, escape, and contamination of captures among depth zones (Harrisson, 1967).

To estimate sources of variability in subsequent analyses, collections were initially pooled by area. They were then grouped within each area by cruise, and finally considered as individual samples. Initially all samples from an area were treated as one large collection. Cruise collections pool those samples taken in an area during each cruise. (Monthly collections used in the analysis of abundance combine the cruise collections taken during the same months over the several years of the study.) Within each area, the collections were also analyzed individually. In this way, for example, vertical and seasonal variation could be estimated.

The standardized fish displacement volumes were used as the index of faunal abundance.

Several types of observations were used to describe faunal diversity: the number of species in a collection; the number of dominant species; the number of frequently captured species; and a probability index of diversity. The species contributing the greatest number of individuals to a collection was considered to dominate that collection. In each area, the number of collections dominated by a particular species and the number of collections in which the species was present were both expressed as percentages of the total number of collections made in the area. The diversity index was computed both for each individual collection and for the pooled collections constituting each cruise collection: Simpson's diversity index as modified by McGowan and Fraundorf (1966).

$$d = 1 - \left[\frac{\Sigma\, n(n-1)}{N(N-1)} \right]$$

where: n = no. individuals of each species
N = total individuals of all species in each collection

The index "d" gives the probability that any two individuals selected randomly and independently from a sample will *not* be of the same species.

The faunal composition was contrasted among the areas by considering

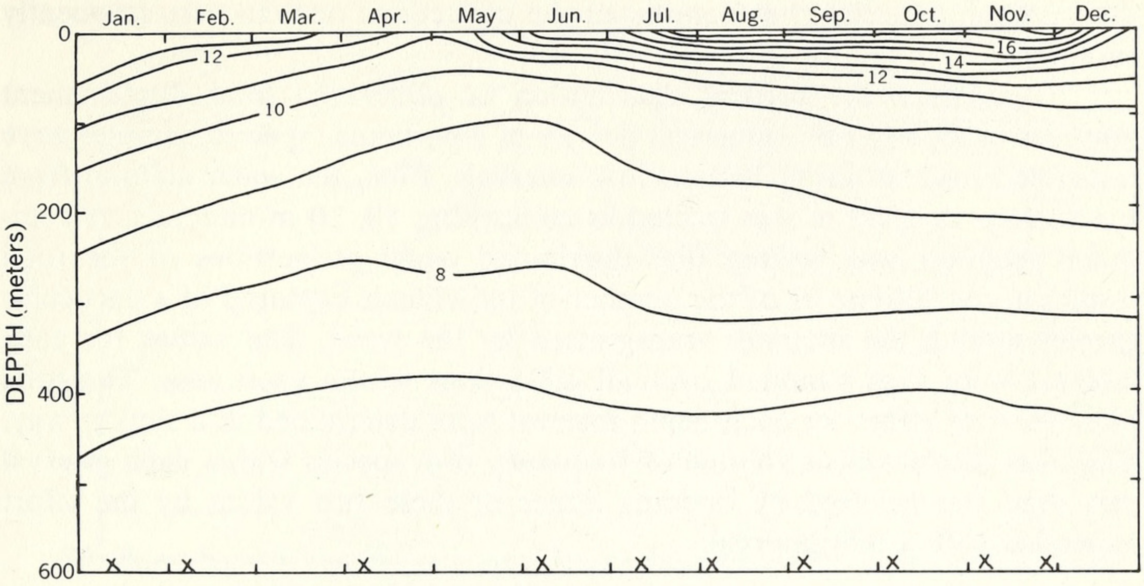

FIGURE 2. Seasonal profile of temperature in the upper 500 m for the Santa Barbara Basin during 1967. The contour interval of isotherms is 1 °C.

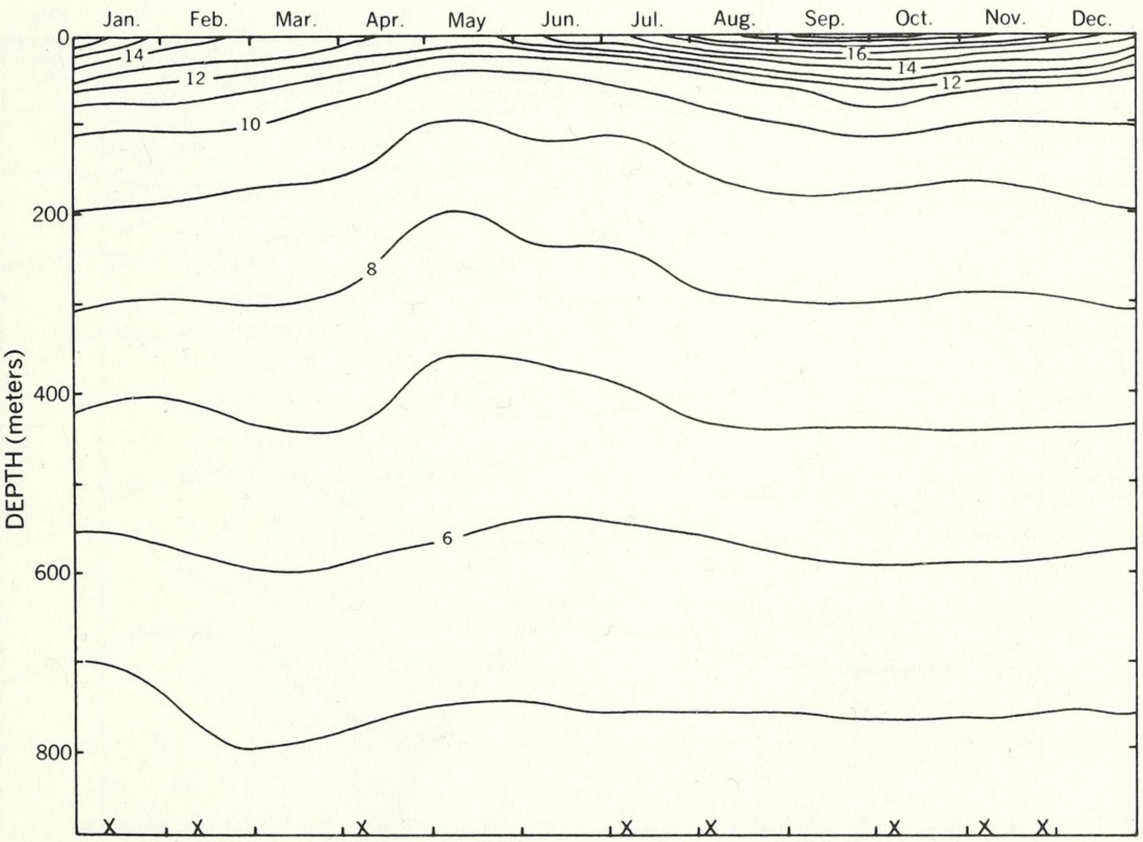

FIGURE 3. Seasonal profile of temperature in the upper 900 m for the Santa Cruz Basin during 1967. Contour interval, 1 °C.

the particular species that dominated the collections or that were frequently captured.

To analyze the vertical distribution of either the total displacement volumes of all fishes or numerical density of a particular species, samples were integrated over arbitrary bathymetric intervals. First, the water column from the surface to 1000 m was treated as comprising 50, 20 m intervals. A computer program was written that distributed equal proportions of the total displacement volume or of the number of individuals captured of a particular species among the intervals transgressed by the trawl. The values for each interval were then summed over all collections within each area. The total kilometers of effort for each depth interval were determined in a similar way. The total displacement volume or frequency of a species within each interval was then standardized by dividing either of these two values by the effort expended within that interval.

RESULTS

Hydrography

Temperature, salinity, oxygen. In the Santa Barbara Basin, the coldest surface water was measured during May when the 11° isotherm reached the

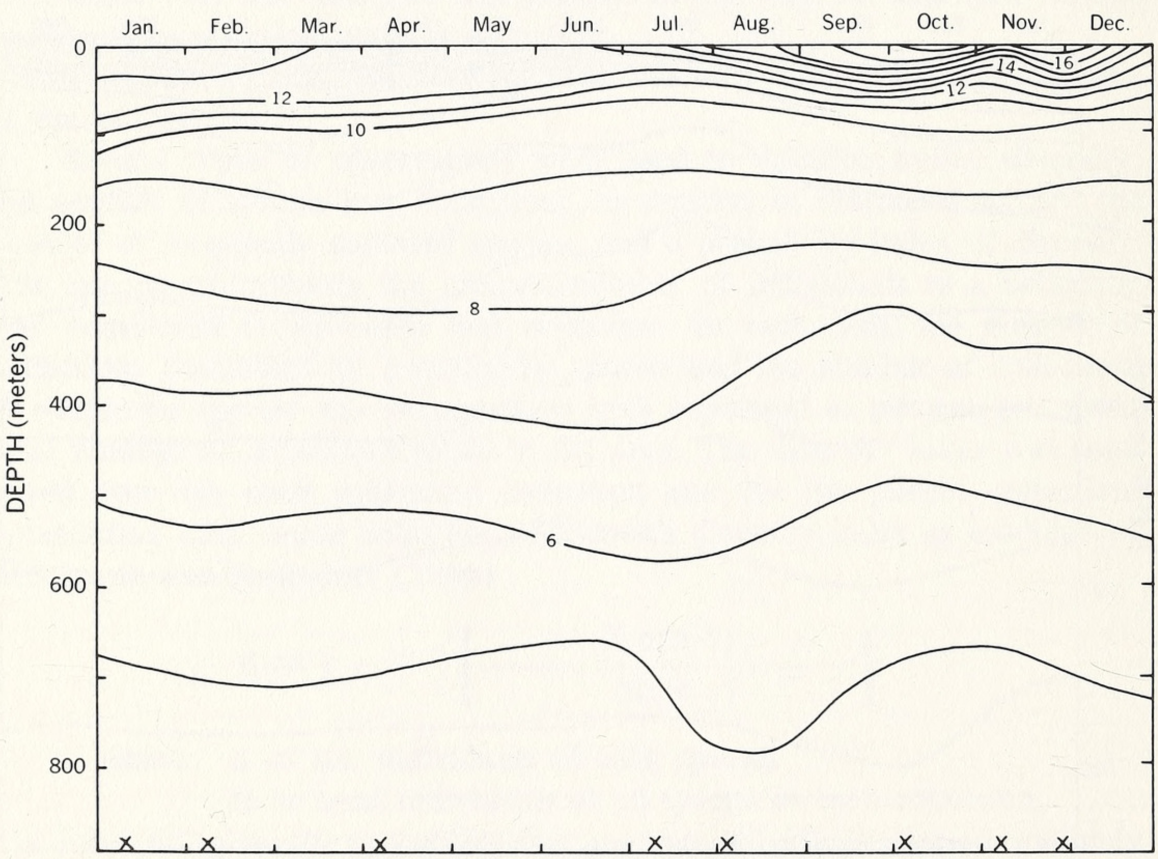

FIGURE 4. Seasonal profile of temperature in the upper 900 m for the Rodriguez Dome area during 1967. Contour interval, 1°C.

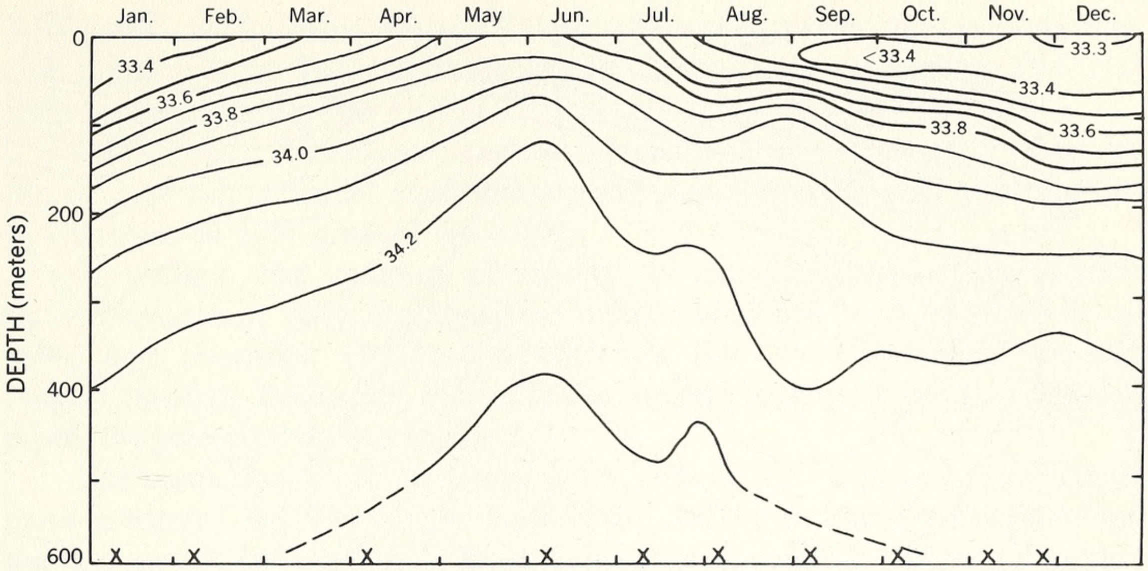

FIGURE 5. Seasonal profile of salinity in the upper 500 m for the Santa Barbara Basin during 1967. Contour interval, 0.1%.

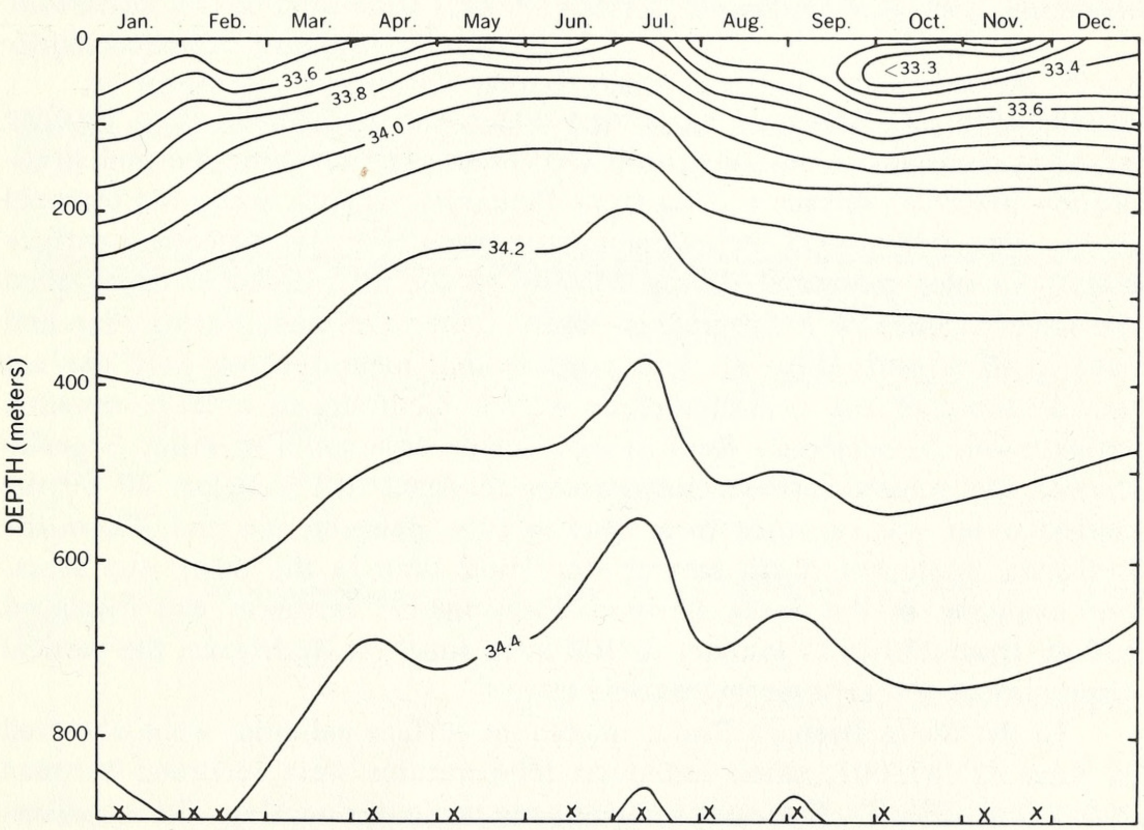

FIGURE 6. Seasonal profile of salinity in the upper 900 m for the Santa Cruz Basin during 1967. Contour interval, 0.1%.

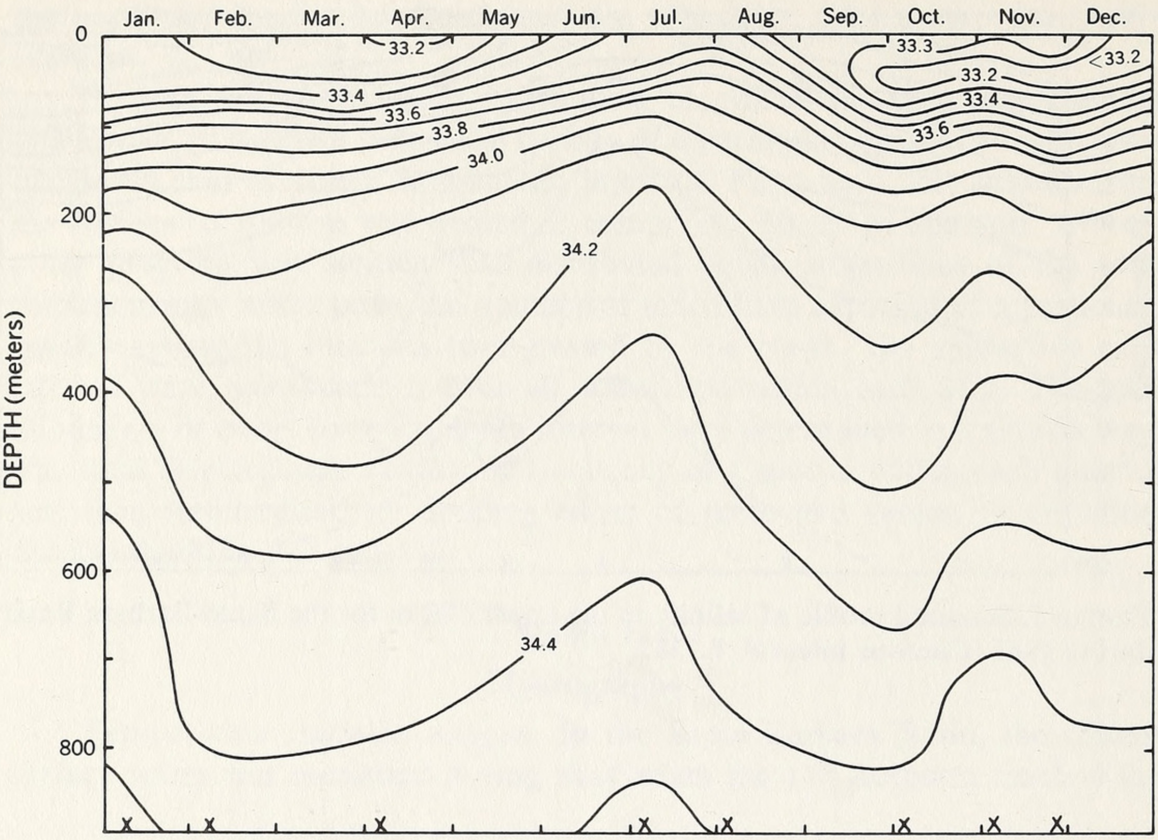

FIGURE 7. Seasonal profile of salinity in the upper 900 m for the Rodriguez Dome area during 1967. Contour interval, 0.1%

surface (Fig. 2). Below 75 m, coldest water was recorded in June. Surface warming continued from June until December. The resulting thermal stratification preceded surface mixing from January to March, when the seasonal thermocline disappeared. In the Santa Cruz Basin (Fig. 3), the coldest surface water was also measured during May when the 12° isotherm approached the surface. Since no hydrographic observations were made during May and June at Rodriguez (Fig. 4), it is possible that measurements here did not include those of the coldest surface waters. Contours of average monthly temperatures presented by Reid (1965) for an area south of Point Arguello showed the coldest surface temperatures in April (12°). Below 30 m, the coldest water was recorded from May to July. Between 100 and 300 m the isotherms fluctuated much less at Rodriguez than in the other two areas. For example, in the Santa Barbara Basin the 9° isotherm was displaced 130 m, from 230 m in January to 100 m in June. At Rodriguez, the vertical displacement of this isotherm was only 60 m.

In the Santa Barbara Basin, maximum surface salinities were observed in June (33.8°/00), when minimum temperatures were recorded between 100-300 m (Fig. 5). No water samples were taken during May. The isohalines gradually deepened from June until January. In the Santa Cruz Basin, the maximum surface salinity was 37.7°/00, recorded in July (Fig. 6). At

Rodriguez, the isohalines below 200 m approached the surface in both July and January (Fig. 7). Maximum surface salinities just exceeding 33.6°/00 were recorded in July and August.

With minor exceptions, seasonal fluctuations of the contours showing the percent saturation of dissolved oxygen generally coincided with changes in salinity in all three areas (Figs. 8-10).

Upwelling. The contours of salinity, temperature, and oxygen suggest the occurrence of three hydrographic periods analogous with those of Monterey Bay (Barham, 1957): May through July, the "upwelling" period; August through December, the period of stratification; and January through April, the period of surface mixing.

The upward slope of the temperature, salinity, and oxygen isopleths indicated intensive upwelling in the Santa Cruz and Santa Barbara basins during the late spring. Mr. Joseph L. Reid, Jr. (personal communication) suggested that this upwelling occurs when a geostrophic low moves toward the coast during this period. This low, which characterizes the hydrography off southern California, constitutes the center of a counterclockwise gyre associated with the borderland. In general, geostrophic lows are identified by surface anomalies expressing central cores of dense water surrounded by less dense water. The redistribution of mass occurs when water moves from the center to the periphery of the gyre. Upwelling is replacement in the central core. Therefore, the movement of the core itself into the study areas causes the observed vertical displacement of isopleths.

At Rodriguez during this period, there occurred little deflection of isotherms, although salinity increased. Mr. Reid suggested that continuously

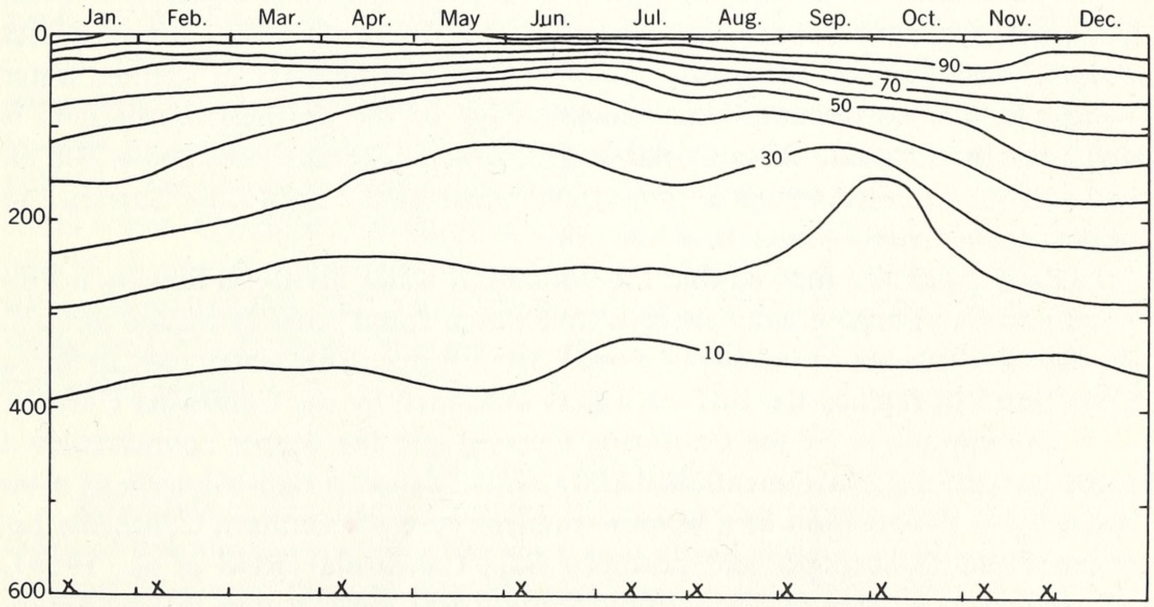

FIGURE 8. Seasonal profile of oxygen concentration percentage in the upper 500 m for the Santa Barbara Basin during 1967. Contour interval, 10% saturation.

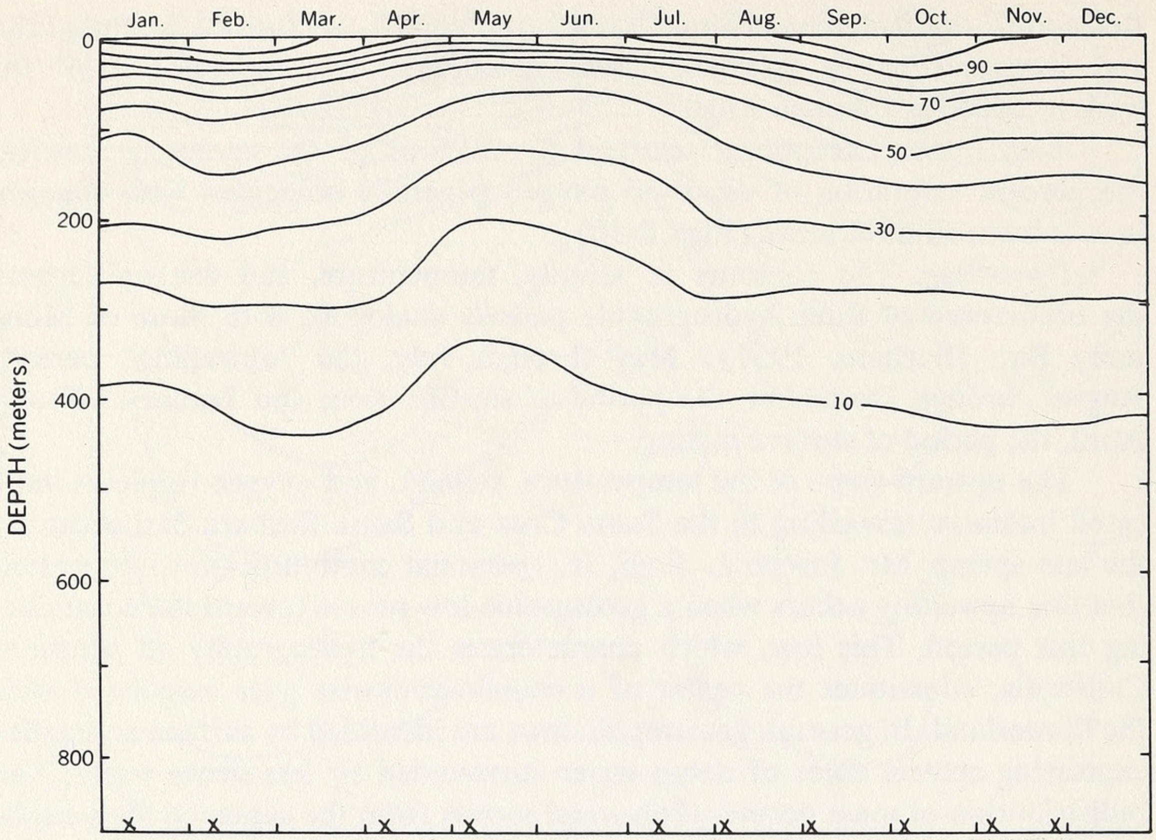

FIGURE 9. Seasonal profile of oxygen concentration percentage in the upper 900 m for the Santa Cruz Basin during 1967. Contour interval, 10% saturation.

warm, more saline central water follows the inshore movement of the hydrographic low.

The southward-flowing California Current is deflected offshore at Point Conception. Emery (1960) pointed out that as the California Current passes Point Conception, it entrains or "pulls with it" a large body of surface water lying over the borderland. The seaward edge of the northern borderland is delimited by the Santa Rosa-Cortez Ridge, which generally rises above 200 m. Obviously, this entrainment of borderland water by the California Current can only occur above this depth in this region.

Emery (1960) showed that the volume of water at 300 m flowing northward past San Diego greatly exceeds that which could possibly escape through the few depressions in the Santa Rosa-Cortez Ridge. This water rises in Santa Cruz Basin to replace the surface waters entrained by the California Current.

The apposition of the California Current and the deeper countercurrent together with the above mentioned entrainment causes a redistribution of mass resulting in the creation of a semi-permanent gyre off southern California between Point Conception and northern Baja California (Reid et al., 1958). Usually centered in the vicinity of the Santa Rosa-Cortez Ridge, this gyre comprises water typical of the upwelled water–high in salinity and inorganic nutrients and low in temperature and ozygen (Emery, 1960).

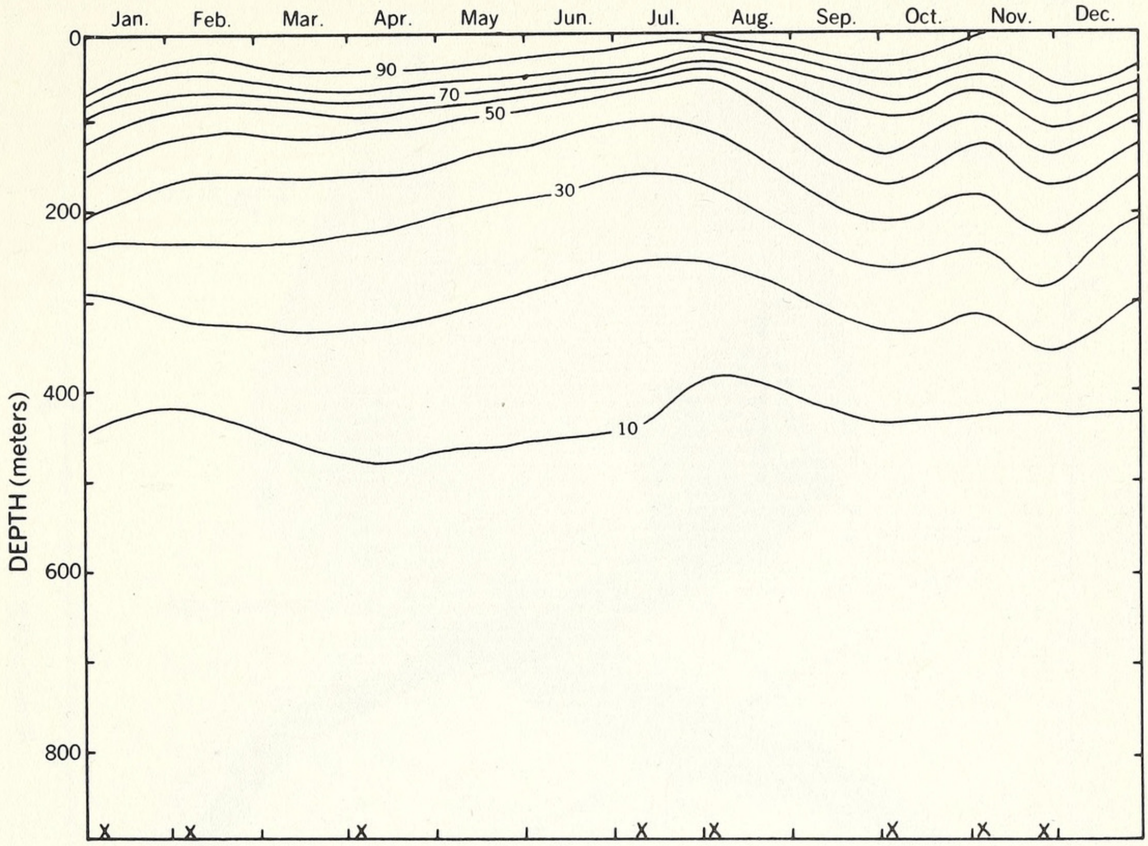

FIGURE 10. Seasonal profile of oxygen concentration percentage in the upper 900 m for the Rodriguez Dome area during 1967. Contour interval, 10% saturation.

These concepts are mutually compatible in that entrainment as conceived by Emery is simply the outward peripheral flow from the geotrophic low as conceived by Reid. Furthermore, the upwelled water replacing that in the center of the low most logically comes from a deep source to the south.

Curves of temperature plotted against salinity substantiate these conclusions. Water mass envelopes were defined for each of the three oceanographic periods by families of these T-S curves (Figs. 11-13). These were compared with T-S relationships from Tibby (1941) which define 30% and 50% equatorial water. Envelopes for all three areas show an increase in a southern component during the upwelling period. In the Santa Barbara and Santa Cruz basins, this probably indicates an influx of deep water from the south. In the Rodriguez area, however, this salinity maximum may indicate an influx of central water as well.

Faunal comparisons

Abundance. The Santa Barbara Basin was the richest area sampled, in terms of fish biomass measured by the standardized displacement volumes. The volumes here were three to four times as large as those from the two offshore areas (Table 2; Figs. 14, 15). Collections from the Santa Barbara Basin were also the most variable, including the most highly successful and empty collec-

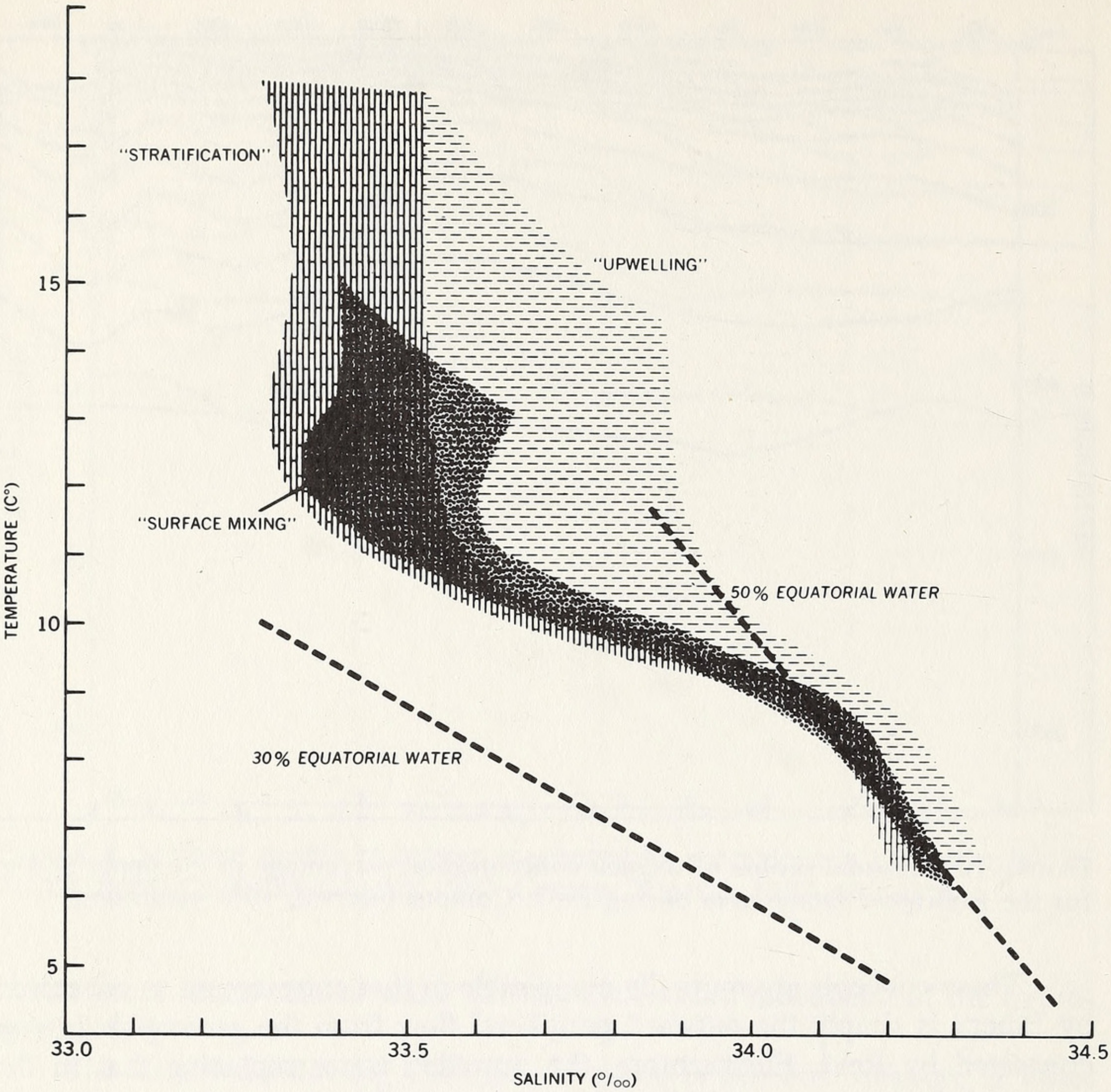

FIGURE 11. Water mass envelopes for three seasonal periods defined by temperature-salinity (T-S) curves for the Santa Barbara Basin: May-June, upwelling period; August-December, stratification period; January-April, period of surface mixing.

tions. They contained the greatest abundance of fish at all depths sampled, although an abundance minimum between 100 and 120 m may separate diel concentrations near the surface at night and at depth during the day (Fig. 14). Seasonally, the collections indicated two periods of maximum abundance in July and November (Fig. 15). The single maximum for the Rodriguez Dome area coincided with the July maximum, while that for the Santa Cruz Basin was one month later than the November maximum.

Diversity. The total number of species captured in each area indicated that the two offshore areas contained a considerably more diverse fish fauna than the Santa Barbara Basin (Table 3; Fig. 16). When the individual collections were pooled by cruise, the increase in the average number of species from Santa Barbara to Rodriguez was accentuated. These averages, but not the total

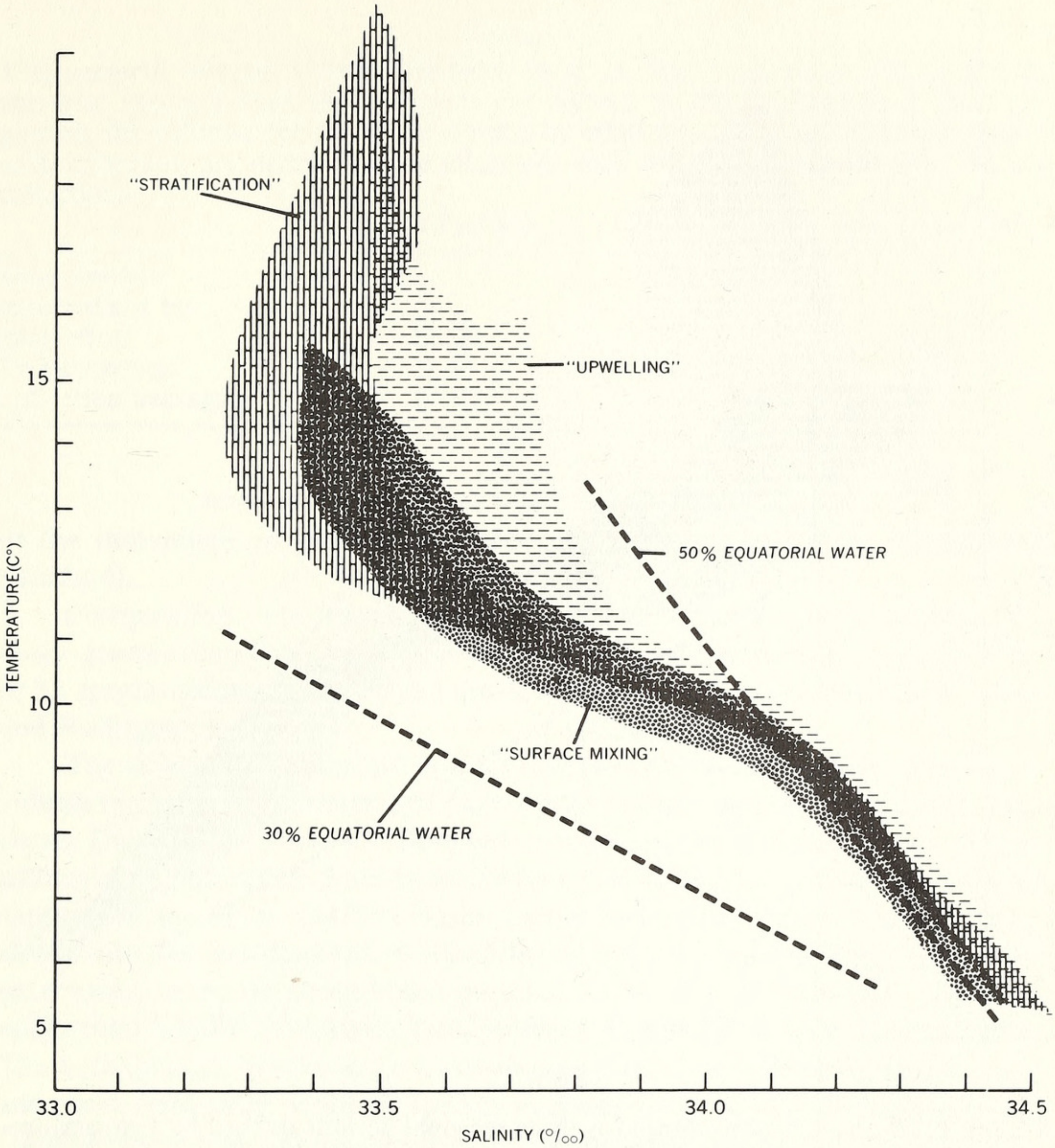

FIGURE 12. Water mass envelopes for three seasonal periods defined by temperature-salinity (T-S) curves for the Santa Cruz Basin (see Fig. 11).

species taken, indicated that Santa Cruz is intermediate in species number. That a greater total number of species was captured in Santa Cruz is probably due to the greater number of collections taken in that area. This would increase the probability of capturing rare species. Also, the relatively steep slope for Rodriguez of a regression of the cumulative total of species captured on the cumulative number of cruises shows that further cruises would undoubtedly take additional species (Fig. 16).

The index of diversity, capture frequency, and dominance hierarchy of species also indicated increased diversity offshore. The diversity index averaged among collections increased from 0.46 for the Santa Barbara Basin, through

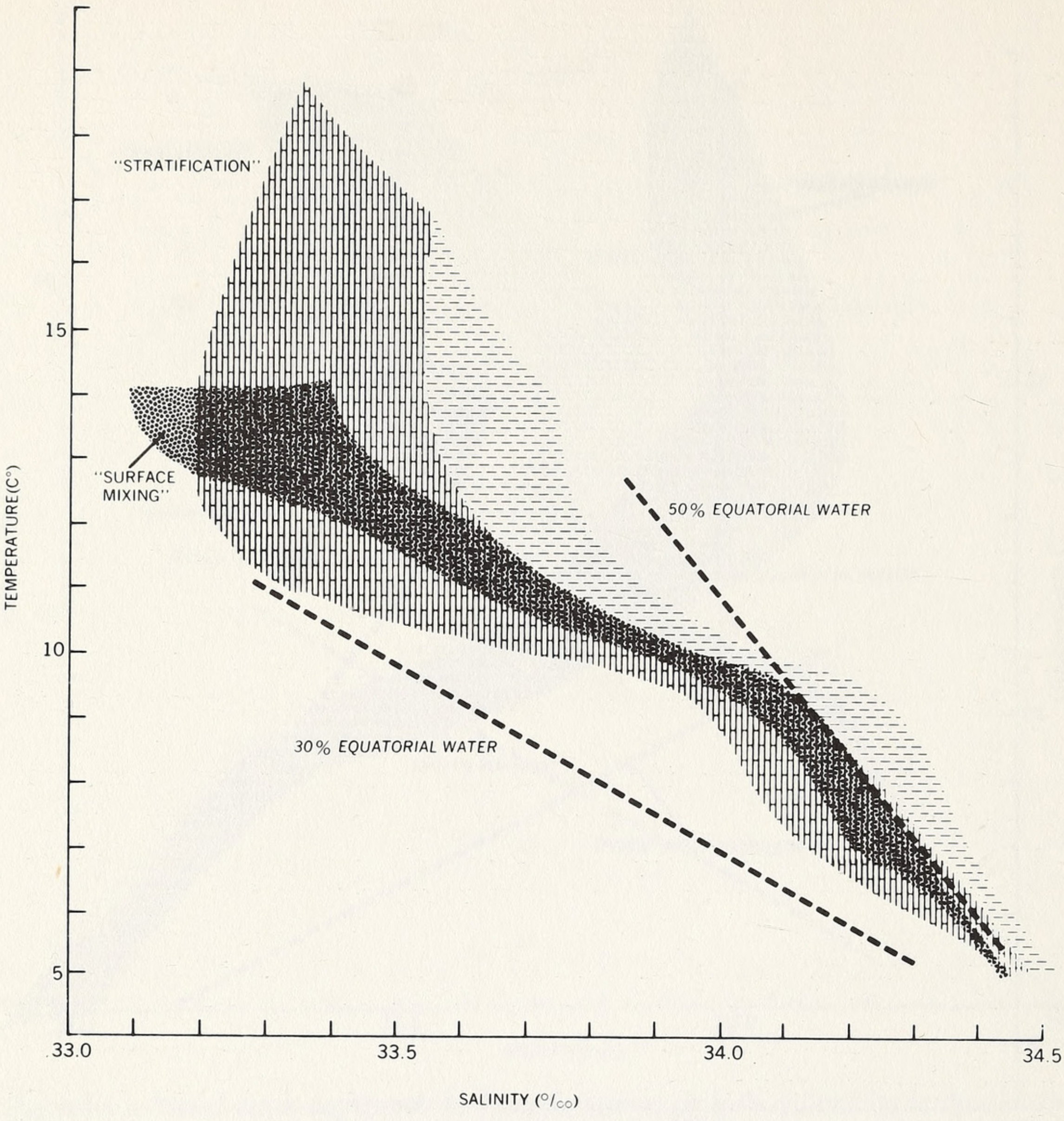

FIGURE 13. Water mass envelopes for three seasonal periods defined by temperature-salinity (T-S) curves for the Rodriguez Dome area (see Fig. 11).

0.58 for the Santa Cruz Basin, to 0.66 for the Rodriguez Dome area. Similarly, the cruise average (pooled among collections) increased from 0.53, through 0.74, to 0.82, respectively. The average collection diversity indices as well as the average numbers of species differed significantly among all three areas ($p < .01$). Furthermore, 12, 19, and 36 species were captured in at least 5% of the collections from Santa Barbara, Santa Cruz and Rodriguez, respectively, while 9, 12, and 21 species were captured during at least 50% of the cruises. Species-abundance curves indicated that relatively few species dominated the Santa Barbara collections, while several species dominated the offshore collections; i.e., the offshore areas showed the more even distributions of species abundance (Fig. 17). In addition, the number of species that constituted 90%

TABLE 2

Displacement volumes of midwater fishes from the three study areas. For each area, the total volumes over all collections are divided by the total trawling effort expended, the volumes per cruise are divided by effort per cruise, and the volumes per each collection are divided by the effort per each collection and averaged over all collections

	Santa Barbara	*Santa Cruz*	*Rodriguez Dome*
Total volume standardized by total effort	47.39	13.17	12.18
Cruise average	55.42	14.19	17.56
Collection average	57.46	14.82	17.75

of the individuals in each of the three areas was 3, 7, and 15, respectively (Table 4).

Composition. The faunal overlap between the two offshore areas was much greater than that of either area with the Santa Barbara Basin. Some 39% of 81 species occurred in all three areas, while 61% occurred in the Santa Cruz and Rodriguez areas only.

The seven most abundant species comprised more than 90% of the individuals in the Santa Barbara and Santa Cruz basins, but only 78% in the Rodriguez Dome area (Table 4). Only two species, the deepsea smelt *Leuroglossus stilbius* and lanternfish *Stenobrachius leucopsarus* made up over 90% of the captures in the Santa Barbara Basin. In the Santa Cruz Basin, however, they, along with the bristlemouth *Cyclothone signata* and lanternfish *Triphoturus mexicanus,* made up about equal proportions of the total fish cath: 11–17% of the total number of individuals captured, taken in 58-69% of the collections. The bathypelagic bristlemouth *Cyclothone acclinidens* was the most abundant and most frequently captured species at Santa Cruz. Two other lanternfishes, *Diaphus theta* and *Lampanyctus ritteri,* were taken less frequently in smaller numbers.

The seven species mentioned above also dominated the Rodriguez fauna, but in a different order. *Cyclothone signata* was the most abundant species

TABLE 3

Total number of species captured among all areas and average number of species captured during each cruise and for each collection

	Santa Barbara Basin	*Santa Cruz Basin*	*Rodriguez Dome Area*
Total number of species captured	44	67	57
Cruise average	9.92	17.83	24.27
Collection average	3.49	5.66	7.20

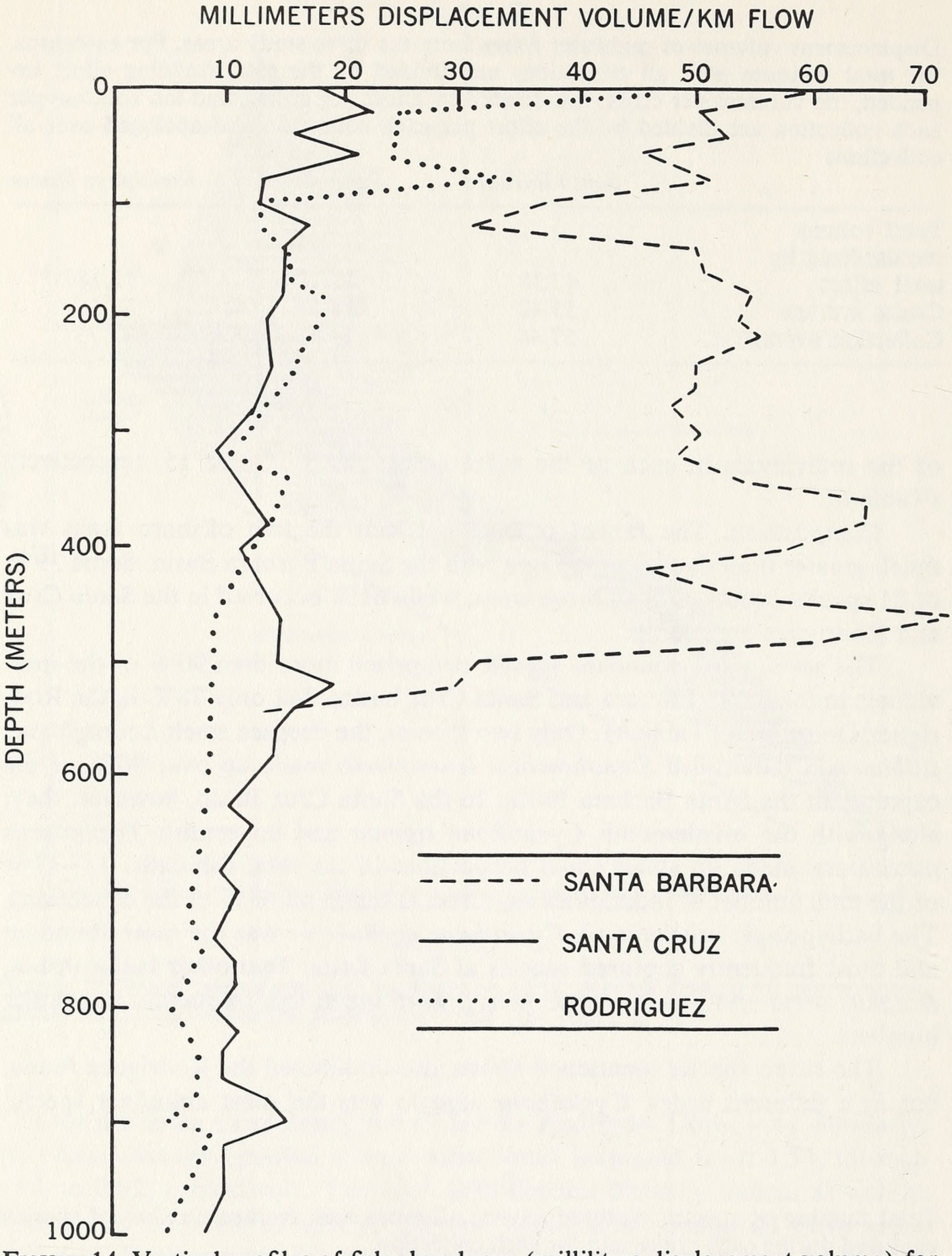

FIGURE 14. Vertical profiles of fish abundance (milliliters displacement volume) for each of the three study areas. Values plotted were computer generated by integrating the displacement volumes over 20 meter depth intervals for the upper 1000 m (see text). The profile for the Santa Barbara Basin is, of course, restricted vertically in this shallow basin.

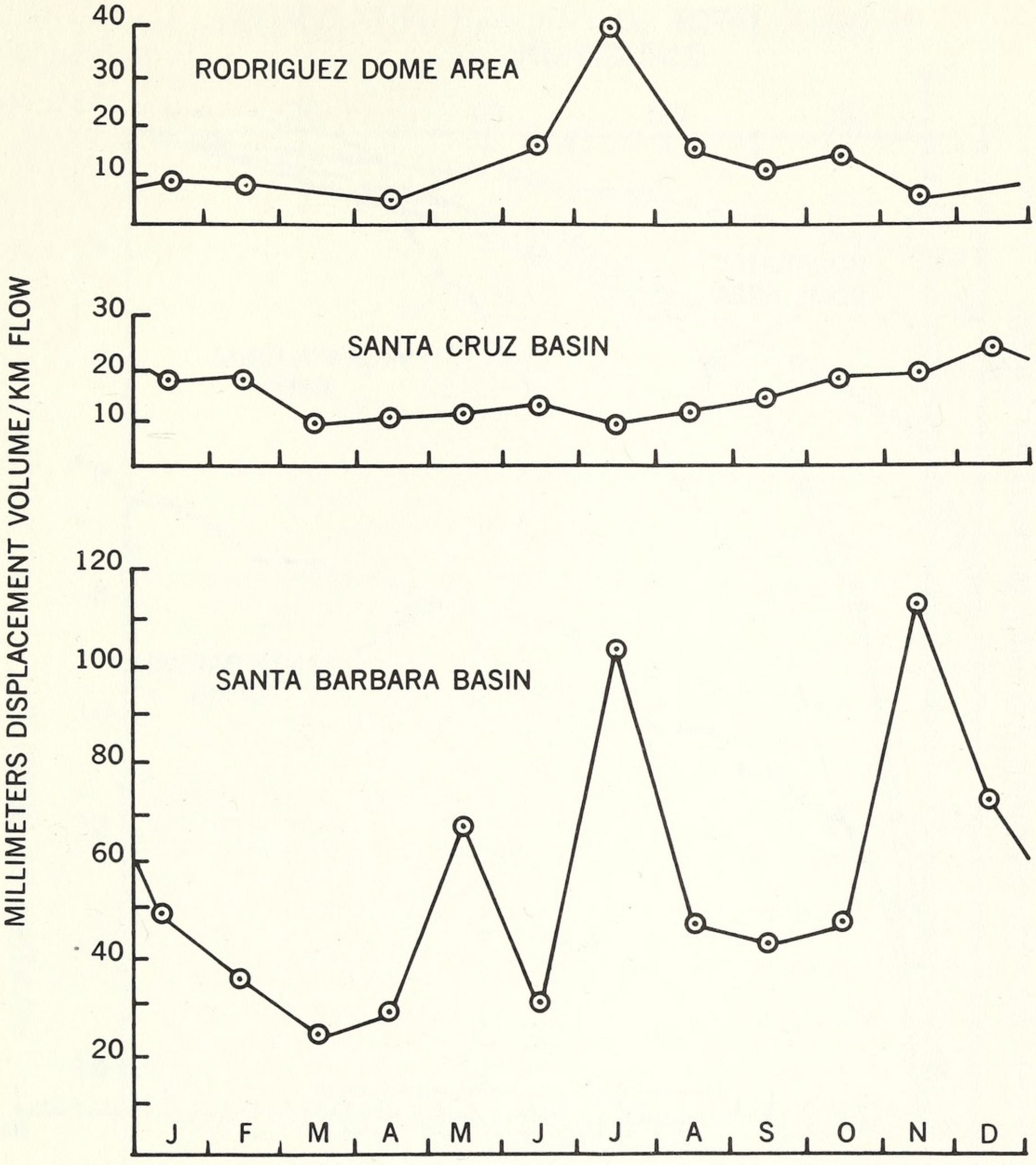

FIGURE 15. Seasonal distribution of fish displacement volumes for the three study areas. Values plotted are the average of the collections pooled by "cruise" for each month in each of the three study areas.

(28%). Next in order, *C. acclinidens* and *S. leucopsarus* comprised 19 and 15% of the total captures, respectively. The other four species comprised much smaller proportions.

Unique and rare species are often quite important in determining faunal intrusions. For example, the distributional center of the alepocephalid *Pellisolus facilis,* taken only in Santa Cruz during the present study, is probably equatorial (Berry and Perkins, 1966). The deep-sea anglerfish *Oneirodes acanthias* and the spookfish *Dolichopteryx longipes* are two other southern

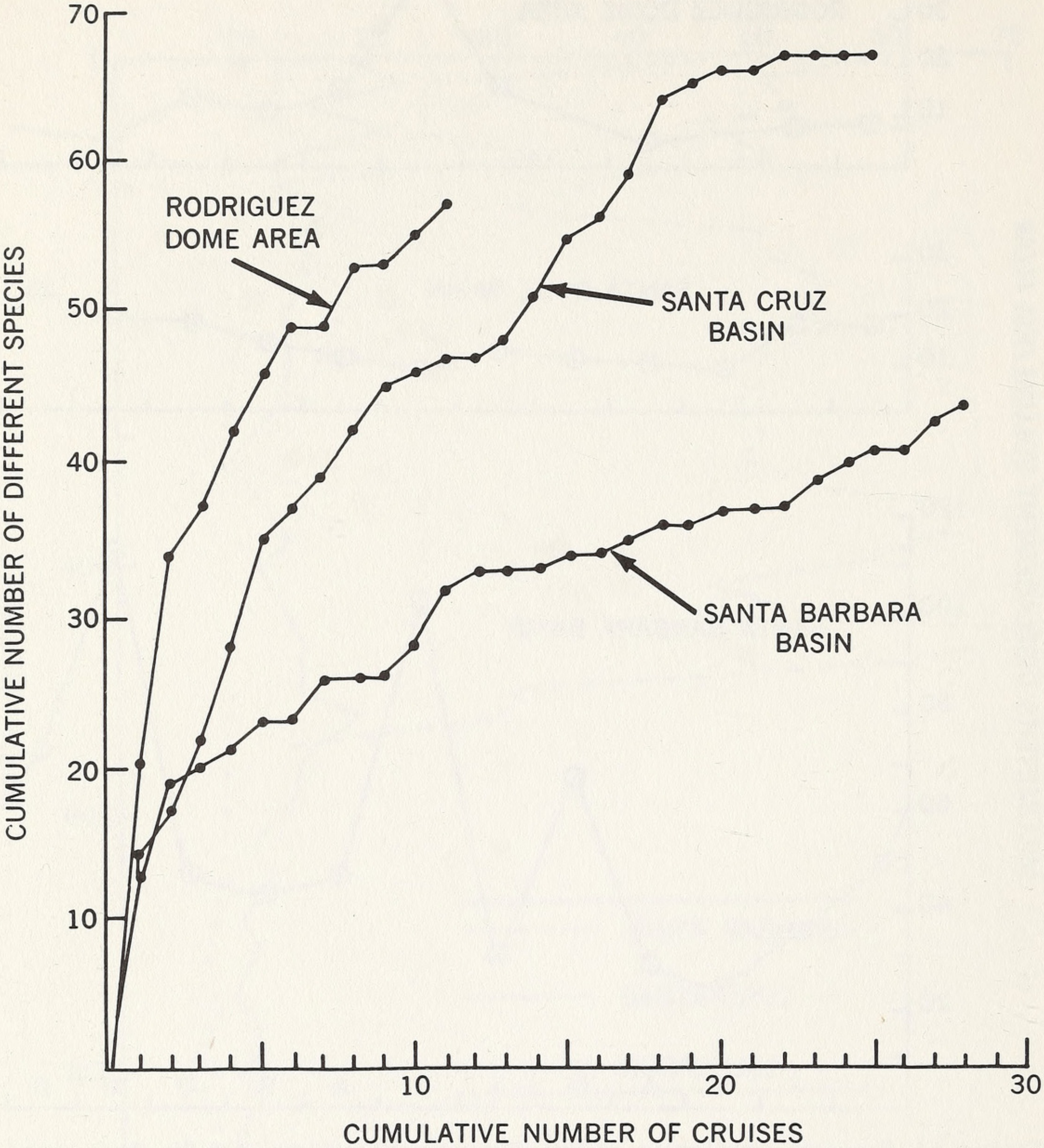

FIGURE 16. Cumulative number of different species plotted against the cumulative number of cruises for each of the three study areas.

species rarely captured as far north over the borderland as the Santa Cruz Basin. However, both species seaward of the borderland are known to occur further north. The stomiatoid *Tactostoma macrops*, three specimens of which were taken at Rodriguez, was among the four most abundant midwater fishes that Pearcy (1964) reported from off the Oregon coast. *Bathylagus ochotensis, Icichthys lockingtoni* and *Macropinna microstoma* are three other northern species occasionally taken at Rodriguez. Among the species taken in but one

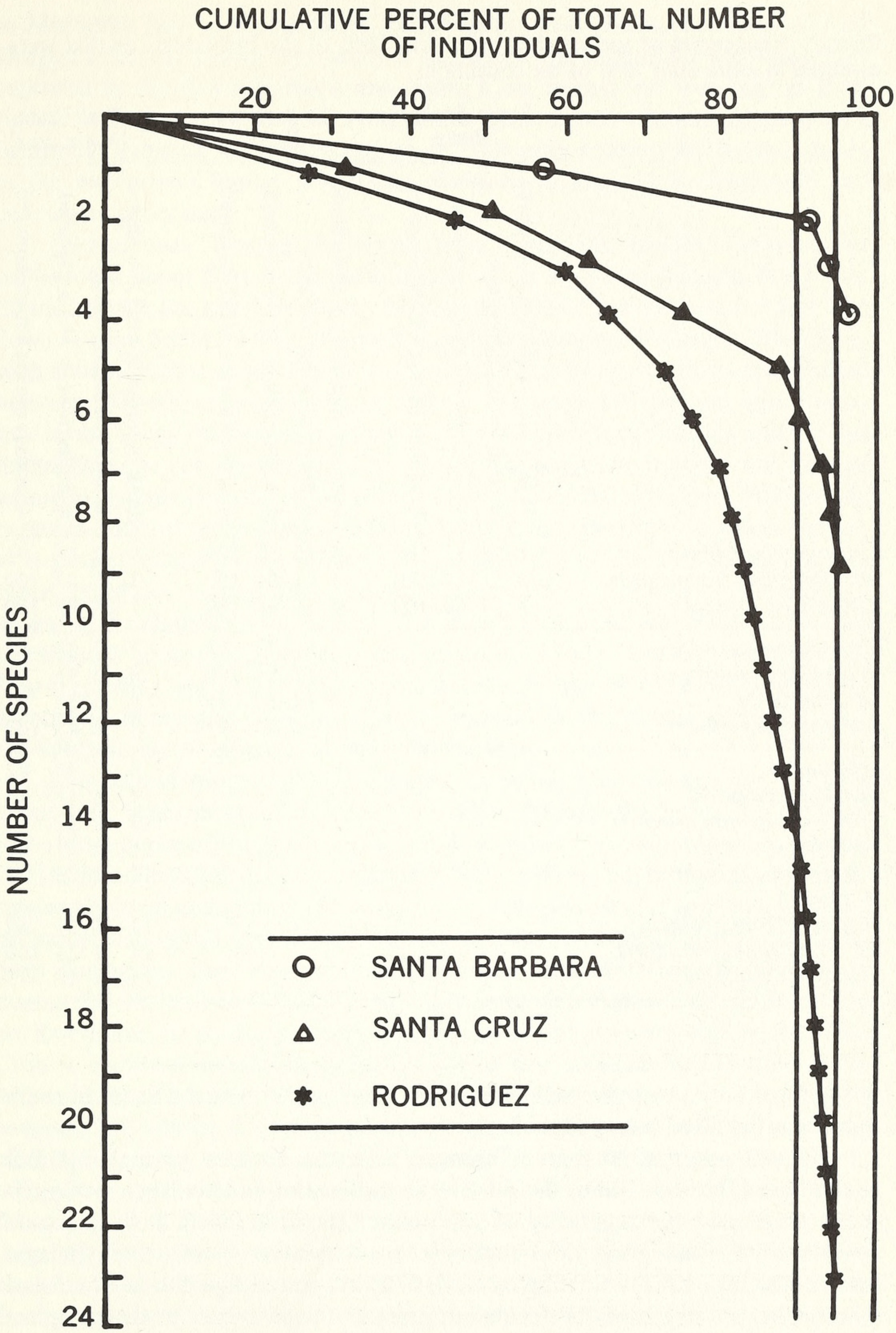

FIGURE 17. Number of species accounting for 95% of the individuals, ranked in descending abundance and plotted as the cumulative percent of total abundance from each of the three study areas.

TABLE 4

Capture frequencies of species that comprised 90% of the individuals or that were captured in more than 50% of the collections

	Santa Barbara Basin				*Santa Cruz Basin*				*Rodriguez Dome area*			
	Rank in terms of total abundance	% total no. of individuals	% collection in which captured	% cruises during which captured	Rank in order of total abundance	% total no. of individuals	% collections in which captured	% cruises during which captured	Rank in terms of total abundance	% total no. of individuals	% collections in which captured	% cruises during which captured
Leuroglossus stilbius	1	58	81	100	3	16	62	100	9	2	31	91
Stenobrachius leucopsarus	2	33	71	100	5	11	64	100	3	15	74	100
Cyclothone signata	3	4	50	100	4	15	69	100	1	28	85	100
Cyclothone acclinidens					1	27	73	92	2	19	88	82
Triphoturus mexicanus					2	17	58	100	8	2	31	82
Diaphus theta					6	4	30	96	5	6	31	91
Lampanyctus ritteri					7	2	34	92	4	6	43	100
Sebastes sp.									6	3	20	82
Larval myctophids									7	2	17	45
Protomyctophum crockeri									10	2	21	82
Bathylagus wesethi									11	2	23	82
Argyropelecus lychnus									12	1	25	73
A. sladeni												
Argyropelecus pacificus									13	1	21	82
Tarletonbeania crenularis									14	1	23	100
Danaphos oculatus									15	1	19	73

of the three areas, only the cat shark *Parmaturus xaniurus* of the Santa Barbara Basin was captured in any abundance.

Several other important differences were the absence of melamphaids in the Santa Barbara Basin, the relative abundance of hatchetfishes in the offshore areas, and the regularity of captures of the lanternfish *Tarletonbeania crenularis* at Rodriguez. Melamphaids are characteristically bathypelagic fishes (Ebeling, 1962). Ebeling et al. (1970) suggested that the hatchetfishes taken in low numbers off California are waifs on the periphery of their tropical distributional centers. Obviously, therefore, their occurrences will increase seaward toward their main ranges. *Tarletonbeania crenularis* is quite abundant in Monterey Bay to the north of Point Conception (Barham, 1957) and off Oregon (Pearcy, 1964). The zoarcid *Melanostigma pammelas* was frequently captured in the Santa Barbara and Santa Cruz basins, but was rare at Rodriguez. It is probably derived from more generalized eelpouts adapted to a benthonic habit on the continental shelf. This may account for its abundance in the borderland basins, which are obviously influenced by benthonic and near shore processes.

Distribution. Among the seven most abundant species, *Leuroglossus stilbius* was about four times more numerous in the Santa Barbara Basin (ca. 20 individuals per km flow effort) than in the Santa Cruz Basin (ca. 5 ind./km flow). In the Santa Barbara Basin it was most abundant between 150–450 m, with a maximum at about 380 m. In the Santa Cruz Basin, it was most abundant between 350–650 m, maximally at 520 m. The several major and minor maxima in the Santa Barbara Basin may represent different age classes and/or diel fluctuations in abundance (Clarke, 1966). Although about equal numbers of young and adult individuals were captured in Santa Barbara, over 70% of the captures were of young individuals in Santa Cruz. Perhaps *L. stilbius* breeds to a greater extent in the offshore areas, then enters the rich Santa Barbara Basin as adults. Young also outnumbered adults at Rodriguez, although all stages were relatively rare there. It has usually been considered as a southern transitional species (Lavenberg and Ebeling, 1967). Barham (1957) and Pearcy (1964) did not record it from Monterey Bay or from off Oregon, respectively. Berry and Perkins (1966) depicted its distributional center over the borderland, to the south of Point Conception.

The second most abundant species, *Stenobrachius leucopsarus,* was also about four times more abundant in the Santa Barbara Basin (ca. 12 ind./km flow) than in the offshore areas (ca. 3 ind./km flow). An abundance minimum at 120 m in Santa Barbara may separate diel maxima and/or age classes. Separate analysis of young and adults, however, revealed similar inflections, which probably distinguish diel concentrations at different depths: shallow at night, deep during the day. Paxton (1967) reported concentrations at 500-700 m during the day and at 100-400 m at night in the San Pedro Basin to the south. At Rodriguez, in contrast, it was always concentrated above 400 m. At Santa Cruz it occurred somewhat deeper, while it was concentrated at only about 250 m in Santa Barbara. Fast (1960) reported a diurnal concentration of adults between 300-500 m, the larvae being restricted to the upper 100 m. The young of *S. leucopsarus,* defined as specimens shorter than 50 mm standard length, comprised approximately 45, 50, and 64% of all individuals of this lanternfish captured in Santa Barbara, Santa Cruz, and Rodriguez, respectively. Like those of *Leuroglossus stilbius,* the young were most abundant offshore. Rodriguez provided the greatest number of unidentifiable larval lanternfishes; Santa Barbara the least. *Stenobrachius leucopsarus* comprised 45% of the individuals reported off Oregon by Pearcy (1964). Aron (1959) noted its abundance in the Gulf of Alaska.

The tiny, light-colored bristlemouth *Cyclothone signata* was captured during every cruise in each of the three areas. At Rodriguez, it was concentrated between 300-500 m (ca. 11 ind./km flow). Similar concentrations were less well defined in the other two areas (ca. 3 ind./km flow at Santa Cruz, ca. one ind./km flow at Santa Barbara). It was always least abundant in the Santa Barbara Basin. Aughtry (1953) described a similar vertical distribution for it in Monterey Bay.

The somewhat larger, black species *Cyclothone acclinidens* was most abundant in the Santa Cruz Basin, with a maximum of ca. 15 ind./km flow at 700-900 m, compared with a maximum of ca. 5 ind./km flow at Rodriguez. The relatively deep bathymetric restriction of this bathypelagic bristlemouth apparently precludes its establishment in the Santa Barbara Basin, even though young and halfgrown individuals were occasionally captured there. The Santa Cruz Basin may serve to concentrate the breeding population. Water flowing into the borderland at depth from the south is funneled between the Santa Rosa-Cortez Ridge and the coast into the Santa Cruz Basin. In the process, bathypelagic and lower mesopelagic species may be concentrated at depth in Santa Cruz as the water finally rises and passes over the northward extension of this ridge. Resident breeding populations would be restrained by the relatively shallow ridge and island chain to the north and west.

The lanternfish *Triphoturus mexicanus* was captured during every cruise in the Santa Cruz Basin, where it was almost 10 times more abundant (ca. 5 ind./km flow at two maxima) than at Rodriguez (ca. 0.5 ind./km flow). Concentrations marked by sharp abundance maxima near the surface and at 500 m indicated that it ascends as relatively dense shoals toward the surface at night. It was seldom captured in the Santa Barbara Basin. It has a southern distribution; very few captures have been noted north of Point Conception.

Diaphus theta was equally abundant in Rodriguez and Santa Cruz (ca. 2.5 ind./km flow at maxima), although its vertical distributions appeared to be quite different between the two areas. It had a relatively shallow distribution in the Santa Cruz Basin at all times, with a distinct abundance maximum between 0-100 m and a lesser maximum at about 200 m (ca. 1.0 ind./km flow). At Rodriguez the order was reversed, with a lesser shallow maximum between 0-250 m (1.5 ind./km flow) and a distinct greater maximum at about 400 m (2.5 ind./km flow). Paxton (1967) concluded that it ascends from 400-600 m into the upper 50 m at night. Although such extensive vertical migrations were suggested by the observed bimodal vertical distribution at Rodriguez, the general pattern was obscure. This somewhat confused diel pattern of movement may reflect what has been called the dynamic nature of the species (Barham, 1957). It may randomly move into and out of the area. Like *Triphoturus mexicanus,* this offshore lanternfish was seldom captured in the Santa Barbara Channel. It has an antitropical distribution, being confined to transitional waters between 25-55°N in the Northern Hemisphere and between equivalent latitudes in the Southern Hemisphere (Bussing, 1965). It comprised 21% of all individuals captured off Oregon during a similar trawling study (Pearcy, 1964).

Lampanyctus ritteri was most abundant at Rodriguez, where it was captured at a rate of ca. 2.5-4.0 ind./km flow, as compared with ca. 1.0 ind./km flow in Santa Cruz at a near-surface maximum. Like the other offshore lanternfishes, it was rarely captured in the Santa Barbara Basin. It appears to be confined to the upper 400-500 m and has a lesser abundance maximum between 100-300 m (ca. 1.5 ind./km flow) in Rodriguez. Berry and Perkins (1966) depicted this species as ranging from Baja California, Mexico to San Francisco, California. Aron (1959) reported captures from the Gulf of Alaska. It may have its distributional center offshore in the transitional water bordering the tropical central region to the west (Pieper, 1967).

DISCUSSION

The Santa Barbara Basin contains a relatively large standing crop of fishes composed of relatively few species. Both offshore areas contain more characteristically oceanic species and a noticeably smaller standing crop. Because the offshore areas are deeper, they support a typical bathypelagic fauna, which cannot invade the relatively shallow Santa Barbara Basin. Brown (1969) showed that more factors, which defined groups of associated species and environmental measures, were needed to describe adequately the offshore faunal assemblages of fishes than to describe the simpler assemblage in the Santa Barbara Basin. Also, in an analysis of both fishes and invertebrates, Ebeling et al. (1971) showed that more "transitory groups" of animals and resident communities were represented in the Santa Cruz Basin than in the Santa Barbara Basin. Both studies showed that fish volumes were invariably correlated with increasing abundances of animals characteristic of the inshore Santa Barbara Basin.

Thus, there is an offshore increase in faunal diversity with contributions from more exotic species. Similarly, Ebeling et al. (1970) showed that the intermediate-deep Santa Catalina Basin to the south has a more diverse and typical oceanic fauna than the shallow inshore San Pedro Basin, which occupies a position analogous to that of the Santa Barbara Basin. Although in the present study the faunas of the two offshore areas resemble each other more than either resembles that of the Santa Barbara Basin, collections from the Rodriguez Dome area did average slightly more species in less abundance than did those from the Santa Cruz Basin. This basin is the northern terminus of a chain of basins progressively filled by deep water flowing up from the south. Therefore, it recruits deep water species from the south more readily than those from the oceanic realm to the west. Central and northern species have more direct access to Rodriguez.

Subsequent collections not included here substantiate the faunal trends discussed above (Brown, 1969). A series of collections taken during November, 1967, generally show the offshore trend in abundance and diversity. Of the 44 collections in this series, 32 were from the offshore areas and 12 were from the Santa Barbara Basin. The cumulative frequencies of displacement volumes and diversities for the test fish collections from inshore and offshore areas were calculated and plotted against the expected frequencies obtained from graphs of cumulative frequency vs all previous collections. The distributions of abundance and diversity based on the 44 test collections, in fact, generally coincided with the distributions based on all the rest. And, as in all previous collections, the 12 inshore test collections were dominated by the deep-sea smelt *Leuroglossus stilbius* and the lantern fish *Stenobrachius leucopsarus,* while the 32 offshore collections were dominated by the bathypelagic bristlemouth *Cyclothone acclinidens,* mesopelagic *C. signata,* or the southern lanternfish *Triphoturus mexicanus.*

Multivariate statistical analyses by Brown (1969) and by Ebeling et al. (1971) resolved a discrete group of intercorrelated measures of water mass change–temperature at given depths, season, and upwelling–which lacked biological correlates of species abundances or total standing crop measured by displacement volumes. Among the physical measures of the environment used, only those of position, such as locality, bottom depth, trawl depth, and trawl temperature, which was a strong correlate of trawl depth, had biological correlates. Depth and physiography, therefore, seem to explain the observed local faunal differences better than major water mass characteristics, which may influence the transitional fauna as a whole, but which are modified locally by nearshore processes. Also, Riley (1963) pointed out that causal relationship among different environmental measures may not be simple, i.e., may not be expressed by a simple linear correlation, because of time lags and complex phase interactions. Therefore, the distinctions among the three faunas are rationalized in terms of four local "positional" characteristics of the three study areas: physiographic isolation; local hydrography; depth differences; and nearness to the coast.

In the relatively rich Santa Barbara Basin, the regeneration and replacement of inorganic nutrients in the surface waters is facilitated by upwelling from the relatively shoal bottom. The presumed high productivity of the surface waters is reflected by a pronounced decrease in dissolved oxygen content below the thermocline to almost zero near the bottom. The adjacent coastal zone is an additional important source of nutrients. The chain of Channel Islands partially isolates the Santa Barbara Basin from the open ocean and thereby inhibits mixing of the inshore water mass with the offshore waters. Therefore, the nutrients are concentrated in this "eutrophic" basin (Robert W. Holmes, personal communication). The physiographic isolation and relatively shallow bottom depth of the basin limit faunal diversity in Santa Barbara. Reduced interaction with surrounding areas restricts faunal intrusions. Bathymetric confinement excludes a true bathypelagic fauna. The wide fluctuation in abundance and diversity observed at Santa Barbara may be due to local effects within the semi-isolated circulation of the area, which is least buffered by the open ocean.

The offshore areas communicate more directly with the open sea. But the relatively high Santa Rosa-Cortez Ridge prevents unlimited oceanic exchange of the deeper Santa Cruz Basin water. Located over the continental slope, the Rodriguez Dome area is directly influenced by the open ocean. Consequently, the primary faunal regions to the north, south, and west contribute exotic species to the area's heterogenous fauna. Its direct contact with the California Current accounts for the regular occurrence of northern and central species in this area, so that the Rodriguez fauna is characteristically the most typical of the open ocean.

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APPENDIX

List of fishes collected during trawling studies off Santa Barbara, California, 1964-67

(Rare species—except for the cat shark *Parmaturus xaniurus,* which was taken 48 times—captured in but one of the three sampled areas: Santa Barbara Basin*, Santa Cruz Basin**, and Rodriguez Dome area***)

Scyliorhinidae (young)
*Parmaturus xaniurus**
Serrivomeridae
*Serrivomer sector***
Nemichthyidae
*Nemichthys scolopaceus***
Clupeidae (larvae)
*Sardinops caeruleus**
Engraulidae (larvae)
Engraulis mordax
Argentinidae
*Argentina sialis**
Nansenia sp.**
Bathylagidae
Leuroglossus stilbius
*Bathylagus ochotensis****
B. wesethi
B. milleri
Opisthoproctidae
*Macropinna microstoma****
*Dolichopteryx longipes***
Gonostomatidae
Cyclothone signata
C. acclinidens
C. pallida
Cyclothone sp.
Danaphos oculatus
Vinciguerria lucetia
Ichthyococcus irregularus
Sternoptychidae
Argyropelecus affinis
A. hemigymnus
A. lychnus
A. sladeni
Sternoptyx diaphana
Melanostomiatidae
*Tactostoma macropus****
Bathophilus flemingi
Malacosteidae
Aristostomias scintillans
Chauliodontidae
Chauliodus macouni
Stomiatidae
Stomias atriventer
Idiacanthidae
Idiacanthus antrostomus
Alepocephalidae (mostly young)
Bajacalifornia burragei
Sagamichthys abei
*Pellisolus facilis****
Holtbyrnia macrops
Holtbyrnia melanocephala
Paralepididae (larvae and young)
Lestidium ringens
Lestidium sp.
Macroparalepis sp.**
Myctophidae
Protomyctophum crockeri
*Diogenichthys atlanticus****
Symbolophorus californiensis
Tarletonbeania crenularis
Diaphus theta
Stenobrachius leucopsarus
Triphoturus mexicanus
Lampanyctus ritteri
Lampanyctus regalis
Parvilux ingens
Myctophid larvae
Scopelarchidae (larvae)
Benthalbella linguidens
Benthalbella dentata
Benthalbella sp.
Neoscopelidae
*Scopelengys tristis***
Oneirodidae
*Oneirodes acanthias***
Gadidae (larvae and young)
Merluccius productus
Zoarcidae
Melanostigma pammelas
Macrouridae
Nezumia stelgidolepis
Prejuvenile macrourid**
Scomberesocidae
*Cololabis saira***
Melamphaidae
Scopelogadus mizolepis bispinosus
Poromitra crassiceps
Melamphaes acanthomus
Melamphaes lugubris
Anoplogasteridae
Anoplogaster cornuta

Syngnathidae (young)
Syngnathus californiensis
Scorpaenidae (larvae and young)
Sebastolobus altivelis
Sebastolobus sp.
Sebastes sp.
Zaniolepididae (larvae)
Zaniolepis sp.*
Cottidae (larvae)
Scorpaenichthys marmoratus
Agonidae (larvae and young)
Cyclopteridae (young)
Paraliparis sp.*
Nectoliparis pelagicus
Carangidae (larvae)
Trachurus symmetricus
Brotulidae (larvae)
*Cataetyx rubrirostris**
Blenniidae* (larvae)
Stromateidae (larvae and young)
*Icichthys lockingtoni****
Peprilus simillimus
Bothidae (larvae)
Citharichthys sordidus
Citharichthys xanthostigma
Citharichthys stigmaeus
Pleuronectidae (larvae)
Microstomus pacificus
Glyptocephalus sp.
Flatfish larvae

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