DISTRIBUTION OF MIDWATER FISHES
AMONG DEEP-WATER BASINS
OF THE SOUTHERN CALIFORNIA SHELF [1]

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THE ENVIRONMENT

Depressions in the relatively narrow continental borderland off southern California provide a nearshore deep-sea habitat extending among the California Islands from Point Conception southward to beyond the Mexican border. Geologic instability of this area has resulted in a tectonic multiplication of ridges delimiting 14 basins, which may be classified as to their depth, physicochemical properties, and distance from shore (Emery, 1960).

Ocean currents in the borderland are complex and marked by the presence of surface eddy patterns. One major current system flowing into the borderland, the southerly moving California Current, is part of the great clockwise circulation of water in the North Pacific Ocean. Subsurface currents derived from the California Current influence the development of eddy systems. A permanent eddy, including the northward-flowing southern California Counter Current, is established over the deep offshore basins and Santa Cruz Basin. Below 500 meters, a deeper counter current flows gradually northward throughout much of the borderlands and approaches the surface during late summer and fall. From spring to fall the California Current predominates, while in late fall through winter the area is influenced by the deeper counter current and local cooling (Sverdrup et al., 1942; Reid et al., 1958).

Upwelling, a transport of cold, deep, nutrient-rich water to the surface, is strongest in the borderland during May and June, when the northwesterly winds prevail. The resulting enrichment of the photosynthetic surface community and, therefore, increased productivity indirectly accounts for the relatively large standing crop of deep-sea animals here.

Borderland water masses ("transitional waters") are derived from three sources (figs. 1, 2). From the north, the component of Subarctic Water ("northern water") is relatively cool, low in salinity, well-oxygenated, and rich in nutrients. This mixes at intermediate depths with a component from the west, the North Pacific Central and Intermediate waters ("central water"), identifiable by its temperature-salinity maximums and low nutrient content. From the south, the component of Pacific Equatorial Water ("southern water") is marked by another salinity maximum. This nutrient-rich but oxygen-poor intrusion fills the depths of the basins below their sills (Sverdrup et al., 1942; Reid et al., 1958; Emery, 1960). In general, therefore, the physicochemical structure of a given water column reflects the varied origin of its vertical components and the individual constitution of its deep waters below sill depth (fig. 1).

Vertically, faunal zones may be defined by light penetration, temperature, and water-mass structure. The thermocline (zone where temperature decreases rapidly with depth) subtends the euphotic epipelagic zone where photosynthesis occurs and temperatures fluctuate greatly both diurnally and seasonally. Nearshore, turbidity restricts this zone to about the upper 50 meters, but it is expanded offshore in the clearer oceanic waters. Within the permanent thermocline, below the compensation depth (depth where photosynthetic anabolism just balances respiratory catabolism), the mesopelagic zone extends to the 6°C isotherm at about 500-600 meters (Bruun, 1956; Hedgpeth, 1957). Although some sunlight filters to the upper mesopelagic in the seasonal thermocline at 100-150 meters, the deeper mesopelagic in the permanent thermocline is lighted only by animal bioluminescence. In the borderland, the lower limit is also marked by the zone at which the water mass first contains more than 50 per cent southern water, so that the interface between the mesopelagic and the next deeper zone (bathypelagic) is a band of mixed northern and southern waters. The bathypelagic extends to near the bottom where, in the borderland, southern water predominates. This deep zone differs from the others by its extensive vertical expansion offshore from the shallow basins, in which it is absent or greatly restricted. In the cold waters filling the basins below sill depth, fishes are black, soft-bodied, and sluggish, as compared with their silvery, active relatives in the mesopelagic (Marshall, 1954, 1960).
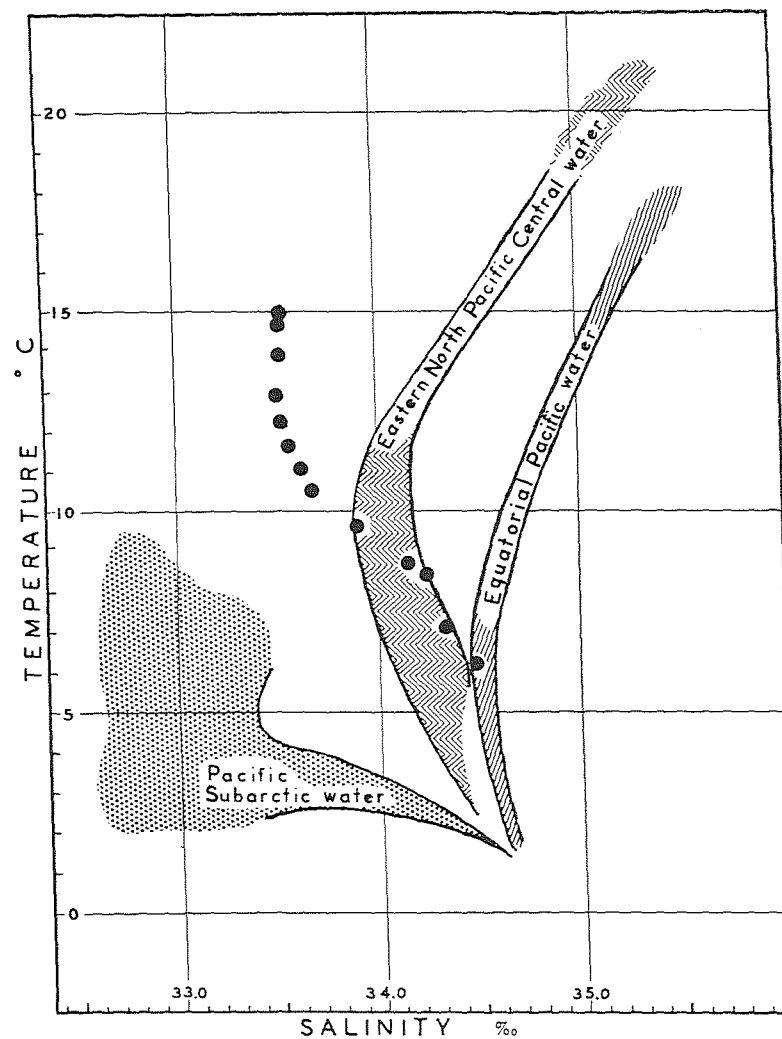

Fig. 1. Water masses of the eastern North Pacific Ocean. The broad lines enclose water-mass envelops, which delimit the extremes in the family of curves of temperature plotted against salinity with depth that defines the oceanic water mass (after Sverdrup et al., 1942). The series of points are temperature-salinity coordinates of mixed "transitional water" in the San Pedro Basin. Note that the deep layer (5-10 °C) is influenced by Pacific Equatorial (southern) Water, the shallow layer by Pacific Subarctic (northern) Water. The intermediate layer may be derived partly from North Pacific Central Water.
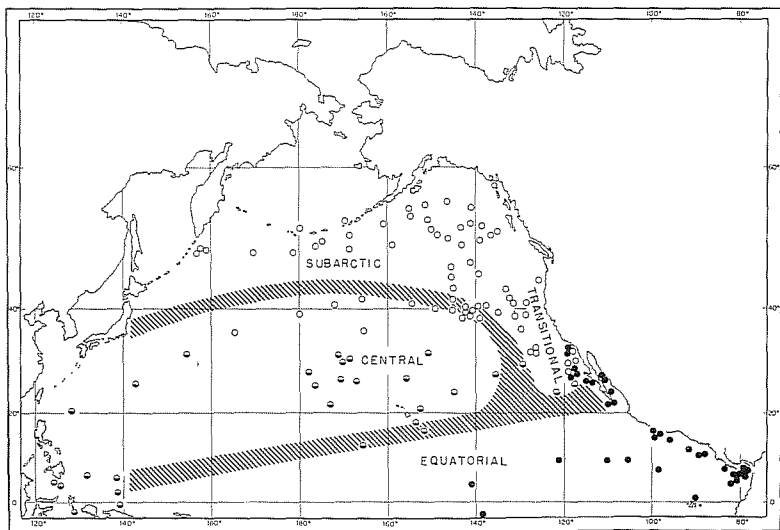
Fig. 2. Distributions of: open circles, a subarctic midwater fish (*Melamphaes lugubris*); solid circles, two equatorial species (*M. acanthomus, M. macrocephalus*); half circles, two central species (*M. simus, M. danae*) (mostly after Ebeling, 1962, with additional eastern Pacific captures of *M. simus* from records of the Scripps Institution of Oceanography, courtesy of Drs. Carl L. Hubbs and Richard H. Rosenblatt). Note the co-occurrence of all faunal elements in the vicinity of the borderland. The hatched bands delimit Pacific Subarctic, Central (partition of eastern and western components omitted), and Equatorial waters. The transitional water off the American Pacific Coast contains components of all three sources.

The shallow inshore basins of the borderland include, from north to south, the Santa Barbara, Santa Monica, and San Pedro basins. Sills ranging in depth from 425 meters in the Santa Barbara Basin to 737 meters in the San Pedro constitute the deepest access to the basins, which range in depth from 627 meters in the Santa Barbara Basin to 912 meters in the San Pedro. Generally they contain two local water types, derivatives of northern surface water and deep southern water. A broad band of mixed water occurs at intermediate depths between 500 and 600 meters. The Santa Barbara Basin contains no southern water and, therefore, has no true bathypelagic zone.

The sills of inshore basins lie within the oxygen minimum layer. Consequently, the oxygen content of subsill water is extremely low, reaching a concentration of no more than 0.2 ml/liter

near the bottom. Hartman and Barnard (1958) suggested that oxygen depletion may impoverish the resident benthic fauna. The poorly represented bathypelagic fauna inhabits a narrow zone between 600 and 900 meters, which usually contains modified but recognizable southern water.

A series of intermediate deep basins includes the Santa Cruz Basin, Santa Catalina Basin, and San Diego Trough. Sills, ranging in depth from 982 meters in the Santa Catalina Basin to 1,085 meters in the Santa Cruz constitute the deepest access to the basin depths, ranging from 1,357 meters in the Santa Catalina Basin to 1,966 meters in the Santa Cruz. In contrast with water masses filling the shallow inshore basins, the more extensive deep waters below sill depth include easily identifiable southern components and contain about 0.5 ml/liter of dissolved oxygen in the oxygen minimum layer. Consequently, the bathypelagic fauna is more diverse over a wider vertical range and the benthic fauna is relatively well developed.

The deep offshore basins include the Tanner, San Nicolas, West and East Cortez, Long, San Clemente, No Name, and Velero basins. They have considerable oceanic exchange over their deep sills, which range in depth from 1,106 meters in the San Nicolas Basin to 1,902 meters in the Velero. The basins range in maximum depth from 1,551 meters in Tanner Basin to 2,571 meters in Velero, the deepest of all borderland depressions. San Nicolas and San Clemente basins are simply extensions of intermediate deep basins. Vertically, they resemble the open ocean, in that the oxygen minimum of 0.7 ml/liter is centered at about 800 meters; recognizable southern water fills the depths; central water is detectable in the intermediate masses; the three depth zones (which support a more diverse deep-sea fauna) are further expanded; and the benthic fauna is richly developed. (The oceanography of the borderland is described in Emery, 1960.)

More than 100 miles offshore, westward and southward of the borderland, vertical organic enrichment around seamounts and islands supports an abundant and typically oceanic deep-sea fauna. Collections from the vicinity of the San Juan Seamount, about 125 miles west of Santa Barbara, resemble more closely those taken near Guadalupe Island, about 160 miles off Baja California, than others from the borderland basins. Here surface waters move southwestward with the California Current, the intermediate water masses of the mesopelagic zone contain distinct central as well as subarctic components, and the deep waters of the fully extended bathypelagic zone comprise North Pacific Intermediate Water (which generally subtends the vast central gyre to the westward) as well as southern water. The composition of these deep waters is characteristic of the bathypelagic zone and is unaltered by semi-isolated basins. The oxygen-minimum layer

between 500 and 1,000 meters is an extension of the vast oxygen-deficient wedge of water at intermediate depths in the eastern tropical Pacific (Weyl, 1965).

The present study of the deep-sea fishes of the borderland was undertaken to analyze, among basins and depths, the contribution of each faunal component (northern, southern, central) to the total heterogeneous assemblage. Considered in particular are the constitutive effects of water masses, diurnal periodicity, and seasonal abundance.

METHOD

Since 1960, marine biologists at the University of Southern California have been comparing the midwater environments among a shallow inshore basin (San Pedro), an intermediate deep basin (Santa Catalina), a deep offshore basin (San Nicolas), and the oceanic deep sea off California and Baja California. Trawling for deep-sea animals was mainly accomplished from the University of Southern California Research Vessel *Velero IV*, with a 10-foot Isaacs-Kidd Midwater Trawl having a continuously open net. The present study is based on nearly 200 such trawls. Supplementing the trawling data, hydrographic and plankton stations are providing correlative information on water-mass structure (temperature, salinity, and oxygen content) and plankton associations. Also, in 1964, the University of California, Santa Barbara, initiated a program of discrete depth sampling (cf. Aron et al., 1964) of the Santa Barbara and Santa Cruz basins, from the chartered General Motors Research Vessel *Swan*. The resulting closed-net samples from narrow depth intervals are being subjected to numerical analyses, which are resolving unit faunal associations.

Geographical and ecological faunal analyses were accomplished in two ways. First, Lavenberg subjectively compared the fish distributions with such factors as locality among the basins, distance offshore, depth, water-mass structure, diurnal period, and season. Exotic species exemplified the heterogeneous constitution of the borderland fauna. Vertical distributions were plotted across profiles depicting the three depth zones.

Next, Ebeling subjected the capture data to a computerized cluster analysis of spatial groupings. Associations of all possible species pairs were calculated as correlation coefficients arranged as a matrix of comparisons. Clusters of ecologically related species were represented as a dendrogram of spatial relationships, which was computed using the unweighted pair-group method of Numerical Taxonomy (cf. Sokal and Sneath, 1963). Neushul (in press) used this method in defining ecological associations of sub-tidal marine vegetation. To examine correlations of these groups with various environmental parameters measured at the time of capture, multiple regressions of their abundance among stations (dependent variable, y) were computed for such factors as depth, time of day, position in latitude and longitude, season, etc. (independent variables, $x_1 \ldots x_n$). In this analysis, total variability in abundance is partitioned into that due to regression (i.e., accountable for by the concordant variability of the independent variables) and an "error term" (i.e., scatter due to random variability), which may be used as an index of sample contamination or of the reliability of the independent variables in predicting group abundances. The variability due to regression is, in turn, partitioned into the partial components of each independent variable (cf. Fager and McGowan, 1963; Seal, 1964).

DISTRIBUTION OF MIDWATER FISHES

The complex hydrographic regime of the borderland, where local, northern, southern, and, to a lesser extent, central water masses mix, accounts for the heterogeneity of the included fauna (fig. 2). Although the deeper northern fishes are somewhat seasonal in distribution, they do, for example, generally co-occur with southern species in the basin depths and are not completely excluded from southern water. Some borderland fishes comprise allochthonous populations of non-reproductive adults, whose breeding grounds occur far to the north or south. Northern and central species may occupy the same intermediate depths, especially in the offshore deep basins and oceanic areas. Notwithstanding this faunal overlap, the origin of all diverse elements can be inferred from their usual water-mass associations and from an examination of their main distributional centers in adjacent water masses. The constituent water masses become progressively altered shoreward. This, together with the inshore restriction of the midwater habitat (especially the bathypelagic zone), probably causes the observed shoreward decrease in midwater species diversity (Pearcy, 1964).

Vertically, these fishes are associated with the bathymetric zones, which, as previously explained, are characterized partly by their contained relative proportions of northern, central, southern, and local water-mass components. But no midwater species is known to occur during photic periods in the epipelagic zone. Various species, especially the mesopelagic fishes, are capable of diurnal interzone migrations (e.g., most lanternfishes and the hatchetfishes *Argyropelecus* and *Sternoptyx*). Bathypelagic fishes may migrate into the mesopelagic zone, especially during the night (e.g., the eel, *Nemichthys scolopaceous*; the bigscale, *Melamphaes acanthomus*; and the eelpout, *Melanostigma pammelas*). These diurnal vertical migrations, of course, tend to obscure the vertical distributions and water-mass associations of certain species.

The Northern Faunal Component

Thirty-two species that generally inhabit the Pacific Subarctic Water Mass comprise the northern component of the borderland fauna (Lavenberg, 1964; Paxton, 1965). Their centers of distribution generally occur outside the borderland in the boreal North Pacific (fig. 2), which contains a highly endemic fauna. Some of these species occur across the Pacific (e.g., the deep-sea smelt, *Bathylagus milleri*, and lanternfish, *Tarletonbeania crenularis*). Others, ranging further south, are mainly restricted to transitional water in the temperate and subtropical eastern North Pacific (e.g., the deep-sea smelt, *Leuroglossus stilbius*, and lanternfish, *Stenobrachius leucopsarus*). Still others are most abundant further offshore, where the peripheral influence of central water is greatest (e.g., the deep-sea smelt, *Bathylagus pacificus*, and lanternfish, *Lampadena urophaos*). Typical indicators of the northern fauna include *B. milleri* and the bigscale, *Melamphaes lugubris* (fig. 2).

Vertically during the day (figs. 3-5), a small group of fishes is associated with the upper mesopelagic zone (e.g., the pencilsmelt, *Nansenia candida*, fig. 3; the barracudina, *Lestidium ringens*, fig. 4; the lanternfishes, *Diaphus theta* and *Protomyctophum crockeri*). Most northern species occur in the lower mesopelagic between 300 meters and the bathypelagic zone (e.g., halfgrown slickhead, *Sagamichthys abei*, fig. 3; *Leuroglossus stilbius*, fig. 3; the lanternfishes, *Lampanyctus ritteri* and *Stenobrachius leucopsarus*). A few inhabit the bathypelagic zone below 600-700 meters (e.g., *Bathylagus milleri*, fig. 3; the stomiatoids, *Aristostomias scintillans* and *Chauliodus macouni*, fig. 4; the lanternfish, *Lampanyctus regalis*). Although often associated with the southern species, most are generally seasonal and are most common during periods of northern water intrusions during late winter and spring. As expected, the bathypelagic species are most common in intermediate deep and deep offshore basins.

The Southern Faunal Component

The 76 species of southern fishes inhabiting the borderland make up the largest faunal component. Their centers of distribution occur to the south and west in the Pacific Equatorial Water Mass (fig. 2), which, like the Subarctic, contains a remarkably endemic fauna. Some southern species, however, are circumequatorial (e.g., the hatchetfish, *Sternoptyx diaphana*, and the bristlemouth, *Cyclothone microdon*) and others are almost cosmopolitan (e.g., the fangtooth, *Anoplogaster cornuta*, and the bigscale, *Poromitra crassiceps*). Some are concentrated in the productive waters over and about the continental shelf (e.g., the eelpout, *Melanostigma pammelas*, and slickhead, *Talismania*
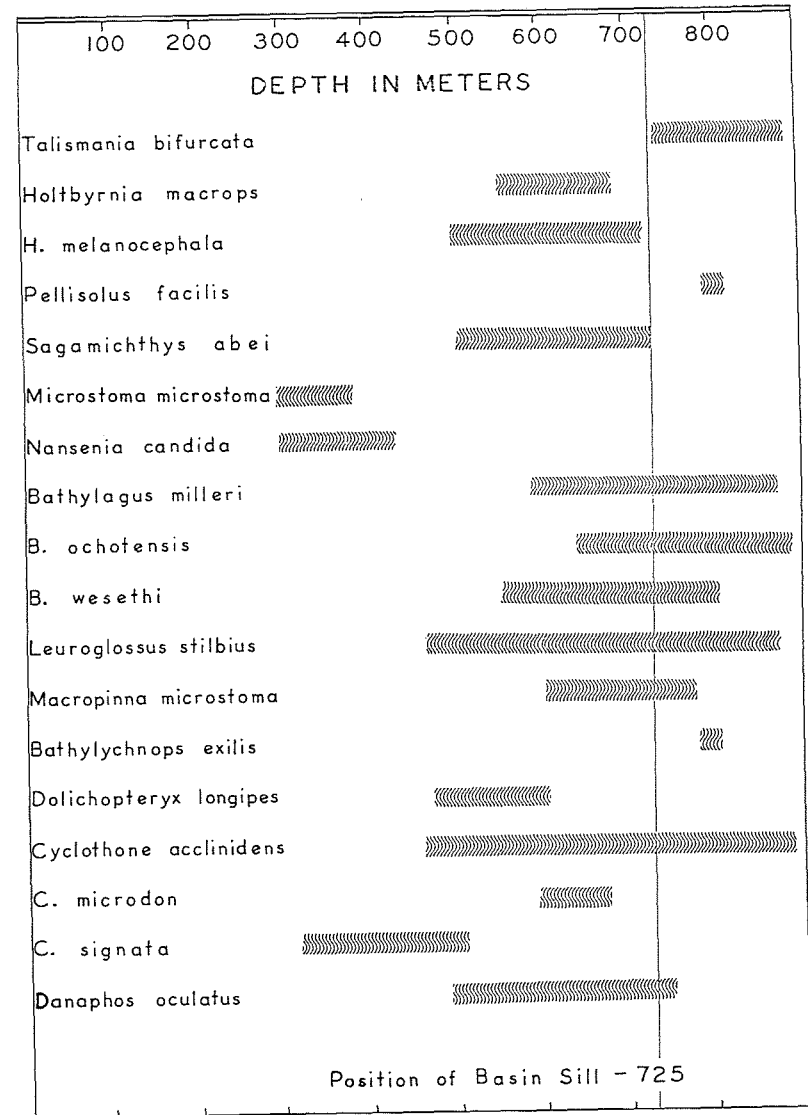

Fig. 3

Figs. 3-5. Vertical ranges (hatched bars) of midwater fishes in the San Pedro Basin. The basin sill depth in meters is indicated by a vertical line at the right of the graph.
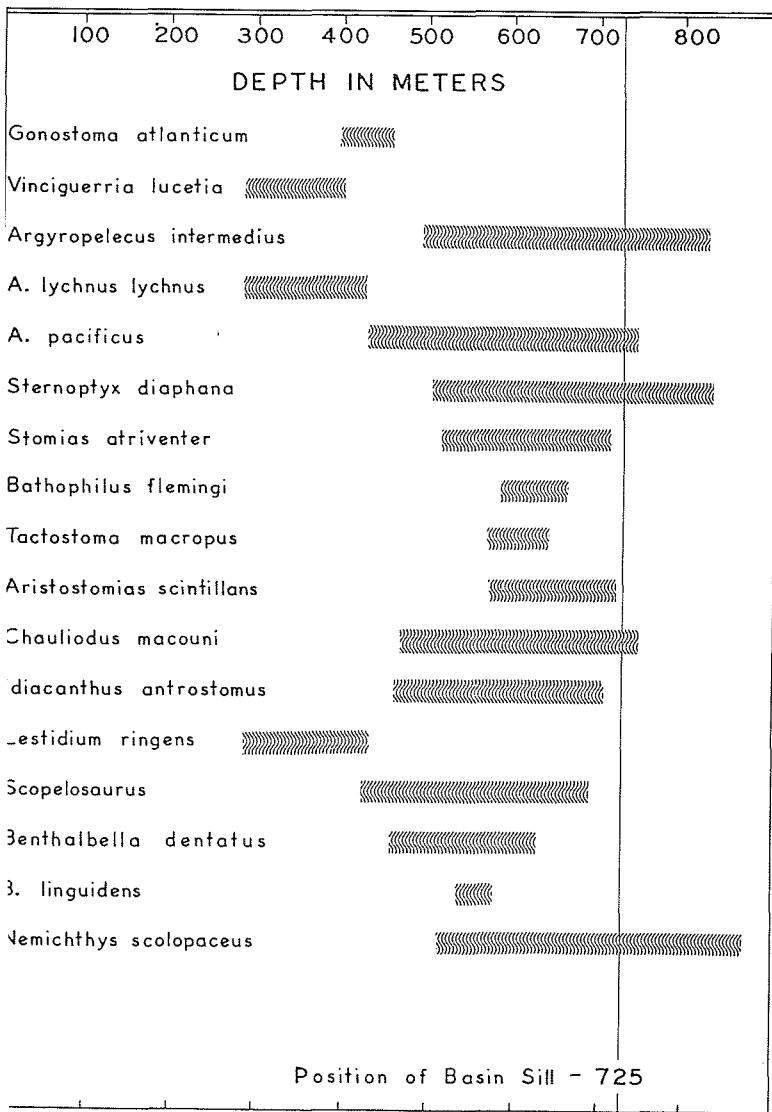
Fig. 4

DEPTH IN METERS

100 200 300 400 500 600 700 800

Gonostoma atlanticum

Vinciguerria lucetia

Argyropelecus intermedius

A. lychnus lychnus

A. pacificus

Sternoptyx diaphana

Stomias atriventer

Bathophilus flemingi

Tactostoma macropus

Aristostomias scintillans

Chauliodus macouni

diacanthus antrostomus

Lestidium ringens

Scopelosaurus

Benthalbella dentatus

B. linguidens

Nemichthys scolopaceus

Position of Basin Sill — 725

Fig. 4

Fig. 5

DEPTH IN METERS

100 200 300 400 500 600 700 800

Serrivomer sector

Chlopsis gilberti

Nezumia stelgidolepis

Melanonus zugmayeri

Merluccius productus

Anoplogaster cornuta

Melamphaes acanthomus

M. lugubris

Poromitra crassiceps

Scopelogadus mizolepis
  bispinosus

Lycodapus fierasfer

Lycodopsis pacificus

Melanostigma pammelas

Cataetyx rubrirostris

Caulophryne jordani

Oneirodes acanthias

O. esrichtii
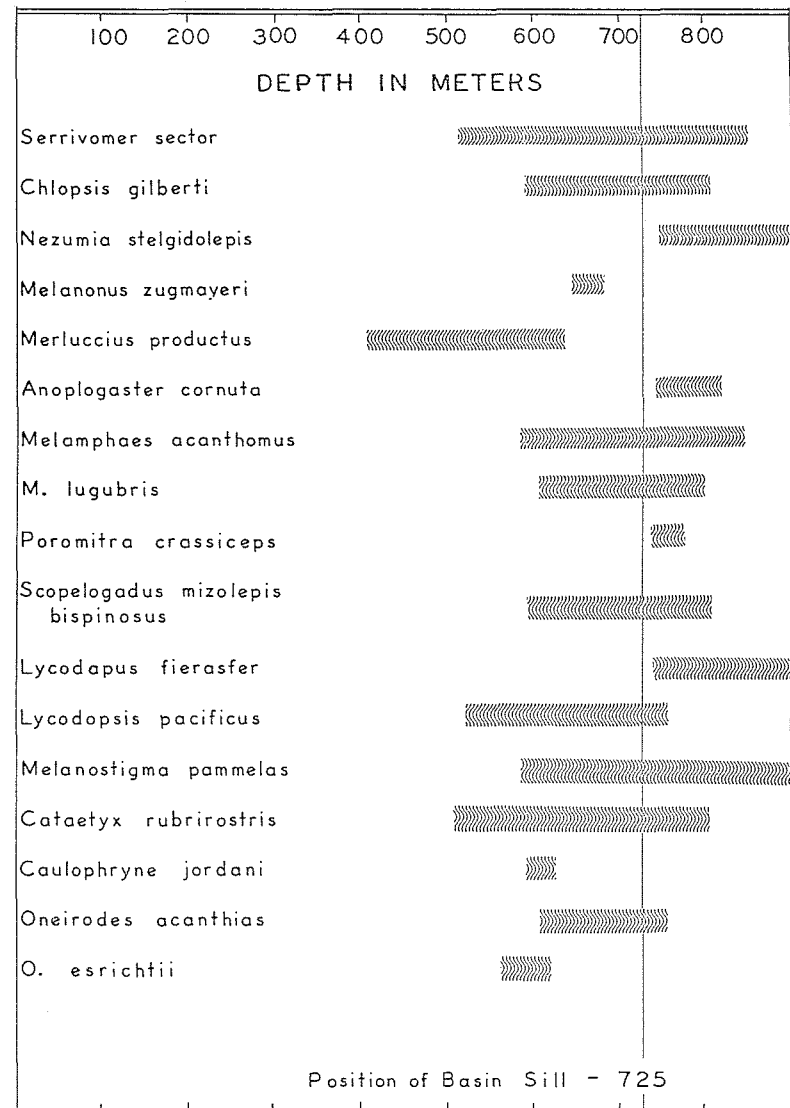
Position of Basin Sill — 725

Fig. 5

furcata). In some species, such as *Melamphaes acanthomus* (fig. 2), many of the large adults are expatriated outside of their breeding grounds and are reproductively lost to the whole species (Ebeling, 1962). Typical indicators of the southern fauna include *Vinciguerria lucetia* and the bigscale, *M. acanthomus*.

Vertically, relatively few southern fishes that invade the borderland are strong migrators. In the inshore and intermediate depth basins, most are bathypelagic (e.g., the slickhead, *Bajacalifornia burragei*, and bigscale, *Scopelogadus mizolepis bispinosus*, fig. 5), although mesopelagic species (e.g., *Vinciguerria*

lucetia, fig. 4, and the lanternfish, *Diogenichthys laternatus*) co-occur with central and northern fishes offshore. Some species are probably seasonal and are most common during periods of deep southern water intrusions during summer and fall.

The Central Faunal Component

With only 16 species, the central component is the smallest of the borderland fauna. The centers of distribution for these species occur in the vast central-tropical region of relatively sterile central water masses (cf. fig. 2), which stretch from the anti-equatorial tropics of the Pacific to the Atlantic Ocean (Ebeling, 1962). Although a few species are endemic to the central current gyres (e.g., *Melamphaes pumilus* in the central North Atlantic; see Ebeling, 1962) that integrate the constituent water-masses of this region, most are nearly circum-tropical (e.g., *Gonostoma atlanticum* and *Melamphaes simus* — fig. 2). Therefore, the central Atlantic and Pacific have more species in common than do the central Pacific and borderland, a relatively few miles to eastward. Typical indicators of the central fauna include *Danaphos oculatus* and the bristlemouth, *Cyclothone pallida*.

Vertically, most central species are mesopelagic (e.g., *Diplophos taenia* and the lanternfish, *Notoscopelus elongatus*). Bathypelagic species inhabiting the intermediate and deep waters below the central waters are often cosmopolitan (e.g., *Anoplogaster cornuta*). A nearshore invasion of central species is often associated with an influx of southern water during late fall. Oceanographically, this represents a "mirror-image" of a similar influx of warm equatorial and/or central water southward to Peru and northern Chile during the same period (cf. Wooster and Gilmartin, 1961). Few captures of central species have been recorded in the nearshore basins.

ASSOCIATIONS OF MIDWATER FISHES

Considering their centers of distribution, affinities with water masses, diurnal distributions with depth, and seasonality, we subjectively assigned the borderland species of midwater fishes into 15 groups, containing three to eight species each. The groups were defined by their general distribution in water masses (i.e., northern-subarctic, northern-transitional, southern, cosmopolitan, central-offshore, central-nearshore), by their depth distributions (i.e., upper-mesopelagic, lower-mesopelagic, bathypelagic, benthopelagic), and by the capacity of their constituent species to undergo diurnal vertical migrations (i.e., migrators, non-migrators). For example, one group comprises seven "southern, bathypelagic, non-migrating species"; another comprises four "northern-transitional, upper-mesopelagic, migrating species".

Next, the compositions of these groups were compared with those of 17 others that were constituted by a computer cluster analysis. Subjective groups and objective clusters were defined by the same terms if their shared species were in the majority. For example, subjective group 8 and cluster 8 each contain four species, of which three are shared; consequently, both were designated "northern-transitional, lower-mesopelagic, migrators." Also, subjective group 6 and cluster 6 contain four and seven species, respectively, of which four are shared; both were designated "central-offshore, lower mesopelagic, migrators", even though two of the unshared cluster species are non-migrators. In this way, 67 per cent of all groups (both subjective groups and clusters) could be mutually defined and 66 per cent of the 80 species included in the analysis were shared, indicating a considerable concordance between the two systems of grouping.

Preliminary analyses of multiple regression confirm expectations that captures are influenced by season, locality, bottom and trawling depths, duration of haul, and time of day. Bathypelagic fishes comprised two groups, one of eight predominantly southern species, the other of six species of more heterogeneous origin, including southern species that extend their ranges northward beyond the Northern Channel Islands (*Cyclothone acclinidens, Melamphaes acanthomus, Melanostigma pammelas*), cosmopolitan species (*Anoplogaster cornuta* and *Poromitra crassiceps*), and a northern species (*Bathylagus milleri*). The among-station abundances of both groups were positively correlated with length of time trawled and fishing depth, i.e., the trawls of longest duration reached the greatest depths, where the bathypelagic species are most common. Whereas the abundance of the southern group was partially correlated with latitude, however, that of the other was correlated with season. Expectedly, the southern group was most abundant in the southerly-most area sampled. The other group, however, was most abundant during the summer and fall, when deep southern waters extend farthest northward. The multiple regressions accounted for 40 and 71 per cent of the variability of the southern and heterogeneous groups, respectively. Obviously, therefore, the distribution of abundances of the heterogeneous group can be largely correlated with the among-station variability of the few simple parameters measured.

The among-station abundances of the mesopelagic groups were variously correlated with time of day as well as the other parameters, probably because most of the constituent species undergo diurnal vertical migrations. In contrast with the bathypelagic groups, mesopelagic groups were inversely correlated with trawling depth, suggesting that deep trawl hauls capture mesopelagic species during lowering or raising, but at depth are fishing under

their main concentrations. The multiple regression accounted for only about 20 per cent of the among-station variability of the northern groups. This indicates either that the most important environmental parameters influencing their abundances had not been considered or that the groups are contaminated and poorly constituted. But almost 80 per cent of the variability of the central-offshore mesopelagic migrators was attributable to the same parameters. Eighty per cent of this, moreover, could be explained by the single parameter of geographical locality as expressed by increasing longitude (distance offshore); i.e., central species are rare in the inshore basins. A multiple correlation analysis among environmental parameters showed that two or more may measure the same trend, e.g., distance offshore may be expressed in increasing values of longitude or increasing depth to bottom. For example, either measurement provided a good index of abundance for groups of central species.

Somewhat different interpretations of seasonal occurrences are implied by the two analyses. The analysis of multiple regression revealed no significant increase in southern bathypelagic species in the borderland during late summer and fall, as suggested by our subjective interpretation of catch data; but such an increase was indicated for southern lower-mesopelagic migrators. It revealed no increase of northern-transitional upper-mesopelagic migrators during spring and summer, as subjectively suggested. However, it revealed a significant increase of central-offshore mesopelagic migrators during winter and spring.

Species that are closely related to members of a particular group may be "competitively excluded" from that group. Fager and McGowan (1963) showed that generic diversity within recurrent ecological groups of North Pacific plankters is significantly greater than might be expected by chance alone. Ebeling (in press) noted that computed clusters of fishes "... usually comprise members of different families or even orders." In the present study, for example, the "heterogeneous group" of six bathypelagic borderland species represents three teleost orders, five families, and six genera.

A preliminary analysis of 100 discrete-depth samples taken from the Research Vessel *Swan* indicated that unit associations of midwater animals may not be as large as those resolved by the analyses of the *Velero IV* open-net captures. Thus although the lanternfish, *Stenobrachius leucopsarus*, and deep-sea smelt, *Leuroglossus stilbius*, were numerically correlated among open-net samples, they were often dissociated in discrete samples made between relatively narrow depth intervals. Dr. William D. Clarke (personal communication) and we have noted that at dawn and dusk, adults of *S. leucopsarus*, which have well-developed photophores, apparently migrate to the upper mesopelagic zone

as a compact shoal (see also Tucker, 1951). However, the adults of *L. stilbius*, which lack photophores, simply broaden their nocturnal vertical distribution.

CONCLUSIONS

The converging of the three main North Pacific water masses over the deep-sea basins in the southern California borderland has created a heterogeneous regime of mixed and stratified water masses. This oceanographic heterogeneity is expressed by the diverse fauna of midwater fishes. Like the water masses, however, the converging subarctic, equatorial, and central faunas are dissociated among depth zones, seasons, and bathymetric groups of basins.

The diversity of the mesopelagic and bathypelagic faunas increases with vertical expansion of their habitats offshore.

The northern component of the fish fauna comprises 32 species, most of which inhabit the mesopelagic zone where northern water predominates. The 76 southern species, which are mostly bathypelagic and lower-mesopelagic, dominate the deep southern intrusions of equatorial water. The central component comprises only 16 species, which are most abundant offshore where central waters invade the mesopelagic zone. Many mesopelagic species undergo diurnal vertical migrations.

Recurrent groups of species subjectively constituted according to their water-mass associations, depth distributions, and capacities to undergo diurnal vertical migrations show considerable concordance with others formed by a computerized cluster analysis of species by species correlations. Within each group, the constituent species are taxonomically more diverse than might be expected.

Multiple regressions of within-group abundances on a series of regularly measured environmental parameters indicates only a small percentage of the variability of most groups to be due to the regression. This implies that relatively unimportant parameters were analyzed, too few parameters were regularly measured, and/or vertical contamination of the open trawl hauls obscured the true species associations. Among borderland associations, the regression most successfully accounts for variability in abundance of bathypelagic groups. Perhaps maximum open-net captures of deep species almost always ensue from long hauls at great depths, but similar success in sampling a vertically unstable group of mesopelagic species is mostly fortuitous. However, the abundance of central-offshore species, which are generally scarce in the borderland, is highly correlated with bottom depth and longitude, both measures of distance offshore.

This substantiates preliminary observations that analyses of

discrete depth samples taken in closing nets will resolve the present recurrent ecological groups into smaller unit associations.

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ADDENDA

Several nomenclatural changes have occurred during the preparation of this manuscript. These changes and errors appearing in fig. 3-5 and in the text should be corrected as follows:

Leuroglossus stilbius	=	*Bathylagus stilbius*
Cyclothone microdon	=	*Cyclothone pseudopallida*
Benthalbella dentatus	=	*Benthalbella dentata*
Chlopsis gilberti	=	*Facciolella gilberti*
Oneirodes esrichtii	=	*Oneirodes eschrichtii.*

Argyropelecus lychnus lychnus as listed in this manuscript is a composite of two closely related species representing individuals of both *A. lychnus* and *A. hawaiensis* populations. The borderland population of *Scopelosaurus* is undescribed.