

DISTRIBUTION OF ICHTHYOPLANKTON OFF SAN ONOFRE, CALIFORNIA, AND METHODS FOR SAMPLING VERY SHALLOW COASTAL WATERS

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ABSTRACT

Spatial abundance patterns of inshore marine fish larvae, together with day-night and ontogenetic changes in these patterns, were investigated at a single site off the southern California coast using neustonic, midwater, and epibenthic samplers. Fifteen of the nineteen most abundant taxa showed statistically significant abundance patterns: Five taxa were principally in the inshore (<2 km from shore) epibenthos, one in the inshore neuston, two in the neuston and midwater less than about 5 km from shore, three to midwater 2-5 km from shore, and four in midwater offshore of about 3.5 km. Abundance patterns for the three most common taxa, *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*, shifted toward shore and toward the bottom with increasing larval size. Comparison of *E. mordax* egg and larval abundances indicated a large excess of larvae over eggs nearshore. Only two taxa showed statistically significant day-night pattern changes; both were lower in the water column during the day.

The existence of inshore abundance maxima implies significant survival value in occupying the nearshore zone. The shallow waters of the southern California coast may represent a nursery area comparable in importance to the estuarine nurseries of the Atlantic coast of North America.

Through the pioneering California Cooperative Oceanic Fish Investigation (CalCOFI) work of the late E. H. Ahlstrom and co-workers (Ahlstrom 1959, 1965), ichthyoplankton of the Southern California Bight are generally well known. However, the CalCOFI effort was concentrated on species found principally offshore of the 100 m isobath, and the larvae of most inshore fishes are rare or missing in the published CalCOFI data. Recent studies of ichthyoplankton in the Southern California Bight inshore of the 100 m isobath (Brewer et al. 1981; Gruber et al. 1982; Brewer and Smith 1982) have indicated that many of these larvae are found in the relatively shallow waters.

In this paper we present methods for sampling quantitatively the entire water column in shallow waters (6-75 m) and describe the spatial abundance patterns of the most commonly occurring larval fishes. Of particular interest was the distribution of larvae in the onshore-offshore vertical plane. Ontogenetic pattern changes were investigated for three abundant species: *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*.

The study was done off San Onofre, Calif., (Fig. 1) from September 1977 to September 1979. Unit 1 of the San Onofre Nuclear Generating Station, a 500-megawatt plant located 1.5 km northwest of the sampling area, was operating continuously throughout the course of the study. However, this plant has been shown to have only very localized effects which have not interfered measurably with the results reported herein (Marine Review Committee 1979³; Bartlett et al. 1981⁴). This study was completed prior to the beginning of operation of Units 2 and 3 of the San Onofre Nuclear Generating Station.

Our sampling methodology resulted from a preliminary study in which we found that a combination of sampling gear was necessary to estimate nearshore larval abundance. The chief purpose of this paper is to present these sampling methods. Results are shown which verify the effectiveness of these methods and further suggest some peculiarities of the nearshore habitat.

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³Marine Review Committee. 1979. Interim report of the Marine Review Committee to the California Coastal Commission. Part 1: General summary of findings, predictions, and recommendations concerning the cooling system of the San Onofre Nuclear Generating Station. In Marine Review Committee Document 79-02, p. 1-20. Marine Review Committee of the California Coastal Commission, 631 Howard Street, San Francisco, CA 94105.

⁴Barnett, A. M., P. D. Sertic, and S. D. Watts. 1981. Final report: Ichthyoplankton preoperational monitoring program. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024, 8 p.

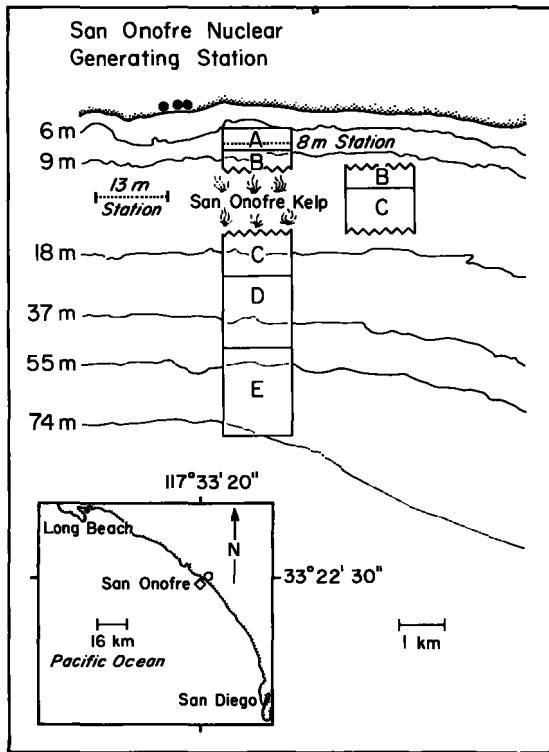


FIGURE 1.—Chart of the sampling area and its position off the southern California coast. The one- and two-dimensional pattern analyses were based on samples taken at a randomly selected isobath in each of the five sampling blocks (A-E) on each sampling date. The study of daily vertical migration was based on samples taken along the 8 and 13 m isobaths (dotted lines).

METHODS

Preliminary Study

In shallow depths, interfaces at the sea surface and seabed comprise a substantial portion of the water column. In addition, concentration of a species at either interface would necessitate sampling the epibenthic and neustonic layers as well as the mid-water column to obtain quantitative abundance estimates.

Neustonic, midwater, and epibenthic samplers were used in a preliminary study⁵ between September and November 1977, to verify their effectiveness and to select mesh size, net design, standard sample

⁵Barnett, A. M., J. M. Leis, and P. D. Sertic. 1978. Report to the Marine Review Committee on the preliminary ichthyoplankton studies. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024.

size, and sampling time for the ensuing full-scale program. The results of this brief study indicated that

1. Filtration efficiency was at least 85% for all nets and lengths of tow.
2. Samples of 400 m³ were adequate to attain asymptotes of numbers of taxa per tow. A sampled volume of 400m³ from the epibenthos was the maximum that could be handled economically.
3. The 12 most abundant larval fish taxa were neither randomly nor evenly distributed with respect to the three vertical strata. Half the taxa were principally epibenthic, while 25% were neustonic and 25% were most abundant in midwater.
4. Only one of these taxa showed a daily vertical migration; *Paraclinus integripinnis*, not a top-ranking species in the ensuing study, tended to descend from midwater to the epibenthic layer at night.
5. Size of individuals and apparent abundance of most taxa increased at night, probably because of visual avoidance during the day.
6. Nitex netting of 0.333 mm mesh retained more fish eggs and smaller anchovy larvae than did 0.505 mm mesh.

From the preliminary results, it was clear that the bongo net alone would undersample significant fractions of many larval populations. Since our goal was to estimate the density and distribution of nearshore ichthyoplankton, we decided to use all three types of gear with 0.333 mm mesh and to filter a target volume of 400 m³.

Sampling Gear

A bongo net was selected for sampling the midwaters, as recommended by Smith and Richardson (1977). An opening-closing 71 cm Brown-McGowan bongo net (total mouth area = 0.79 m²) was used. A General Oceanics⁶ (GO) flowmeter was mounted in the starboard frame. The bongo net, as conventionally used, is placed on the wire some distance above a weight and towed astern. The geometry of this arrangement and the circular net mouths make the gear ill-suited for sampling the plankton in the neustonic and epibenthic strata near the sea surface and seabed, respectively. Therefore, specially designed samplers, described below, were used to sample these layers.

We chose the brown manta net (Brown and Cheng

⁶Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

1981) as our neustonic sampler. This net had an 88 cm wide mouth and fished to a depth of 16 cm. Fiberglass-covered styrofoam floats kept the top of the net out of water, and a 3 m spar and asymmetrical bridle kept the gear outboard of the bow wave. A weight suspended from the end of the wire held the bridle well below the surface, out of the path of the net. The sampler was launched and recovered off the quarter by means of a tag line. Both a Tsurumi-Seiki (TSK) flowmeter and a GO flowmeter were mounted in the mouth of the net. The GO meter served as a back-up for the TSK, which sometimes fouled with kelp and eelgrass.

The Auriga net,⁷ used to sample the epibenthic layer, consisted of a rectangular net frame (0.5 m high × 2 m wide) attached to a chassis equipped with a pair of side-mounted, 2 m diameter wheels. The device rolled on the bottom so that the mouth of the net was 10 cm (original design) or 17 cm (later versions) above the bottom of the wheels. A series of 12 cm diameter plastic rollers below the mouth of the net helped prevent the sampler from digging into the bottom and presumably minimized escapement below the net. Both GO and TSK flowmeters were mounted within the mouth of the Auriga net. The Auriga net was towed off the stern. Divers have observed (M. Sowby⁸) that the mouth of the Auriga assumes a horizontal attitude when the wheels are off the bottom. We therefore believe that contamination of the epibenthic samples by midwater plankton was minimal during launch and recovery, when the main component of (relative) water movement was across, rather than through, the mouth. Any contamination that did occur should have been a function of depth, which was always <20% of the length of an epibenthic tow (this potential source of error has been ignored in the density calculations).

Although serious clogging was not apparent in the preliminary study, denser plankton concentrations at other times of the year might clog the nets before 400 m³ of water could be filtered. Clogging would be most serious for oblique bongo tows, because it would result in undersampling of the upper part of the water column. In anticipation of this possibility, the area of mesh in all nets was increased according to the criteria suggested by Smith et al. (1968, equation 5) in order to sample 500 m³ (bongo), 400 m³ (Auriga), and 200 m³ (Manta) for "green" coastal waters. The filtering ratios ($R = \text{mesh pore area/net mouth area}$) of bongo, Auriga, and Manta nets were increased to

7.8, 6.6, and 10.7, respectively, by adding mesh cylinders ahead of the conical portions of the nets. External flowmeters were not used in the subsequent surveys, but tows were carefully timed. Internal flowmeter readings were checked upon recovery, and samples were repeated if the readings differed by more than 20% from expected values.

Except for the limited study of daily vertical migration, all sampling was done at night. The deck lights were always off during the neuston tows. All samplers were launched, towed, and recovered with the vessel underway at about 1 m/s. For bongo tows, wire was paid out (scope about 2:1) until the weight, located 1.5 below the center of the net frame, bumped the bottom. Then the nets were opened, and a stepped oblique tow was made consisting of 18 30-s steps. The Auriga sampler was towed with a scope of 3:1 and recovered after 6.5 min on the bottom. With the small-mouthed Manta net, the volume of 400 m³ was achieved by towing two nets simultaneously, off port and starboard, for 20 min (about 1.4 km).

Samples were preserved in 5-10% seawater-Formalin.

Sampling Locations and Frequency

Since we eventually wanted to assess the effects of a power plant cooling system, it was necessary to concentrate much of our sampling effort within the depth contours encompassing the cooling structures. At the same time, in order to estimate the abundance of nearshore species, we needed to sample far enough from shore to delimit their centers of abundance. We decided upon a stratified random sampling design (Snedecor and Cochran 1967) wherein, on each sampling date, the neustonic, midwater, and epibenthic layers were sampled along a randomly chosen depth contour in each of five blocks (Figs. 1, 2). The five blocks were defined by depth contours: A) 6-9 m, corresponding to cooling water intake locations; B) 9-12 m and C) 12-22 m, both corresponding to future diffuser discharge locations; D) 22-45 m, corresponding to a faunal break between inshore and coastal zooplankton assemblages (Barnett and Sertic⁹); and E) 45-75 m, chosen a priori as the likely offshore limit of most nearshore larval fishes.

The sampling transect thus consisted of 15 strata: Three depth layers in each of five blocks (Fig. 2). To

⁷Marine Biological Consultants, Inc., 947 Newhall Street, Costa Mesa, CA 92627.

⁸M. L. Sowby, Marine Biological Consultants, Inc., 947 Newhall Street, Costa Mesa, CA 92627, pers. commun. 1979.

⁹Barnett, A. M., and P. D. Sertic. 1979. Spatial and temporal patterns of temperature, nutrients, seston, chlorophyll-a and plankton off San Onofre from August 1976 - September 1978, and the relationships of these patterns to the SONGS cooling system. *In* Marine Review Committee Document 79-01, p. vii through 9-89. Marine Review Committee of the California Coastal Commission, 631 Howard Street, San Francisco, CA 94105.

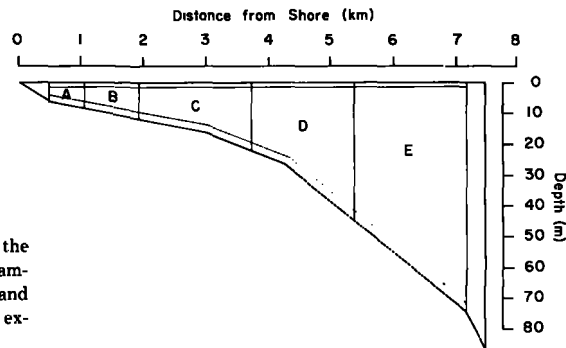


FIGURE 2.—Diagrammatic profile of the study transect showing the 15 strata sampled off San Onofre, Calif. Neustonic and epibenthic layers are vertically exaggerated.

avoid the San Onofre kelp bed, some of the tows in the B and C blocks were offset by about 1 km. Wilcoxon signed rank tests of samples taken from B block and B offset (Fig. 1) showed no significant differences in species abundances ($P > 0.05$) between the main block and the offset which could not be related to the inshore-offshore patterns discussed below.

The transect was sampled monthly in January and February 1978, fortnightly from March through August 1978, and again monthly through September 1979. During each of these 28 sampling periods, the five blocks were surveyed once each night for 1-3 nights, giving a total of 57 sampling dates for the 21-mo study.

As noted above, we chose a standard sampled volume of 400 m^3 based on the preliminary study. This volume was large enough to assure a representation of all abundant species throughout the year. Volume was used as the sampling unit, although an argument based on the scale of patchiness could be made for length of tow (i.e., 400 m in each water layer) as the criterion, rather than volume filtered (P. Smith¹⁰). Most tows were at least 400 m long.

Laboratory Procedures

Samples were sorted for fish eggs and larvae under dissecting microscopes at $10\times$ magnification. The choice of 400 m^3 as the sampled volume was made at a time of year when ichthyoplankton abundance was low (Walker et al.¹¹); consequently the samples from other times of year were larger than necessary to rep-

resent the nearshore assemblage. Samples with large plankton volumes were subsampled, using a Folsom plankton splitter before sorting. The size of the subsample was set to include at least 100 non-engraulid larvae (the mean number of larvae counted per subsample was 277, of which 62.8% was *E. mordax*). This fraction was usually one-fourth and was seldom smaller than one-eighth. Eggs were sorted from 1%, 5%, or 10% (to get at least 100 eggs) of the residue of the fraction sorted for larvae. Sorting efficiency was maintained above 90%.

Some epibenthic samples contained so much sand and detritus that it was necessary to clean them before sorting, using a flotation technique adapted from Ladell (1936). After removal of large fish and debris, such a sample was mixed with a 40% MgSO_4 solution (specific gravity = 1.2) in a large separator fashioned from a 19 l (5-gal) plastic carboy with the bottom cut off and the neck fitted with a rubber hose and ball valve. Most detritus sank, while plankton floated to the top. The heavy material was drained off and processed once or twice more to ensure separation of the plankton. Checks of the heavy residue of three such samples showed that more than 99% of the larvae were separated by flotation.

All larvae were identified to the lowest taxonomic category currently possible. Eggs were identified as *Engraulis mordax* or "other". In some larval categories (e.g., Atherinidae, Goby Type A), our ability to discriminate among species or larval types (sensu Richardson and Pearcy 1977) improved as the study progressed. However, not all of the old collections were reprocessed. When mixed taxa showed seasonal and spatial coherence, they were retained for the analyses presented here.

Pattern Analysis

All counts of eggs and larvae were standardized to number/ 400m^3 . Thus the standardized numbers

¹⁰P. E. Smith, La Jolla Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038, pers. commun. 1979.

¹¹Walker, H. J., A. M. Barnett, and P. D. Sertic. 1980. Seasonal patterns and abundance of larval fishes in the nearshore Southern California Bight off San Onofre, California. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024.

were roughly the same as the actual numbers of eggs and larvae caught, a desirable situation for analysis with transformed data (Murphy and Clutter 1972). These values were transformed by $\log(X + 1)$ before analysis for offshore and vertical pattern. The results were back-transformed, resulting in geometric means with asymmetric confidence bounds, and presented as number/100m³.

To describe the cross-shelf abundance patterns of ichthyoplankton, a procedure was adopted involving Hotelling's T^2 test and a series of *a posteriori* *t*-tests (Morrison 1976) to divide the 15 strata into groups. These parametric methods allowed us to detect significant differences in mean abundance among components of a pattern and to determine confidence bounds on the means.

Hotelling's T^2 test was selected over an analysis of variance (ANOVA) because the covariance structures in the data tended not to meet the assumptions of standard ANOVA models (i.e., errors were not independent; the abundances of neighbor strata were likely to be correlated). The T^2 -test allows this correlation by using the sample covariance matrix, rather than (as in ANOVA) assuming a specified covariance pattern (Winer 1971; Morrison 1976).

With a significant T^2 test result obtained ($P \leq 0.05$), *a posteriori* multiple *t*-tests were used to separate strata into groups having significantly different abundances. The strata were contrasted in a series of *t*-tests using the Bonferroni statistic, $t(0.05)_{k,s}$, where k = potential number of contrasts, s = number of sampling periods - 1, and 0.05 = overall type I (α) error. The value of k was set as the number of all possible contrasts among m strata plus 5, for further tests employing combinations of the initial strata: i.e., $k = \frac{(m)(m-1)}{2} + 5$. Bonferroni *t*-values were taken from Myers (1972, table A-12).

After the initial series of *t*-tests of all possible comparisons, strata found not to differ significantly were pooled into initial groups. The time-averaged abundance of each stratum was used to calculate the initial groups' mean abundance

$$Z_j = \sum_{i=1}^n Z_i/n$$

where Z_j is the initial group mean, n is the number of strata in the initial group, and Z_i are the means of individual strata. Further *t*-tests (the total of all tests $\leq k$) were made to contrast the resulting initial groups. If more than one final grouping was possible, the final set of groups selected was that which maximized the *t*-statistic.

Both the Hotelling T^2 and the *t*-test assume normally distributed data. Excessive zero values in a data set violate this assumption in a way that cannot be corrected by transformations. The methods used here were robust with respect to zero values in zooplankton data (Barnett et al.¹²); nevertheless, some sampling dates for 12 of the 19 ichthyoplankton taxa analyzed were deleted in one of two ways in order to reduce the number of zero observations. The preferred method, useful for eight seasonally abundant taxa, was to eliminate from analysis all consecutive samples taken when the annual abundance cycle was lowest. In these cases, the number of survey dates was ≤ 57 (Fig. 3), and means and confidence bounds presented (Table 1) apply to the "season of abundance". The second method, used for four sporadically abundant taxa, was to include only those

¹²Barnett, A. M., A. E. Jahn, and P. D. Sertic. 1980. Long term average spatial patterns of zooplankton off San Onofre and their relationship to the SONGS cooling system. MEC01380994. Marine Ecological Consultants of Southern California, 531 Encinitas Boulevard, Encinitas, CA 92024.

TABLE 1.—Geometric mean abundance (no./100m³) with 96% confidence bounds (C.B.) for the 15 larval fish taxa showing statistically significant cross-shelf patterns off San Onofre, Calif. Groups of strata which differ significantly in mean abundance are ranked from highest to lowest. Refer to Figure 3 for locations of these groups.

Mean abundance: Strata groups: 95% C.B.:	Highest-----Lowest											
	1			2			3			4		
	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper
<i>Gibbonsia</i> sp. A	0.15	0.35	0.86	0.00	0.01	0.03						
<i>Seriphus pollitus</i>	5.47	22.71	91.93	1.15	2.67	5.85	0.19	0.67	1.66	0.07	0.24	0.50
<i>Gobiesox rhesodon</i>	0.81	2.07	4.84	0.13	0.32	0.60	0.00	0.02	0.05			
Goby Type A	1.09	2.70	6.28	0.35	0.88	1.88	0.09	0.28	0.56	0.01	0.04	0.07
<i>Genyonemus lineatus</i>	8.36	37.21	162.71	0.84	2.65	7.46	0.17	0.68	1.78	0.04	0.23	0.57
Atherinidae	9.71	23.11	54.54	1.37	4.17	11.83	0.27	0.66	1.32	0.00	0.05	0.11
<i>Hypsopsetta guttulata</i>	0.06	0.27	0.63	0.01	0.03	0.08						
<i>Hypsoblennius</i> spp.	0.44	1.03	2.13	0.03	0.09	0.17						
<i>Engraulis mordax</i>	44.03	88.49	177.60	21.78	47.81	104.56	8.41	19.58	45.19	1.67	3.93	8.86
<i>Paralichthys californicus</i>	0.66	1.81	4.40	0.15	0.38	0.75	0.04	0.12	0.23			
<i>Pleuronichthys verticalis</i>	0.04	0.13	0.24	0.00	0.02	0.05						
<i>Citharichthys</i> spp.	0.06	0.20	0.40	0.00	0.03	0.07						
<i>Sebastes</i> spp.	0.42	1.28	3.22	0.07	0.30	0.69	0.00	0.03	0.07			
<i>Stenobrachius leucopsarus</i>	0.24	0.83	2.14	0.01	0.05	0.11						

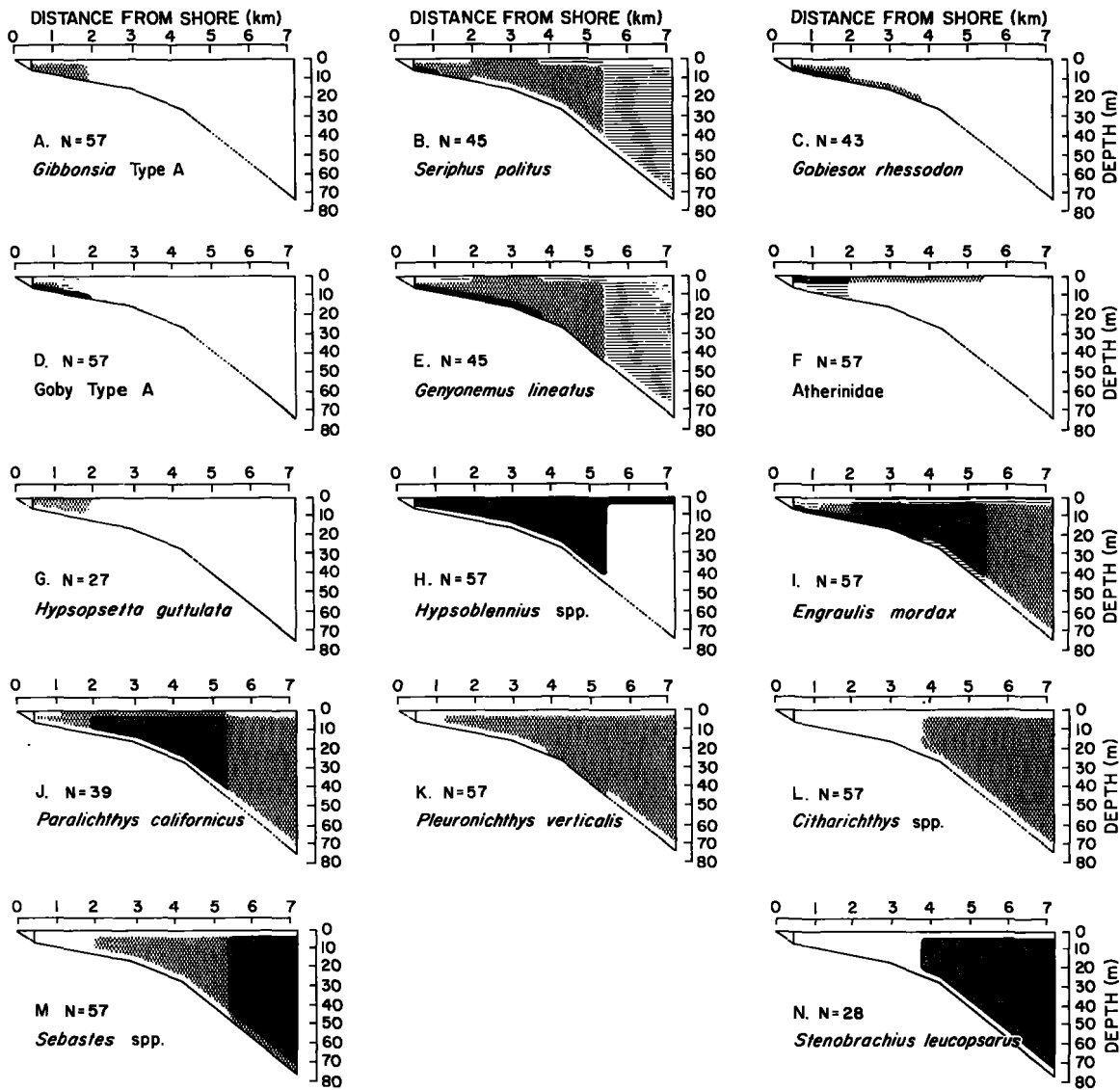


FIGURE 3.—Cross-shelf abundance patterns for the 14 most common larval fish taxa off San Onofre, Calif. Shading indicates relative abundance in groups of strata differing significantly in mean abundance. Heavier shading indicates higher abundance; the darkest shading (black) is used for centers of abundance with larval densities > 3 individuals/400 m³ (0.75/100 m³). N = Numbers of surveys used in analysis. Geometric mean abundances with 95% confidence bounds for each of these groups are given in Table 1.

dates when a taxon was present. The latter method was used only to obtain cross-shelf patterns; in these cases, mean abundances in the various parts of the pattern are relative numbers, and confidence bounds were not calculated (Table 1).

All testing was done on the basis of abundance alone, without regard to the strata being grouped. Final groupings of strata are shown in diagrams of the cross-shelf transect (Fig. 3). Occasionally, non-abutting strata were members of the same statistical

group. These are depicted as being physically connected when such an interpretation is reasonable. In all cases, shading is used to indicate groups of strata which differ significantly.

RESULTS

Cross-Shelf Patterns

The 19 larval taxa analyzed were those which rank-

ed among the 10 most abundant in any of the 5 sampling blocks. Fourteen taxa showed significant differences among the strata which were resolved into spatial patterns (Table 1, Fig. 3). Taxa with centers of abundance nearest shore tended to be concentrated in either the epibenthic or the neustonic layer. Of the five epibenthic taxa, four (*Gibbonsia* Type A, *Seriphus politus*, *Gobiesox rhessodon*, and Goby Type A [consisting of *Ilypus gilberti* and *Quietula y-cauda*]; Fig. 3A-D) had centers of abundance within 2 km of shore. The fifth, *Genyonemus lineatus*, was most abundant out to about 4 km (Fig. 3E). Atherinidae (Fig. 3F) were neustonic and most abundant within 2 km of shore. *Hypsopsetta guttulata* (Fig. 3G) was abundant in the neustonic and midwater layers out to 2 km. It had the most nearshore pattern of any midwater taxon. *Hypsoblennius* spp. were concentrated in the neustonic and midwater layers out to about 5 km and in the neustonic layer beyond 5 km from shore (Fig. 3H).

The remaining six taxa with discernible patterns were all most concentrated in midwater. The centers of abundance of *Engraulis mordax* and *Paralichthys californicus* (Fig. 3I, J) extended from 2 to ~5 km from shore, while those of *Pleuronichthys verticalis*, *Citharichthys* spp., *Sebastes* spp., and *Stenobrachius leucopsarus* appeared to extend seaward of the sampling area (Fig. 3K-N).

Five taxa (*Chromis punctipinnis*, *Paralabrax* spp., *Parophrys vetulus*, *Peprilus simillimus*, and *Pleuroichthys ritteri*) were not shown to have patterns by this analysis.

Vertical Migration

Because the basic study plan called for nighttime sampling, the patterns described would pertain to nighttime distributions. The preliminary study found little evidence of daily vertical migration; nevertheless, we conducted a further small study of vertical migration to test whether the vertical component of the patterns remained the same during daylight hours. The study was conducted at two inshore locations (Fig. 1). A description of the vertical study is given in the Appendix.

There was no indication of vertical migration at the 8 m station, but at the 13 m station two taxa, *Hypsoblennius* spp. and *Paralichthys californicus*, showed significant ($P < 0.05$) vertical shifts downward in the water column during the day (Fig. 4). The low probability (0.055) of the F value for *Gobiesox rhessodon* (App. Table 2), though higher than the customary rejection level of 0.05, suggests a daily change in vertical distribution. The data indi-

cate this species may, like *Paraclinus integripinnis* in the preliminary study, tend to migrate or settle from midwater into the epibenthic layer at night.

Onshore-Offshore Abundance

The analysis of cross-shelf pattern assumes that larvae are uniformly distributed throughout each midwater stratum, an assumption that becomes increasingly untenable with depth of stratum. Layering of ichthyoplankton within the midwater zone will cause an apparent decrease in density in the seaward blocks, as more of the volume used in the density calculations comes from deeper waters where a species may be rare. To eliminate bias in the cross-shelf patterns due to inclusion of noncontributing depths in the density calculations, one-dimensional abundances were calculated based on the estimated number of larvae under a unit (100 m²) of sea surface in each offshore block

$$N = \sum_{i=1}^3 n_i d_i$$

where n = larvae/100 m³ in stratum i and d = vertical thickness of stratum i in meters (0.16 m, neustonic; 0.50 m, epibenthic; depth of water column - 1 m, midwater).

The one-dimensional patterns, which emphasize numbers of larvae (Table 2), provide a useful comparison to the two-dimensional patterns which emphasize larval density (Table 1, Fig. 3). All epibenthic and neustonic taxa had similar onshore-offshore centers of abundance as determined by both methods. This was expected, since their cross-shelf abundance patterns were essentially one-dimensional. *Gibbonsia* Type A, *Seriphus politus*, *Gobiesox rhessodon*, Goby Type A, and Atherinidae, all with abundance centers within 2 km of shore in the two-dimensional analysis (Fig. 3), likewise had one-dimensional maxima shoreward of 2 km. With the exception of *S. politus*, these taxa were less than half as abundant beyond 2 km. *Genyonemus lineatus*, most concentrated in the epibenthic layer within about 4 km of shore, had a one-dimensional maximum at 2-4 km but remained abundant ($> \frac{1}{2}$ maximum) out to ~5 km.

Of the eight midwater taxa, only two had one-dimensional patterns which differed from their two-dimensional patterns. *Engraulis mordax* appeared more abundant farther offshore in one dimension (cf. Table 2 and Fig. 3I). The steady increase in abundance of *E. mordax* with distance from shore is at odds with its two-dimensional pattern (Fig. 3I) and

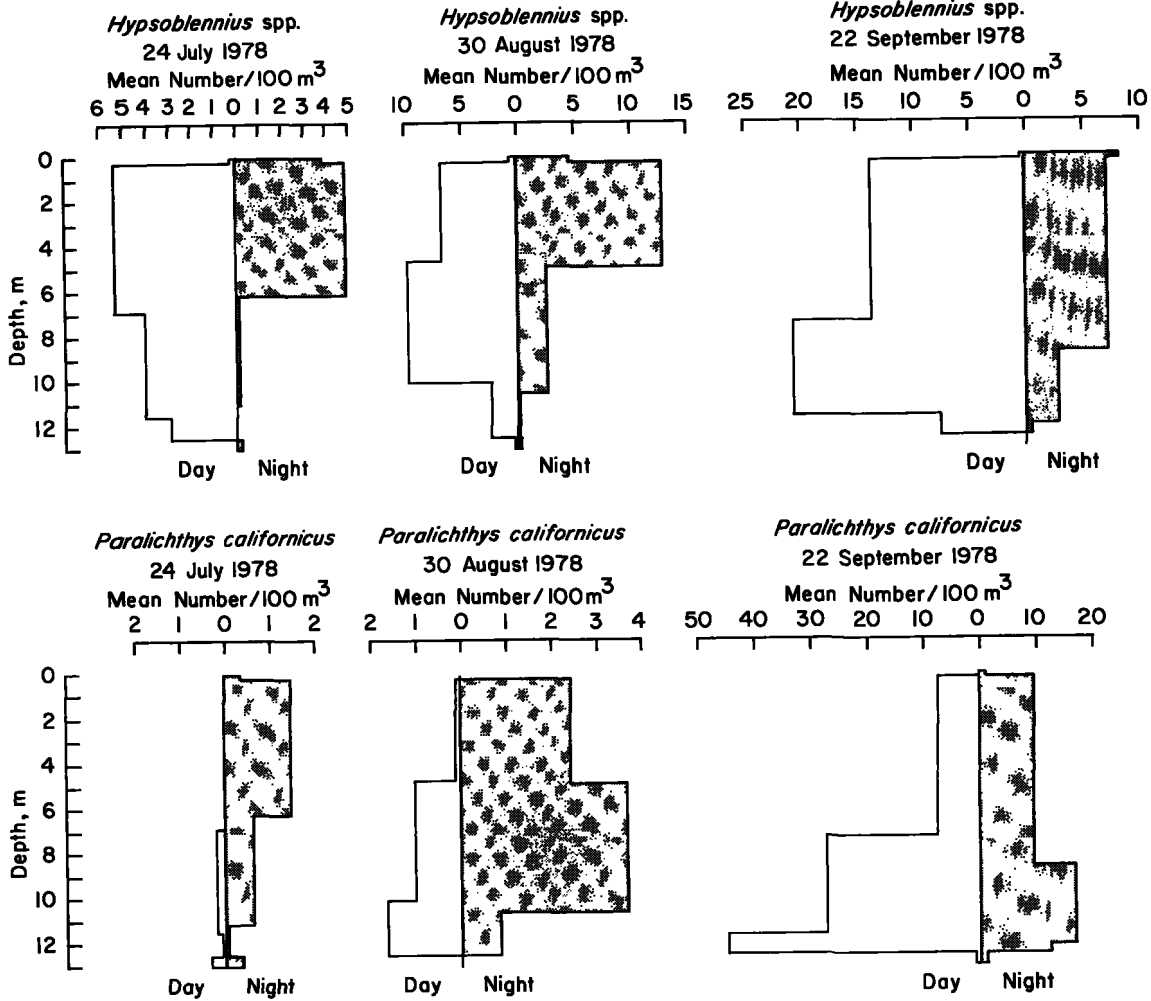


FIGURE 4.—Average vertical abundance profiles of *Hypsoblennius* spp. and *Paralichthys californicus* during the study of daily vertical migration off San Onofre, Calif. The depth ranges of the five sampling strata are the averages (based on four to six profiles) for each sampling period. Note that the horizontal (abundance) scale varies.

TABLE 2.—Numbers of larvae under 100 m² of sea surface in the five sampling blocks, averaged over 57 cruises, off San Onofre, Calif.

Sampling block: Offshore limits (km):	A 0.5-1.1	B 1.1-1.9	C 1.9-3.7	D 3.7-5.4	E 5.4-7.2
<i>Gibbonsia</i> Type A	6.4	10.3	1.5	0.3	1.1
<i>Seriphys politus</i>	273.9	103.9	217.9	118.9	93.7
<i>Gobiesox rhesodon</i>	4.8	12.1	5.3	1.1	3.0
Goby Type A	24.5	17.5	3.5	2.9	1.1
<i>Genyonemus lineatus</i>	132.7	312.4	823.3	566.5	221.1
Atherinidae	35.7	28.1	11.7	8.9	4.9
<i>Hypsopsetta guttulate</i>	3.1	3.2	3.9	0.6	0.7
<i>Hypsoblennius</i> spp.	27.5	26.9	48.1	63.0	36.9
<i>Engraulis mordax</i>	970.0	1,833.4	6,454.4	9,250.2	10,263.5
<i>Paralichthys californicus</i>	4.3	11.4	90.0	103.2	42.4
<i>Pleuronichthys verticalis</i>	0.4	2.3	13.4	36.4	11.7
<i>Pleuronichthys ritteri</i>	<0.1	0.2	5.6	30.9	13.9
<i>Citharichthys</i> spp.	2.9	3.5	9.9	17.9	31.0
<i>Sebastes</i> spp.	<0.1	<0.1	18.2	77.7	518.6
<i>Stenobrachius leucopsarus</i>	0.1	0.4	4.4	28.1	106.1
<i>Chromis punctipinnis</i>	0	0	0.8	6.6	53.3
<i>Paralabrax</i> spp.	0.1	0.8	34.3	97.8	84.1
<i>Parophrys vetulus</i>	0.5	0.3	0.1	7.3	33.6
<i>Peprilus simillimus</i>	2.0	4.1	3.6	10.0	17.4

indicates that this species must be vertically stratified beyond the 45 m contour. This agrees with the findings of Ahlstrom (1959) in which the majority of *E. mordax* larvae occurred above 50 m. In contrast, *Pleuronichthys verticalis* peaked in abundance at 4-5 km rather than extending offshore as in the two-dimensional analysis (cf. Table 2 and Fig. 3K). This result may have occurred because the tests used in the two-dimensional analyses failed to distinguish between offshore blocks due to the small number (27) of non-zero observations for this species.

Four of the five taxa lacking statistically significant two-dimensional patterns (*Chromis punctipinnis*, *Paralabrax* spp., *Parophrys vetulus*, *Peprilus similimus*) appeared to be most abundant beyond 4-5 km when considered in one dimension (Table 2). The fifth, *Pleuronichthys ritteri*, peaked in abundance at 4-5 km from shore.

Ontogenetic Pattern Changes

Larvae of the three most abundant species were divided into size groups, which were analyzed separately for spatial pattern. To prevent temporal bias in the patterns, only 1978 data were used since they covered a full year. Larvae of two sciaenids, *Genyonemus lineatus* and *Seriphus politus*, were each divided into groups corresponding to developmental stages. Preflexion larvae, with straight notochords and no hypural development, were analyzed separately from more fully developed, and presumably more mobile, flexion and postflexion larvae. Hypural development was found to begin at 3.8 mm for *G. lineatus* and at 4.1 mm for *S. politus*. Similarly, *Engraulis mordax* larvae were divided into early and late developmental stages, but this was done on the basis of size alone and did not correspond to flexion of the notochord. Early preflexion larvae (<6 mm), termed "early stage", were analyzed separately from

other larvae, termed "late stage". One hundred larvae or all specimens, whichever was less, were measured for each species in each collection. When only the first 100 larvae were measured, the proportions of the various size classes were applied to the total.

To examine the ratio of older to younger larvae, the total number in each sampling block (Fig. 1) was calculated, using a longshore dimension of 1 m, i.e., number in block,

$$N_b = N \cdot L,$$

where *N* is number under 100 m² of sea surface in the block, and *L* is the onshore-offshore extent of the block in hundreds of meters.

The patterns of all three species were more nearshore and epibenthic for older larvae (Table 3, Fig. 5). The ratio of older to younger larvae was about 1:2 for all three species (transect totals, Table 4). This ratio increased in the shoreward blocks for *G. lineatus* and *S. politus*, reaching maxima in blocks A and B. The ratio of older to younger *E. mordax* larvae was maximum in blocks C and D. The remarkable aspect of the *E. mordax* data is that there were far too few eggs in the nearshore zone to account for the numbers of larvae. The ratio of total *E. mordax* larvae to eggs was about 28:1. The median size of the larvae was about 6 mm, corresponding to an average age of roughly 10 d (Methot and Kramer 1979). Zweifel and Lasker (1976) found a time to hatching of 2.5 d (at about 16°C). The ratio of 10-d-old larvae to eggs thus has an upper limit of the order 4:1 in the absence of mortality, implying at least a sevenfold excess of larvae in these nearshore samples. The minimum diameter of *E. mordax* eggs during the months of maximum egg abundance is about twice the mesh opening of the plankton nets used, so that sampling deficiencies for these immobile objects should be negligible.

TABLE 3.—Geometric mean abundance (no. 100m³) with 95% confidence bounds (C.B.) for younger and older age groups of larvae of *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*, showing statistically significant cross-shelf patterns off San Onofre, Calif. Groups of strata which differ significantly in mean abundance are ranked from highest to lowest. Refer to Figure 5 for locations of these groups.

Strata groups:	Mean abundance: Highest.....Lowest											
	1			2			3			4		
95% C.B.:	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper
<i>Engraulis mordax</i>												
early stage larvae	2.33	13.21	70.06	0.52	3.31	16.24	0.22	1.10	3.63			
late stage larvae	23.43	62.42	165.65	5.53	14.34	36.60	0.92	2.99	8.72			
<i>Genyonemus lineatus</i>												
Preflexion stage larvae	1.55	7.42	32.40	0.73	3.15	11.52	0.33	1.11	2.93	0.04	0.26	0.64
flexion and postflexion stage larvae	7.46	30.88	125.51	0.53	1.56	3.97	0.10	0.62	1.90	0.02	0.08	0.14
<i>Seriphus politus</i>												
preflexion stage larvae	0.58	1.37	2.90	0.15	0.49	1.12	0.04	0.16	0.33			
flexion and postflexion stage larvae	4.31	20.64	95.57	0.50	1.90	5.86	0	0.10	0.22			

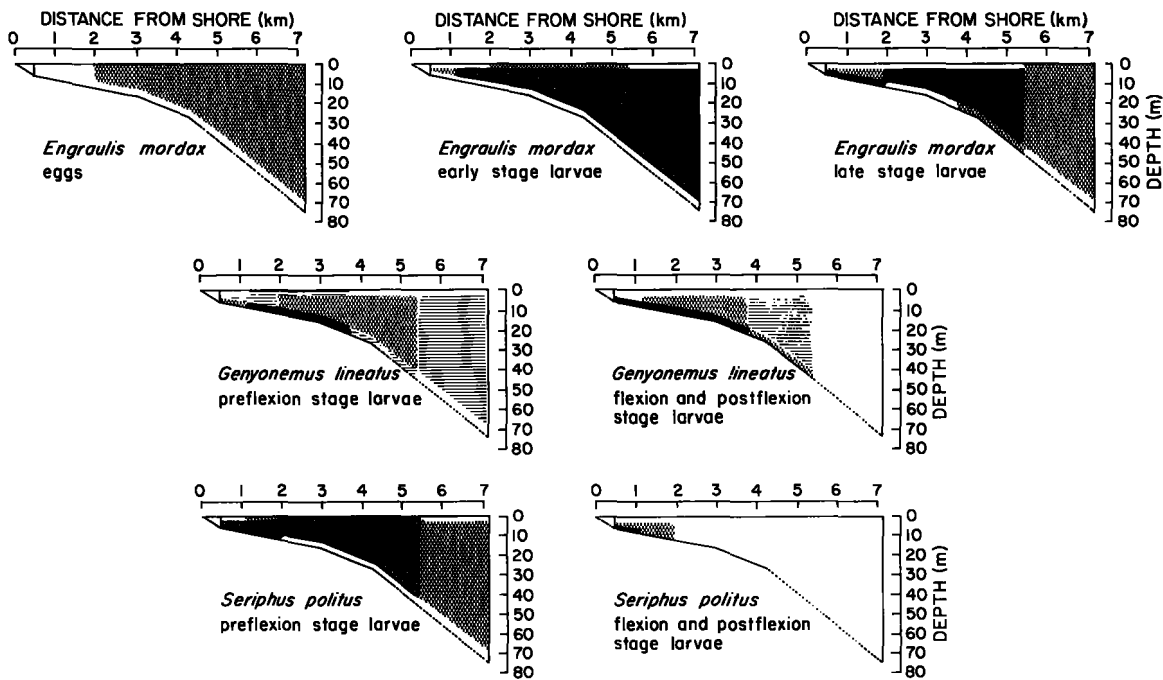


FIGURE 5.—Changes with development stage in the cross-shelf abundance patterns of *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus* off San Onofre, Calif. Shading indicates relative abundance in groups of strata differing significantly in mean abundance. Heavier shading indicates higher abundance; the darkest shading (black) is reserved for densities >3 individuals/400 m³ (0.75/100 m³). Geometric mean abundance and 95% confidence bounds for each group are given in Table 3.

TABLE 4.—Early life stages of *Engraulis mordax*, *Genyonemus lineatus*, and *Seriphus politus*, for 1978 off San Onofre, Calif. See Figure 1 for description of sampling blocks.

Species	Sampling block (avg. no./m of coastline)					Total average no.
	A	B	C	D	E	
<i>Engraulis mordax</i>						
eggs	3,100	25,334	85,372	75,238	95,782	284,826
larvae <6 mm	85,302	363,002	1,387,638	1,770,549	1,770,939	5,377,430
larvae >6 mm	42,970	86,977	816,941	1,164,417	607,805	2,719,110
<i>Genyonemus lineatus</i>						
preflexion larvae	463	688	7,440	9,290	3,724	21,605
flexion and postflexion larvae	464	2,969	4,198	2,699	107	10,437
<i>Seriphus politus</i>						
preflexion larvae	592	490	4,200	2,137	2,103	9,522
flexion and postflexion larvae	2,214	809	779	197	96	4,095

DISCUSSION

The methods we have employed for sampling very shallow inshore waters, though not without shortcomings, have proven satisfactory in that they clearly emphasize the degree to which many larval fishes are concentrated in different layers, especially near bottom. Any quantitative sampling of nearshore fish larvae over soft bottom (at least) in the Southern California Bight must clearly include the epibenthic layer. However, our method of doing so may leave

room for improvement. The Auriga net probably does not sample the 17 cm immediately above the substrate, unless the rollers induce an avoidance response such that larvae swim upward and into the mouth. Moreover, we have not determined the thickness of the epibenthic microhabitat or whether it is the same for all species. The sharpness of some abundance patterns suggests this layer may be no more than 1 m thick (the bongo net tows began about 1 m above the bottom), but small errors in this determination, and failure to sample obliquely from the

top of the range of the epibenthic gear, could make large differences (by a factor of 2) in the abundance estimates of some taxa.

Other studies from the Southern California Bight have shown cross-shelf patterns similar to those which we describe. For example, Gruber et al. (1982; sampling neuston and midwater) and Brewer et al. (1981; sampling the entire water column) both showed vertical and cross-shelf changes in species composition. In both studies, atherinid larvae were principally neustonic. Brewer et al. (1982) took 69% of all larvae on their surveys from the epibenthic stratum. Both studies showed that clinids, most gobiids, sciaenids, and atherinids were most prevalent nearer shore. Such inshore-offshore patterns have also been shown further north along the west coast (Pearcy and Meyers 1974; Richardson and Pearcy 1977).

Icanberry et al. (1978) conducted a distributional study of ichthyoplankton above the epibenthic stratum at two nearshore stations off Diablo Canyon, about 100 km northwest of the Southern California Bight. Though there is taxonomic overlap between their study and ours, their sampling was too nearshore to delimit the offshore extent of any species in our study. Published data on widely (offshore) ranging species are contained in the CalCOFI atlas series (Kramer and Ahlstrom 1968; Ahlstrom 1969, 1972; Ahlstrom and Moser 1975) and complement some of the offshore patterns reported here.

Engraulis mordax, one of these widely ranging species, spawns principally offshore (Richardson 1981; Brewer and Smith 1982). The number of excess *E. mordax* larvae (over those which can be accounted for by eggs) in the nearshore zone must come from outside the sampling area, and these larvae must begin moving shoreward at an early age. Richardson (1981) suggested that currents might be a mechanism through which larvae of the northern subpopulation of *E. mordax* are redistributed. We presently cannot identify a mechanism for the redistribution off San Onofre. However, if one assumes it involves some behavioral response to environmental cues, it is worth considering just how far a larval anchovy might swim. Hunter (1972) estimated cruising speed on the order of one-half body length/s. At this speed, a 6 mm larva would swim about 250 m/d, far enough to move several kilometers along an environmental gradient during the larval period. Any behavior allowing larvae to remain in the nearshore zone (e.g., orientation toward the bottom), once encountered, could help explain their observed concentration.

The increased concentration of older larvae of *E. mordax*, *Genyonemus lineatus*, and *Seriphys politus* nearshore and near the bottom is reminiscent of the invasion and retention of larval and postlarval fishes in estuaries and tidal creeks of the Atlantic coast (cf. Chao and Musick 1977; Weinstein et al. 1980). Older larvae of *Paralichthys californicus*, although too rare for statistical analysis, also appeared more concentrated nearshore than did the younger larvae. Whatever the mechanisms for such ontogenetic redistribution, they must be at least partly behavioral. Weinstein et al. (1980) found vertical movements in response to tides, whereby postlarvae became more concentrated near the bottom during ebb flows, thus taking advantage of the slower seaward current in the boundary layer. In the Southern California Bight the mean nearshore flow is alongshore, with relatively weak cross-shelf components (Hendricks 1977; Reitzel 1979¹³; Parrish et al. 1981; Winant and Bratkovich 1981). The major source of cross-shelf water motion is internal waves of tidal frequency (Winant and Olson 1976) which propagate toward shore. For these waves to propagate, the water column must be stratified. It is notable that larval *S. politus*, which displayed the most intense ontogenetic redistribution, is most abundant during late summer-early fall (Walker et al. footnote 11), the season of maximum thermal stratification in the Bight (Cairns and Nelson 1970). Thus it may be that *S. politus* and other semi-planktonic organisms of the shallow shelf waters take advantage of internal tides in somewhat the same way that the estuarine fauna use the surface tide to regulate position. It is conceivable that due to dissipation of energy, seaward motions in the boundary layer are slower than shoreward motions.

A similar internal wave mechanism for shoreward migration has been suggested by Norris (1963). He hypothesized that postlarval *Girella nigricans* might swim ahead of the cold waters of the incoming internal wave fronts, thus producing the observed early shoreward migration of that species.

Brewer and Smith (1982) estimated that the numbers of *E. mordax* larvae spawned in the nearshore waters were approximately proportional to the area the nearshore waters represented in the total waters inhabited by the central subpopulation. They concluded that the nearshore region off southern

¹³Reitzel, J. 1979. Physical/chemical oceanography. In Interim report of the Marine Review Committee to the California Coastal Commission. Part II: Appendix of technical evidence in support of the general summary. MRC Document 79-02(II), p. 6-23. Marine Review Committee of the California Coastal Commission, 631 Howard Street, San Francisco, CA 94105.

California was not a preferred habitat for adult spawning during 1978-80. Our ratios of *E. mordax* eggs to early larvae support this conclusion.

On the other hand, larval survivorship may be enhanced in these nearshore waters. Hjort (1914), Lasker (1975), and Brewer and Smith (1982) pointed out that the number of eggs and larvae surviving to recruitment may vary independently of spawning stock size. Brewer and Smith (1982) indicated that the shallow coastal region's importance as a nurseryground for *E. mordax* is not yet clear. Their preliminary length-frequency data show relatively high numbers of large size classes nearshore, which are rare further offshore. Our preliminary length-frequency data corroborate this. The onshore ontogenetic shift of these larvae is a conspicuous and persistent feature of our data set (fig. 5). Thus nearshore environmental conditions may enhance growth or survivorship or both for *E. mordax* larvae as well as for other larvae with typically inshore patterns.

The larval taxa discussed in this paper represent some 12% of the types identified in the course of this study. Less common taxa were omitted for statistical reasons, but inspection of the data suggests that the patterns of abundance shown here are typical. Larvae of many species found in our study are most abundant in shallow water within a few kilometers from shore. Laroche and Holton (1979), noting the inshore abundance of 0-age *Parophrys vetulus* off the Oregon coast, suggested a nursery function for those open, nearshore areas. Concentration of juvenile fishes well inshore of adult depth ranges is also well known along the southern California coast (Limbaugh 1961; Feder et al. 1974).

Whether such patterns result from behavioral mechanisms leading to nearshore concentration, from differential onshore-offshore mortality, or simply from random movements away from very localized spawning sites, their evolution and maintenance imply significant value in occupying nearshore waters. Eppley et al. (1978) found higher concentrations of phytoplankton inshore of the 50-100 m depth contours, and Lasker (1975, 1978) showed that nearshore abundance of suitable-sized phytoplankton can be an important determinant of year-class strength in *E. mordax*. Gruber et al. (1982) noted that Pacific sardine, *Sardinops caeruleus*, once spawned over wide areas of the California Current region, but the reduced stock now concentrates its spawning effort nearshore. They suggested the productive nearshore zone may be especially important to recovering fish stocks, a situation which might apply to northern anchovy at some future date.

Pearcy and Myers (1974) noted that a number of studies found estuaries of northern California and Oregon to be important nurseries. However, estuaries in the Southern California Bight, as along much of the Pacific coast of North America, are small and far between. Enhanced productivity in the shallow waters of the open coast seems to provide a nursery area for many Southern California fishes analogous to the estuarine nurseries of other regions.

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LITERATURE CITED

- AHLSTROM, E. H.
 1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. Fish Wildl. Serv., Fish. Bull., U.S. 60:107-146.
 1965. Kinds and abundance of fishes in the California Current region based on egg and larval surveys. Calif. Coop. Oceanic Fish. Invest. Rep. 10:31-52.
 1969. Distributional atlas of fish larvae in the California Current region: jack mackerel, *Trachurus symmetricus*, and Pacific hake, *Merluccius productus*, 1951 through 1966. Calif. Coop. Oceanic Fish. Invest. Atlas 11, xi + 187 charts.
 1972. Distributional atlas of fish larvae in the California Current region: six common mesopelagic fishes — *Vinciguerra lucetia*, *Triphoturus mexicanus*, *Stenobrachius leucopsarus*, *Leuroglossus stilbius*, *Bathylagus wesethi*, and *Bathylagus ochotensis*, 1955 through 1960. Calif. Coop. Oceanic Fish. Invest. Atlas 17, xv + 306 charts.
- AHLSTROM, E. H., AND H. G. MOSER.
 1975. Distributional atlas of fish larvae in the California

- Current region: flatfishes, 1955 through 1960. Calif. Coop. Oceanic Fish. Invest. Atlas 23, xix + 207 charts.
- BREWER, G. D., R. J. LAVENBERG, AND G. E. MCGOWEN.
1981. Abundance and vertical distribution of fish eggs and larvae in the Southern California Bight: June and October 1978. In R. Lasker and K. Sherman (editors), Symposium on the early life history of fish. Introduction and background, Woods Hole, April 1979, Vol. 178, p. 165-167. Rapp. P.-V. Réun. Cons. Int. Explor. Mer.
- BREWER, G. D., AND P. E. SMITH.
1982. Northern anchovy and Pacific sardine spawning off southern California during 1978-1980: preliminary observations on the importance of the nearshore coastal region. Calif. Coop. Oceanic Fish. Invest. Rep. 23:160-171.
- BROWN, D. M., AND L. CHENG.
1981. New net for sampling the ocean surface. Mar. Ecol. Prog. Ser. 5:225-227.
- CAIRNS, J. L., AND K. W. NELSON.
1970. A description of the seasonal thermocline cycle in shallow coastal water. J. Geophys. Res. 75:1127-1131.
- CHAO, L. N., AND J. A. MUSICK.
1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. Fish. Bull., U.S. 75:657-702.
- EPPLEY, R. W., C. SAPIENZA, AND E. H. RENGER.
1978. Gradients in phytoplankton stocks and nutrients off southern California in 1974-76. Estuarine Coastal Mar. Sci. 7:291-301.
- FEDER, H. M., C. H. TURNER, AND C. LIMBAUGH.
1974. Observations on fishes associated with kelp beds in southern California. Calif. Dep. Fish Game, Fish Bull. 160, 144 p.
- GRUBER, D., E. H. AHLSTROM, AND M. M. MULLIN.
1982. Distribution of ichthyoplankton in the Southern California Bight. Calif. Coop. Oceanic Fish. Invest. Rep. 23:172-179.
- HENDRICKS, T. J.
1977. Coastal currents. In Southern California Coastal Water Research Project, Annual Report, p. 53-62. El Segundo, Calif.
- HJORT, J.
1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 20:1-228.
- HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.
- ICANBERRY, J. W., J. W. WARRICK, AND D. W. RICE, JR.
1978. Seasonal larval fish abundance in waters off Diablo Canyon, California. Trans. Am. Fish. Soc. 107:225-233.
- KRAMER, D., AND E. H. AHLSTROM.
1968. Distributional atlas of fish larvae in the California Current region: northern anchovy, *Engraulis mordax* Girard, 1951 through 1965. Calif. Coop. Oceanic Fish. Invest. Atlas 9, xi + 268 charts.
- LADELL, W. R. S.
1936. A new apparatus for separating insects and other arthropods from the soil. Ann. Appl. Biol. 23:862-879.
- LAROCHE, W. A., AND R. L. HOLTON.
1979. Occurrence of 0-age English sole, *Parophrys vetulus*, along the Oregon coast: an open coast nursery area? Northwest Sci. 53:94-96.
- LASKER, R.
1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453-462.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:212-230.
- LIMBAUGH, C.
1961. Life-history and ecologic notes on the black croaker. Calif. Dep. Fish Game 47:163-174.
- METHOT, R. D., AND D. KRAMER.
1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull., U.S. 77:413-423.
- MORRISON, D. F.
1976. Multivariate statistical methods. 2d ed. McGraw-Hill, N. Y., 415 p.
- MURPHY, G. I., AND R. I. CLUTTER.
1972. Sampling anchovy larvae with a plankton purse seine. Fish. Bull., U.S. 70:789-798.
- MYERS, J. L.
1972. Fundamentals of experimental design. 2d ed. Allyn and Bacon, Boston, 466 p.
- NORRIS, K. S.
1963. The functions of temperature in the ecology of the percid fish *Girella nigricans* (Ayres). Ecol. Monogr. 33:23-62.
- PARRISH, R. H., C. S. NELSON, AND A. BAKUN.
1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1:175-203.
- PEARCY, W. G., AND S. S. MYERS.
1974. Larval fishes of Yaquina Bay, Oregon: A nursery ground for marine fishes? Fish. Bull., U.S. 72:201-213.
- RICHARDSON, S. L.
1981. Spawning biomass and early life of northern anchovy, *Engraulis mordax*, in the northern subpopulation off Oregon and Washington. Fish. Bull., U.S. 78:855-876.
- RICHARDSON, S. L., AND W. G. PEARCY.
1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull., U.S. 75:125-145.
- SMITH, P. E., R. C. COUNTS, AND R. I. CLUTTER.
1968. Changes in filtering efficiency of plankton nets due to clogging under tow. J. Cons. Int. Explor. Mer 32:232-248.
- SMITH, P. E., AND S. L. RICHARDSON.
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. 175, 100 p.
- SNEDECOR, G. W., AND W. G. COCHRAN.
1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 593 p.
- SOKAL, R. R., AND F. J. ROHLF.
1969. Biometry. The principles and practice of statistics in biological research. W. H. Freeman, San Franc., 776 p.
- WEINSTEIN, M. P., S. L. WEISS, R. G. HODSON, AND L. R. GERRY.
1980. Retention of three taxa of postlarval fishes in an intensively flushed tidal estuary, Cape Fear River, North Carolina. Fish. Bull., U.S. 78:419-436.
- WINANT, C. D., AND J. R. OLSON.
1976. The vertical structure of coastal currents. Deep-Sea Res. 23:925-936.
- WINANT, C. D., AND A. W. BRATKOVICH.
1981. Temperature and currents on the Southern California shelf: a description of the variability. J. Phys. Oceanogr. 11:71-86.
- WINER, B. J.
1971. Statistical principles in experimental design. 2d ed. McGraw-Hill, N.Y., 907 p.
- ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—a general model. Fish. Bull., U.S. 74:609-621.

APPENDIX 1

On 24 July, 30 August, and 22 September 1978, vertically stratified samples were taken at one station along the 8 m isobath and at another along the 13 m isobath. A sample set, or profile, consisting of five strata was sampled at each station: Neustonic, three midwater strata, and the epibenthic layer (the midwater strata were chosen with regard to the depths of power plant cooling structures). At the 8 m station, the midwater strata were 1) the lower 3 m of the water column, 2) 3 m above the bottom, and 3) the water column above stratum 2. At the 13 m station, the lower midwater stratum was the lower 2 m of the water column, while the upper two depended on the vertical thermal structure. When a thermocline was present, as during the September cruise and intermittently during the August cruise, the middle stratum extended from 2 m above the bottom to the base of the thermocline, and the upper stratum from the top of the thermocline to just below the surface. In the absence of a well-defined thermocline, the water column above 2 m from the bottom was divided into two equal parts. Sample sets were replicated four to six times in the day and again at night, resulting in 325 samples in the vertical migration study.

Data from the two stations were analyzed separately, since all sampling depths (except the neustonic layer) differed between stations. No analysis was done of the effects of the thermocline, since its extreme movements with respect to the vertical scale of interest would require a more intensive sampling program. In this analysis nominal sampling depths were treated as constants.

Because of patchy distributions of ichthyoplankton and movements of the thermocline (August and September), inherent variability was expected among the sets of profiles taken on a given date. In order to separate this variability from variability due to sam-

pling date (cruise), time of day, and "error", we analyzed the data in a repeated-measures type analysis of variance design (App. Table 1). In this design, the depth effect was contained within the fixed-effect time of day and the random-effect cruise. The questions addressed were 1) whether there was a depth effect, i.e., significant differences among strata, within cruise \times time-of-day blocks, and 2) if a depth effect did exist, whether there was a significant depth \times time-of-day interaction. This interaction, interpreted (when significant) as daily vertical migration, was evaluated as the F -ratio of the depth \times time of day to the depth \times time of day \times cruise mean square errors. When the three-way term was insignificant (in this case, $P > 0.75$), the error sums of squares and the three-way sum of squares were pooled, and this pooled term was used as the denominator in the F -ratio (Sokal and Rohlf 1969: 266).

The 10 most frequently occurring taxa were analyzed (App. Table 2). (A high frequency of occurrence was important to keep cell variances relatively homogeneous.) To reduce the effect of day-night differences in apparent abundance (most likely from visual net avoidance), we reduced each profile to a set of differences, or Δ 's between adjacent strata, e.g.

$$\Delta_1 = (\text{abundance at depth 1}) - (\text{abundance at depth 2}).$$

Abundance was expressed as $\log_{10}(X + 1)$, where X = larvae/100m³. Any daily change in the relative abundance in two strata would thus be manifest in a change in sign and/or magnitude of the corresponding Δ .

APPENDIX TABLE 1.—ANOVA model applied in the analysis of daily vertical migration. The last two terms can form the error estimate (e) in Appendix Table 2.

$$\bar{Y}_{ijkm} = \mu + C_i + T_j + P_{m(lj)} + D_k + CT_{(ij)} + CD_{(ik)} + TD_{(jk)} + DP_{(m(lj)k)} + CTD_{(ijk)} + \epsilon_{ijkm}$$

where Y_{ijkm}	=	Density
μ	=	Mean effect
C_i	=	Sampling date (cruise) effect
T_j	=	Time-of-day effect (day-night)
$P_{m(lj)}$	=	Depth profile within cruise and time-of-day
D_k	=	Depth effect
$CT_{(ij)}$	=	Interaction, cruise \times day-night period
$CD_{(ik)}$	=	Interaction, cruise \times depth
$TD_{(jk)}$	=	Interaction, day-night period \times depth
$DP_{(m(lj)k)}$	=	Depth k for profile m within cruise and time-of-day
$CTD_{(ijk)}$	=	Interaction, cruise \times day-night period \times depth
ϵ_{ijkm}	=	Residual error

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APPENDIX TABLE 2.—F-table for the 10 most frequently occurring larval fish taxa off San Onofre, Calif.: repeated-measures ANOVA. *D* = depth, *TD* = day-night period X depth, *CTD* = cruise X day/night period X depth. When the *CTD* mean square error (MSE) was insignificant ($P > 0.75$), the *CTD* and Error (ϵ) sums of squares were pooled. The *TD* interaction term, when significant ($*P \leq 0.05$; $**P < 0.01$), is interpreted as daily vertical migration. Frequency refers to the number of samples in which a taxon occurred out of 325 total samples. Results are presented for the 13 m station only.

Taxa	Freq.	Source	df	MSE	F	P
<i>Engraulis mordax</i>	251	<i>D</i>	3	0.79065	4.101	0.010
		<i>TD</i>	3	0.18989	0.335	0.801
		<i>CTD</i>	6	0.56687	2.940	0.013
		ϵ	69	0.19281		
<i>Seriophilus politus</i>	232	<i>D</i>	3	1.72110	8.943	<0.001**
		<i>TD</i>	3	0.06644	0.045	0.986
		<i>CTD</i>	6	1.46510	7.613	0.000
		ϵ	69	0.19246		
<i>Hypsoblennius</i> spp.	206	<i>D</i>	3	3.93932	19.586	<0.001
		<i>TD</i>	3	2.37801	12.344	0.000**
		<i>CTD</i>	6	0.09508	0.473	0.826
		ϵ	69	0.20113		
<i>Genyonemus lineatus</i> ¹	148	<i>D</i>	3	1.56249	11.853	<0.001
		<i>TD</i>	3	0.82790	5.377	0.100
		<i>CTD</i>	3	0.15403	1.168	0.332
		ϵ	45	0.13183		
<i>Cheilotrema saturnum</i>	144	<i>D</i>	3	1.15593	13.838	<0.001
		<i>TD</i>	3	0.03663	0.145	0.929
		<i>CTD</i>	6	0.25185	3.015	0.011
		ϵ	69	0.08353		
<i>Menticirrus undulatus</i>	125	<i>D</i>	3	2.52228	31.968	<0.001
		<i>TD</i>	3	0.03333	0.294	0.829
		<i>CTD</i>	6	0.11325	1.435	0.214
		ϵ	69	0.07890		
<i>Paralabrax</i> spp.	122	<i>D</i>	3	1.86818	15.383	<0.001
		<i>TD</i>	3	0.60921	1.802	0.247
		<i>CTD</i>	6	0.33768	2.781	0.018
		ϵ	69	0.12144		
<i>Paralichthys californicus</i>	119	<i>D</i>	3	2.97375	15.609	<0.001
		<i>TD</i>	3	0.76462	4.873	0.047*
		<i>CTD</i>	6	0.15653	0.822	0.557
		ϵ	69	0.19051		
<i>Gibbonsia</i> Type A	114	<i>D</i>	3	1.25337	25.265	<0.001
		<i>TD</i>	3	0.20486	1.742	0.258
		<i>CTD</i>	6	0.11763	2.371	0.039
		ϵ	69	0.04961		
<i>Gobiesox rhessodon</i>	113	<i>D</i>	3	3.52655	103.984	<0.001
		<i>TD</i>	3	0.17248	4.528	0.055
		<i>CTD</i>	6	0.03806	1.122	0.359
		ϵ	69	0.03391		

¹The analysis of *G. lineatus* differed from those of other taxa. At the 13m station, the 24 July cruise was eliminated because the extremely low abundance of *G. lineatus* on that date caused the variance to be unacceptably heterogeneous (by inspection).