TEMPORAL AND SPATIAL PATTERNS OF NEARSHORE DISTRIBUTION AND ABUNDANCE OF THE PELAGIC FISHES OFF SAN ONOFRE-OCEANSIDE, CALIFORNIA

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ABSTRACT

The pelagic fishes off San Onofre-Oceanside, California, were sampled nearshore (within 0.5-3.0 km of shore) during September 1979 to March 1981, using standardized lampara net gear. Sixty-two taxa were collected in 643 net-hauls systematically partitioned among three depth strata during day and night periods. *Engraulis mordax* dominated the catch and accounted for about 81% of all fishes. *Seriphus politus*, *Genyonemus lineatus*, *Peprilus simillimus*, and one species complex (atherinid spp.), together with *E. mordax*, made up >98% of the total numerical catch. Total catch per unit effort (CPUE) was greatest during the summer months (June-September), due mainly to the increased abundance of *Engraulis mordax*. The CPUE of other common species fluctuated little throughout the year except for a general decline during October-December because of the decreases in catches of *Seriphus politus* and *Genyonemus lineatus*. Four species groups were defined by quantitative clustering. Species Group I contained the above five most abundant and ubiquitous species. Groups II and III consisted of periodic species that occurred nearshore primarily during warmer and cooler water months, respectively. Group IV was composed of nine species of relatively rare bottom-oriented fishes.

The most conspicuous pattern exhibited by the common species in the assemblage involved a marked shift in depth over a diel period. *Engraulis mordax*, *Seriphus politus*, *Genyonemus lineatus*, and, to a lesser extent, *Peprilus simillimus* schooled in shallow water (5-11 m depths) during the day and dispersed offshore of these depths at night. Analysis of gut fullness during day and night suggested that *Seriphus politus*, and possibly *Genyonemus lineatus* and *Engraulis mordax*, disperse at night in part to feed on nocturnally active prey.

The marked depth and diel patterns of abundance that were observed could only be attributed in small part to depth-specific differences in water clarity and diel differences in catch efficiency.

Knowledge of pelagic fish assemblages that inhabit the waters off California is limited to general accounts from commercial catch records, larval fish studies and surveys (reviewed in Lasker 1982), and hydroacoustic surveys of adults (Mais 1974). These sources have provided general information on composition, distribution, and behavior of the offshore component of the pelagic ichthyofauna. This fauna is heavily dominated in numbers and biomass by the schooling clupeiform—northern anchovy, *Engraulis mordax*—especially within 37 km of the coast between Santa Barbara and San Diego (Mais 1974). Jack mackerel, *Trachurus symmetricus*; Pacific mackerel, *Scomber japonicus*; Pacific sardine, *Sardinops sagax*; Pacific saury, *Cololabis saira*; and Pacific hake, *Merluccius productus*, are also important components of this fauna, although their relative abundances are poorly known (Mais 1974). Information on the relative abundances of pelagic fish stocks of nearshore (<3.0 km from shore) waters was limited to a few unpublished reports prior to the initiation of the present study.

Little is known about the diel and seasonal movements of fishes within the Southern California Bight, although the diel activity patterns of some fishes associated with kelp beds in the Bight have been documented (Ebeling and Bray 1976; Hobson and Chess 1976; Hobson et al. 1981). Several of these species (queenfish, *Seriphus politus*; salema, *Xenistius californiensis*; walleye surfperch, *Hyperprosopon argenteum*) are known to make diel migrations between kelp beds and nearshore pelagic and other coastal (e.g., sandy surf zone) habitats (Hobson and Chess 1976).

This study is the first direct, systematic assessment of the pelagic fish assemblage inhabiting nearshore (<3 km) waters off southern California. The specific purposes of this paper are to characterize this assemblage by 1) species composition, 2) major spatial and temporal patterns of abundance and distribution, 3) species associations, and 4) important environmental factors.

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METHODS

Field Sampling

Two longshore locations were sampled in the nearshore waters (0.5-3.0 km offshore) between San Onofre and Oceanside in southern California (Fig. 1). Fish abundances at these locations were monitored as part of an environmental impact assessment of the San Onofre Nuclear Generating Station (SONGS), located about 5 km downcoast of San Clemente, performed for the Marine Review Committee of the California Coastal Commission. The upcoast location is situated several kilometers downcoast of SONGS and the downcoast location ~18 km downcoast (Fig. 1). The sand and sand-cobble bottom in the area slopes gradually from shore with an increase in depth of about 5 m/km. The upcoast location is ~0.5-1.5 km downcoast of the San Onofre kelp bed (designated by stippling, Fig. 1).

Samples (net-hauls) were taken at randomly chosen positions within each of three depth blocks (shallow: 5-11 m; mid: 12-16 m; and deep: 18-27 m) at both locations during day (1-6 h after dawn) and night (1-6 h after sunset) periods from September 1979 to March 1981, inclusive. (Samples could not be taken in January-February 1980, when our sampling vessel was drydocked for repairs.) The three depth blocks used were chosen as most appropriate for partitioning onshore/offshore variation in catches, based on the results of prior (May 1978-August 1979) lampara sampling at various depths in the general area. The number of cruises ($N = 1$-4) and net-hauls ($N = 4$-8) per month differed between diel periods and depth blocks, with most samples allocated to the daytime period and shallow depth block wherein catches were most variable. Because we suspected a significant date (cruise) effect on our catches, a paired sampling design was established in which the same depth blocks were sampled during the same diel period at both longshore locations on each cruise.

Two sizes of lampara net (semipursing round haul, Scofield 1951) were used: 1) A small net with each of two wings 118 m long of 15 cm stretch mesh, tapering to a bag of 1.25 cm mesh, was used to sample surface-to-bottom within the 5-11 m and 12-16 m depth blocks. The small net sampled about 4,600 m² of sea surface area. 2) A large net with wings each 136 m long of mesh identical to the small net was used to sample the 18-27 m depth block, wherein it also fished surface-to-bottom. The large net sampled about 6,200 m² of sea surface area. Catch was standardized to the area of the small lampara net. Both nets took about 10 min to set and retrieve, using a commercial fishing vessel. The same vessel and procedures of net deployment were used for the duration of the study.

Fishes collected in net-hauls were transferred by dip net to a holding tank on the vessel and were then identified and counted. Subsamples of major species were taken for life history analysis, and other fishes were returned to the sea as soon as possible. Large catches were subsampled with standard bait brailers.

In order to evaluate the potential effects of variable net catch efficiencies under varying water clarity conditions during the day, an index of water clarity (visibility to shipboard observer of 30 cm Secchi disk) was measured immediately following most net-hauls. Potential diel differences in catch efficiency were evaluated on the basis of the percentage recapture of marked *Seriphus politus* in net-hauls made during a pilot (June-September 1978) study. A constant number (50) of fin-clipped adult *S. politus*, captured on the previous net-haul, were released within the center of the area being encircled as the net was deployed. Test releases were made in all depth blocks, both at the surface and near bottom (via a messenger-tripped holding cage), and during both day and night. Secchi disk indices of water clarity were measured at night between test net-hauls, using a standard shipboard light source.

Data Analysis

Analyses were carried out using the Statistical Analysis System (SAS) installed at the Marine Review Committee's Computer Center in Solana Beach, Calif.

Preliminary tests (t-test for paired comparisons, $P > 0.05$) failed to detect significant differences between locations in all but a few of the common species using log-transformed catch data. Log transformation ($\log_{10} X + 1$) of catch data was necessary to satisfy the parametric assumptions of normality and equality of variances within depth blocks and diel periods. The general lack of longshore differences allowed us to pool the data at both locations for subsequent analyses.

Catch per unit effort (CPUE) was calculated by month based on log-transformed catch data for individual depth blocks and diel periods. Combined CPUE of all three depth blocks was expressed as the grand mean and associated standard error of depth means.

Comparisons of untransformed catch data between depths, diel periods, and dates were made by using Wilson's nonparametric analysis of variance (Wilson
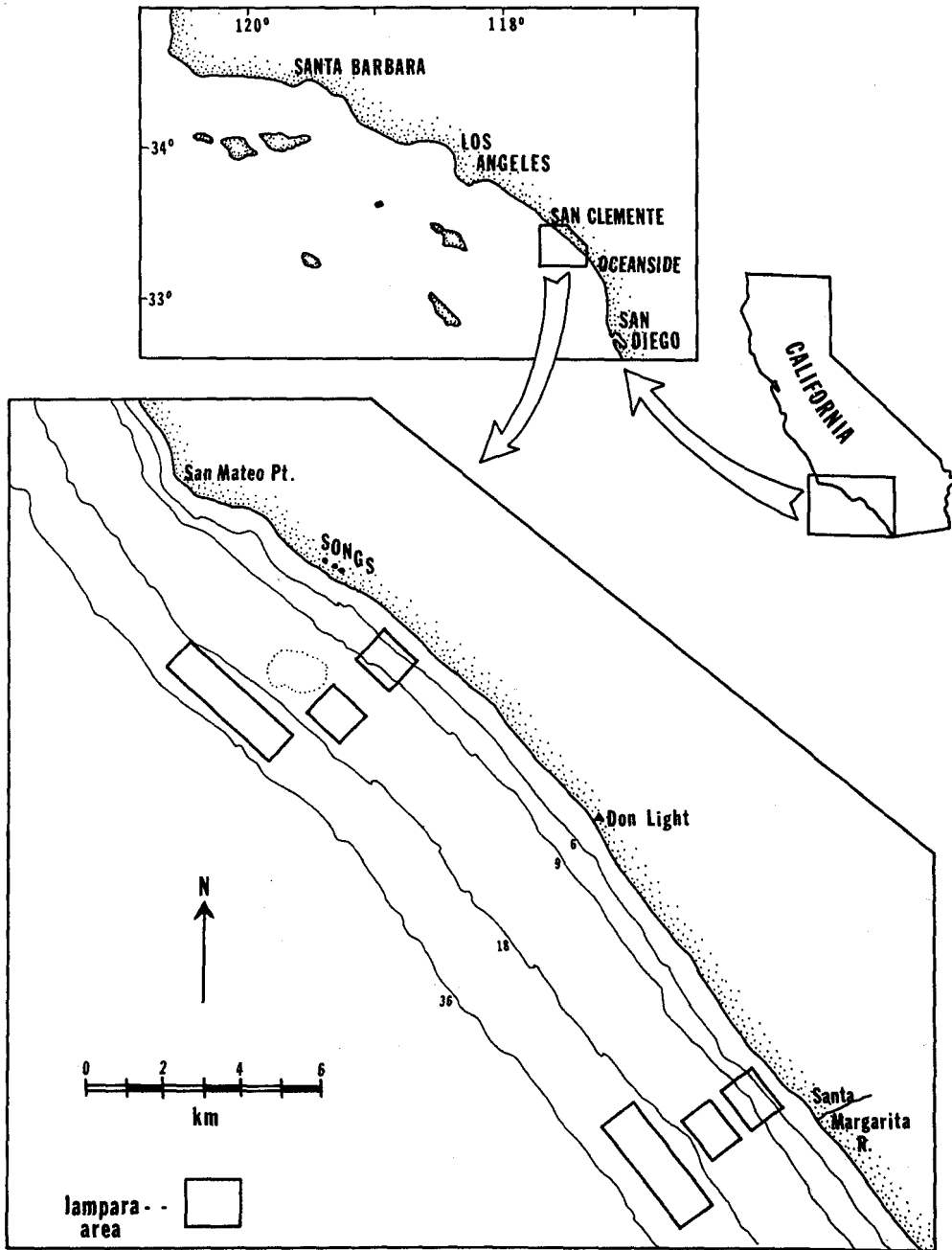
FIGURE 1.—Map of the study area, San Onofre-Oceanside, Calif. Rectangles represent the various depth blocks sampled at the two longshore locations; note that all depth blocks are 1 km distance in onshore-offshore extent. Stippled area represents the location of the San Onofre kelp bed.

1956), available in the IMSL Library's[3] statistical package. Variances of catches were heteroscedastic among depth blocks and between diel periods, which precluded use of parametric analysis of variance. Wilson's three-way ANOVA's (either with unequal replication or without replication) were used, depending on the category (e.g., total individuals or species counts) or species being considered.

Quantitative clustering of species was carried out using the Ecological Analysis Package (EAP)[4]. Mean abundance of species by cruise date, depth, and diel period was transformed by its square-root in order to counter the tendency of the Bray-Curtis Index (Clifford and Stephenson 1975) to overemphasize abundant species. Flexible sorting was used to maximize the separation between groups. Only species with a minimum total occurrence of 20 were considered in this analysis.

Spearman's rank correlations (r_s) were calculated to examine the relationships between diel period, water depth, and surface water temperature and CPUE for 1) total individuals, 2) total individuals minus *E. mordax*, 3) certain major species, and 4) species counts. CPUE data for taxonomic categories 1-3 were related to water clarity by using Spearman's rank test within each depth block; in addition, a parametric analysis of covariance (ANCOVA), with water clarity as covariate of CPUE and depth block as the treatment effect, was performed to estimate the general magnitude of the potential influence of depth-specific differences in water clarity on daytime catches. Diel catch efficiency data for *Seriphus politus* were related to water clarity by parametric or Spearman rank correlation, as appropriate.

Day-Night Comparison of Foregut Fullness

Preliminary examination of the variance: mean ratios of CPUE data indicated that fishes were dispersed more at night than during the day. In order to investigate the possible role of feeding behavior in this nocturnal dispersal pattern, we examined archived stomachs from paired day (1000-1300 h) and night (2100-0100 h) samples of fishes of comparable sizes for the five most abundant taxa (*E. mordax*; *Seriphus politus*; white croaker, *Genyonemus lineatus*; Pacific butterfish, *Peprilus simillimus*; and atherinid spp., the latter represented by jacksmelt,

Atherinopsis californiensis). Contents of the foregut were removed, either dried at 40°C (for *E. mordax*, *S. politus*, and *G. lineatus*) or blotted dry (*P. simillimus* and *A. californiensis*), and weighed. A contents index (CI) was then calculated for each specimen as follows:

$$CI = (\text{weight contents/weight of fish}) \times 10^5.$$

Diel overlap in gut evacuation did not create a major problem except that it tended to make the analysis more conservative (i.e., more difficult to detect day-night differences).

The CI's for day-caught versus night-caught fishes were compared by either Wilcoxon signed-ranks test for paired comparisons or Wilcoxon two sample test, depending on the number and temporal distribution of samples.

RESULTS

Species Composition

Sixty-two taxa representing 33 families of teleost and elasmobranch fishes were collected in 643 net-hauls partitioned among the three depth blocks and two diel periods made during the 19-mo period, September 1979-March 1981 (Table 1). The catch was overwhelmingly dominated by *E. mordax*. *Seriphus politus*, *G. lineatus*, *P. simillimus*, and a species complex of silversides (atherinid spp.) were also abundant in the catch. These top five taxa accounted for >98% of the numbers of total individuals sampled (Table 1). The atherinid species complex was a composite of three species (*Atherinopsis californiensis*; topsmelt, *Atherinops affinis*; California grunion, *Leuresthes tenuis*) that were not readily identifiable in the field. Subsamples of "atherinid spp." field catches were about 48% *Atherinopsis californiensis*, 42% *L. tenuis*, and 10% *Atherinops affinis*.

Location Comparison

Location differences were insignificant ($P > 0.05$) for most categories and species within depth blocks and diel periods based on *t*-tests for paired comparisons. Differences were detected in the following cases: 1) Atherinids were more abundant at night in the upcoast area ($P < 0.01$); 2) Pacific barracuda, *Sphyraena argentea*, occurred in greater numbers at night upcoast ($P < 0.01$); 3) *T. symmetricus* was more abundant both day and night upcoast ($P < 0.01$); and 4) *Scomber japonicus* was also caught in greater numbers upcoast ($P < 0.05$), but only at night during the

period November 1980-March 1981. *Xenistius californiensis* was consistently more common upcoast ($N = 170$ sample fish) than downcoast ($N = 13$) at night, although its low frequency of overall occurrence precluded a statistical test for longshore differences.

TABLE 1.—Number of individuals and frequency of occurrence of 62 species/taxa in 643 lampara net samples on 129 cruises from September 1979 to March 1981, inclusive. Species/taxa are ranked according to total number of individuals.

Species/taxa	Number	Percent number	Frequency	Percent frequency
Engraulis mordax	819,872	80.79	440	68.4
Seriphus politus	80,513	7.93	413	64.2
Genyonemus lineatus	53,994	5.32	335	52.1
Peprilus simillimus	26,003	2.56	238	37.0
Atherinid spp.	15,811	1.56	326	50.7
Scomber japonicus	7,386	0.73	194	30.2
Trachurus symmetricus	2,750	0.27	92	14.3
Anchoa compressa	1,915	0.19	85	13.2
Sarda chiliensis	1,394	0.14	115	17.9
Sphyraena argentea	1,066	0.11	99	15.4
Hyperprosopon argenteum	936	0.09	106	16.5
Phanerodon furcatus	665	0.07	101	15.7
Myliobatis californica	455	0.04	212	33.0
Menticirrhus undulatus	412	0.04	117	18.2
Umbrina roncador	269	0.03	38	5.9
Amphistichus argenteus	211	0.02	51	7.9
Xenistius californiensis	182	0.02	25	3.9
Paralichthys californicus	139	0.01	79	12.3
Sardinops sagax	130	0.01	15	2.3
Paralabrax nebulifer	108	0.01	56	8.7
Cymatogaster aggregata	86	0.01	34	5.3
Squalus acanthias	66	0.01	23	3.6
Scorpaena guttata	57	0.01	28	4.3
Urolophus halleri	34	<0.01	19	2.9
Citharichthys stigmaeus	28	<0.01	16	2.5
Otophidium scrippsi	27	<0.01	19	2.9
Rhinobatos productus	22	<0.01	12	1.9
Platyrhinoidis triseriata	21	<0.01	18	2.8
Anisotremus davidsoni	19	<0.01	8	1.2
Medialuna californiensis	19	<0.01	5	0.8
Torpedo californica	18	<0.01	15	2.3
Cynoscion nobilis	17	<0.01	12	1.9
Pleuronichthys verticalis	12	<0.01	13	2.0
Raja inornata	12	<0.01	8	1.2
Rhacochilus toxotes	11	<0.01	4	0.6
Porichthys myriaster	9	<0.01	5	0.8
Porichthys notatus	8	<0.01	4	0.6
Alopias vulpinus	8	<0.01	5	0.8
Pleuronichthys ritteri	8	<0.01	5	0.8
Embiotoca jacksoni	8	<0.01	6	0.9
Sebastes auriculatus	7	<0.01	1	0.1
Roncador stearnsi	6	<0.01	2	0.3
Hypsopsetta guttulata	6	<0.01	5	0.8
Dorosoma petenense	4	<0.01	4	0.6
Paralabrax clathratus	4	<0.01	4	0.6
Damalichthys vacca	4	<0.01	1	0.1
Leptocottus armatus	4	<0.01	3	0.5
Syngnathus spp.	4	<0.01	4	0.6
Citharichthys xanthostigma	3	<0.01	3	0.5
Triakis semifasciata	3	<0.01	3	0.5
Raja binoculata	2	<0.01	1	0.1
Xystreurys liolepis	2	<0.01	2	0.3
Heterostichus rostratus	2	<0.01	2	0.3
Cypselurus californicus	2	<0.01	2	0.3
Heterodontus francisci	1	<0.01	1	0.1
Sebastes rastrelliger	1	<0.01	1	0.1
Balistes polylepis	1	<0.01	1	0.1
Synodus lucioceps	1	<0.01	1	0.1
Symphurus atricauda	1	<0.01	1	0.1
Mugil cephalus	1	<0.01	1	0.1
Icichthys lockingtoni	1	<0.01	1	0.1
Mustelus californicus	1	<0.01	1	0.1
Grand total	1,014,762		643	

Monthly and Longer Temporal Patterns

CPUE for total individuals, number of *E. mordax*, and total individuals minus *E. mordax*, when plotted on a monthly basis, revealed general temporal patterns of abundance (Fig. 2). Catches were generally higher at night for all three categories (see below). Day catches were generally much more variable than night catches, as the standard errors indicate (Fig. 2). The longer term (i.e., "seasonal") temporal changes in the catch of total individuals largely reflect the increase in primarily juvenile-sized (<10 cm standard length, Hunter and Leong 1981) *E. mordax* during the summer months. When the abundances of all species other than *E. mordax* are combined, the catch remained relatively constant throughout the study period except for a general decline in numbers during October-December of both 1979 and 1980.

The abundances of *Seriphus politus* and *G. lineatus* also remained relatively constant except for the October-December declines. These two species (Fig. 3) were primarily responsible for the pattern observed for total individuals minus *E. mordax*. Night catches were higher than day catches for *G. lineatus* and (especially) *S. politus*. The abundances of *P. simillimus* and atherinids in general showed patterns which were similar in terms of seasonality. Both were usually more abundant during cooler water months (December-April). Three species of higher level (mainly piscivorous) carnivores showed dissimilar patterns of nearshore abundance (Fig. 3). *Scomber japonicus* was more abundant in warmer water months from about June to October. Pacific bonito, *Sarda chiliensis*, occurred in greatest numbers from March to August, but only during the day. *Sphyraena argentea* was more abundant during the cooler water months of October through March.

Diel and Depth Patterns

Day and night catches of total individuals varied among depth blocks throughout the study (Fig. 4). Day catches were consistently highest at 5-11 m depths, but the variability in catches was high. Night catches did not differ ($P > 0.05$, Wilcoxon's signed rank test) from day catches in the shallow depth block. However, night catches were higher and less variable than day catches in both the 12-16 m and 18-27 m depth blocks (Fig. 4).

All categories and species common enough to test showed significant diel, depth, and date (cruise) main effects, as well as diel × depth interactions, based on Wilson's three-way ANOVA with unequal replication
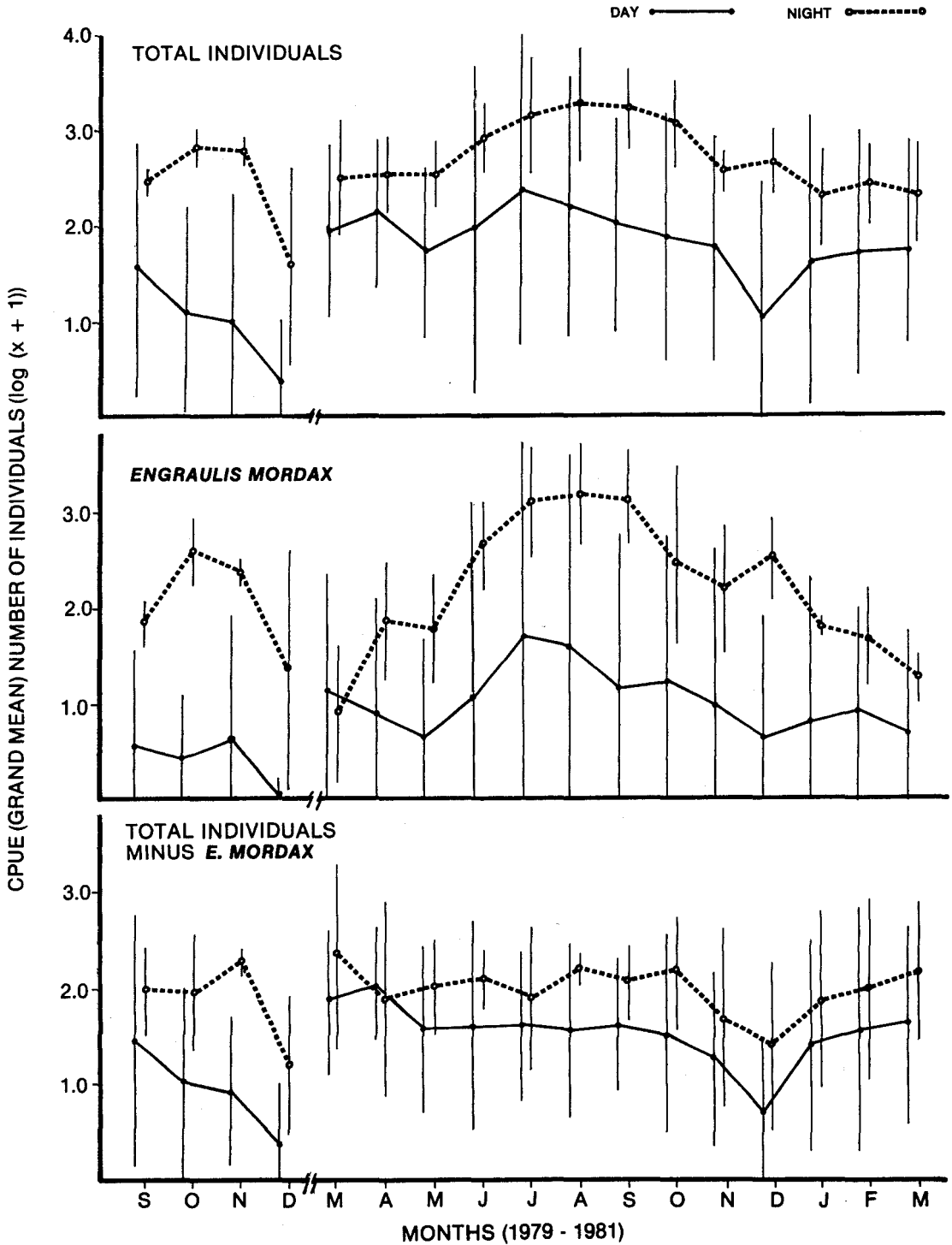
FIGURE 2.—Monthly variation in the abundance (CPUE) of total individual fishes, *Engraulis mordax*, and total individuals minus *E. mordax* over the study period. Each value represents the grand mean of $\log_{10}(X+1)$ transformed catches from day and night net-hauls. Vertical bars depict ±2 standard errors of the respective grand mean.
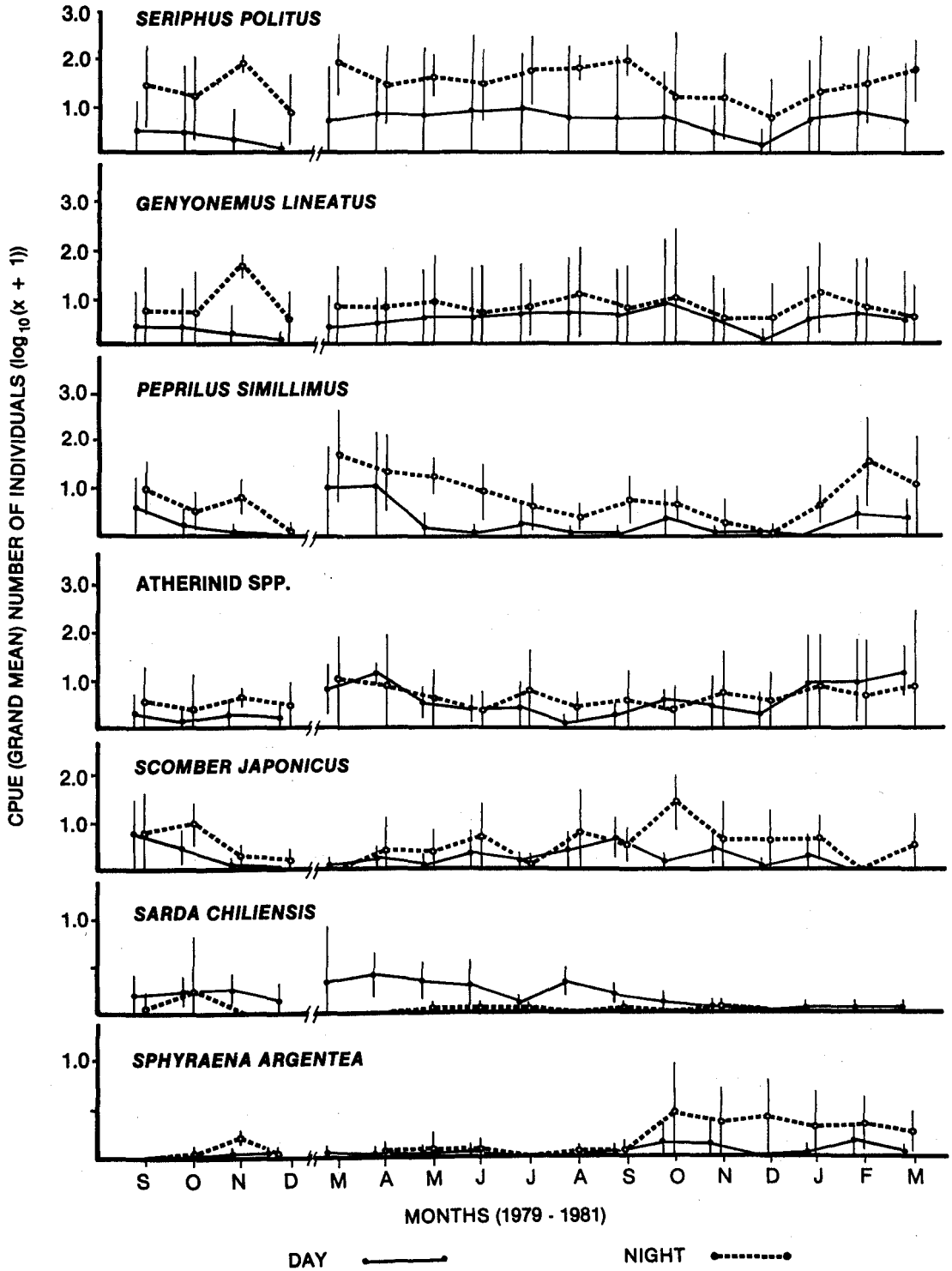
FIGURE 3.—Monthly variation in day and night catches of seven common species and one taxon of fishes over the study period. Each value represents the grand mean of $\log_{10} (X + 1)$ transformed catches from day and night net-hauls. Vertical bars depict ±2 standard errors of the respective grand mean.
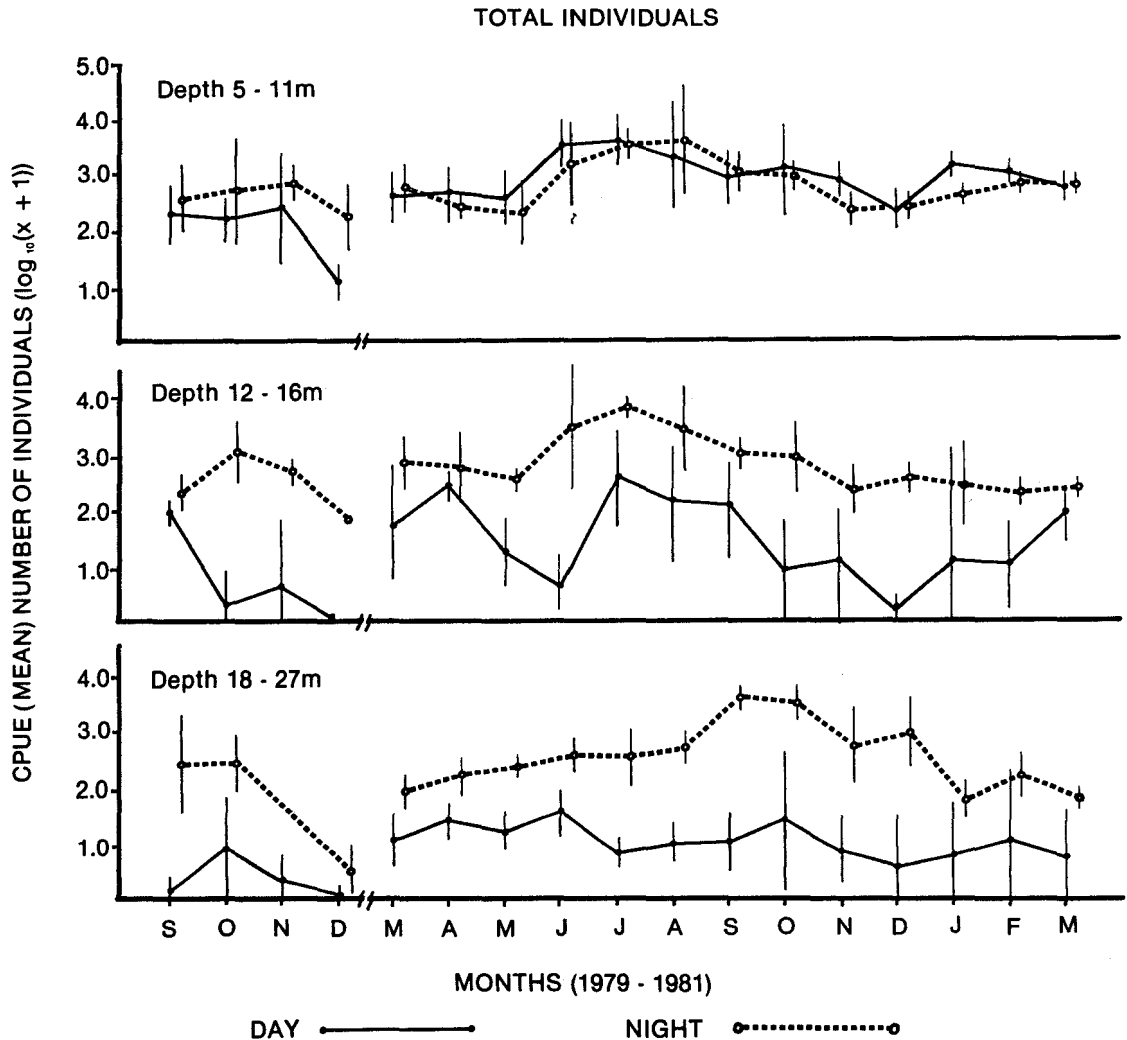
TOTAL INDIVIDUALS

FIGURE 4.—Monthly variation in the total number of individual fishes captured during the day and night in each of three depth blocks over the study period. Each value represents the grand mean of $\log_{10} (X + 1)$ transformed catches from day and night net-hauls. Vertical bars depict ±2 standard errors of the respective grand mean.

(Table 2). The probability for a date effect on *E. mordax* was marginal at $P = 0.09$.

Diel, depth, and date effects were variously important for four other common taxa or categories (Table 3). Interactions between main effects could not be evaluated for these species because we were forced to use Wilson's ANOVA without replication in order to minimize the number of zeros in the catch data. *Peprilus simillimus* was more abundant at night (diel effect) and on certain cruises during the study period (date effect). Catches of *G. lineatus* were higher at night and at the shallow depth. *Scomber japonicus* was more abundant offshore and at certain times of year.

Species Associations

Quantitative clustering of species by sample abundance among depth blocks and diel periods produced four distinct groups within 21 species (Fig. 5). The largest dichotomy (~160% distance) occurred between members of Groups I-II and Groups III-IV. Separation within both Groups I-II and Groups III-IV occurred at ~65% distance.

In Group I *E. mordax* was most dissimilar, fusing with other group members at ~55% distance. *Seriphus politus* and *G. lineatus* formed a very close association, being linked at ~12% distance. *Peprilus*

TABLE 2.—Summary of significant chi-square values from Wilson's three-way ANOVA with unequal replication for three categories and two species of fishes present in lampara net samples, September 1979-March 1981, inclusive (*=$P<0.001$). Dashes indicate insignificant ($P<0.05$) results.

Category or species	Diel	Depth	Date	Diel × depth	Diel × date	Depth × date	D×D×D
Total individuals	42.7**	58.9**	22.6*	29.3**	—	—	—
Total individuals minus *Engraulis mordax*	8.1*	87.4**	24.9*	10.6*	—	—	—
Species counts	26.2**	90.9**	26.8*	22.4**	—	—	—
Engraulis mordax	82.4**	22.2**	—	37.7*	—	—	—
Seriphus politus	63.4**	79.4**	26.0*	32.6*	—	—	—
df	1	2	13	2	13	26	26

TABLE 3.—Results of Wilson's three-way ANOVA without replication for four species that were common in lampara net samples, September 1979-March 1981, inclusive. (* = $P \leq 0.05$; ** = $P \leq 0.001$.)

Factor	x^2	df	P
Peprilus simillimus			
Diel	17.30	1	<0.001**
Depth	1.15	2	0.563
Date	24.36	13	0.028*
Genyonemus lineatus			
Diel	4.76	1	0.029*
Depth	48.29	2	<0.001**
Date	8.00	13	0.844
Atherinid spp.			
Diel	0.05	1	0.827
Depth	27.86	2	<0.001*
Date	13.64	13	0.400
Scomber japonicus			
Diel	2.34	1	0.126
Depth	8.90	2	0.012*
Date	25.70	13	0.019*

(December-February) as would be expected in a temperate marine habitat. Sampling depths ranged from 5 to 25 m. Day collections were made between 0700 and 1300 h and night collections between 1900 and 0100 h.

Spearman rank correlations of 2 categories and 21 individual species (Table 4) with time of collection, depth of water column, and sea surface temperature yielded numerous significant relationships. Depth (20 significant values) and time of collection (14) were important factors for most categories or species. Temperature was significantly correlated with 10 categories or species. The total individuals category was significantly correlated with all three abiotic factors (negative with depth). Species counts correlated only with depth (negative) and time of collection. In general, both the numbers of individuals and numbers of species were greatest at

simillimus and atherinid spp. also formed a close association (~18% distance).

Sarda chiliensis was the most dissimilar member of Group II, and linked to *Scomber japonicus* and *T. symmetricus* at ~40% distance.

The four species in Group III formed a relatively tight group with a maximum dissimilarity of only 38% distance (yellowfin croaker, *Umbrina roncador*, to the other three species). *Sphyraena argentea* and *X. californiensis* were most closely associated (~20% distance), with deepbody anchovy, *Anchoa compressa*, occupying the intermediate position.

Group IV was composed of nine bottom-oriented species which were relatively rare in the samples.

Influences of Diel Period, Surface Water Temperature, and Depth

Sea surface temperature ranged from about 14.2° to 24.0°C during the study period. Highest water temperatures were encountered during the summer months (July-September) and lowest in winter

TABLE 4.—Summary of Spearman's rank correlation (r_s) values and significance levels for 2 categories and the 21 abundant species/taxon collected. Time = time of collection (military time); Depth = bottom depth (m); Temp = surface water temperature (°C). (df = 210; * = $P \leq 0.05$; ** = $P \leq 0.0001$.)

| Category or species/taxon	Time	Depth	Temp.	Species group
Total individuals	0.44**	−0.46**	0.22*	—
Species counts	0.43**	−0.62**	0.11	—
Engraulis mordax	0.48**	−0.33**	0.22*	I
Seriphus politus	0.46**	−0.56**	0.11	I
Genyonemus lineatus	0.31**	−0.71**	0.08	I
Peprilus simillimus	0.54**	−0.21*	0.04	I
Atherinid spp.	0.16*	−0.52**	−0.22*	I
Scomber japonicus	0.12	0.28**	0.40**	II
Trachurus symmetricus	0.15*	0.25**	0.08	II
Sarda chiliensis	−0.27**	0.05	0.27**	II
Anchoa compressa	−0.01	−0.52**	−0.14*	III
Sphyraena argentea	0.20*	−0.25**	−0.14*	III
Umbrina roncador	0.11	−0.32**	−0.14*	III
Xenistius californiensis	0.12	−0.14*	−0.06	III
Myliobatis californicus	0.04	−0.22**	0.26**	IV
Phanerodon furcatus	0.14*	−0.46**	−0.02	IV
Hyperprosopon argenteum	0.05	−0.54**	−0.01	IV
Menticirrhus undulatus	−0.09	−0.60**	0.06	IV
Amphistius argenteus	−0.17*	−0.45**	0.01	IV
Cymatogaster aggregata	0.14*	−0.35**	0.07	IV
Paralichthys californicus	0.07	−0.48**	0.01	IV
Paralabrax nebulifer	−0.03	0.01	0.22**	IV
Scorpaena guttata	0.27**	−0.11	0.02	IV
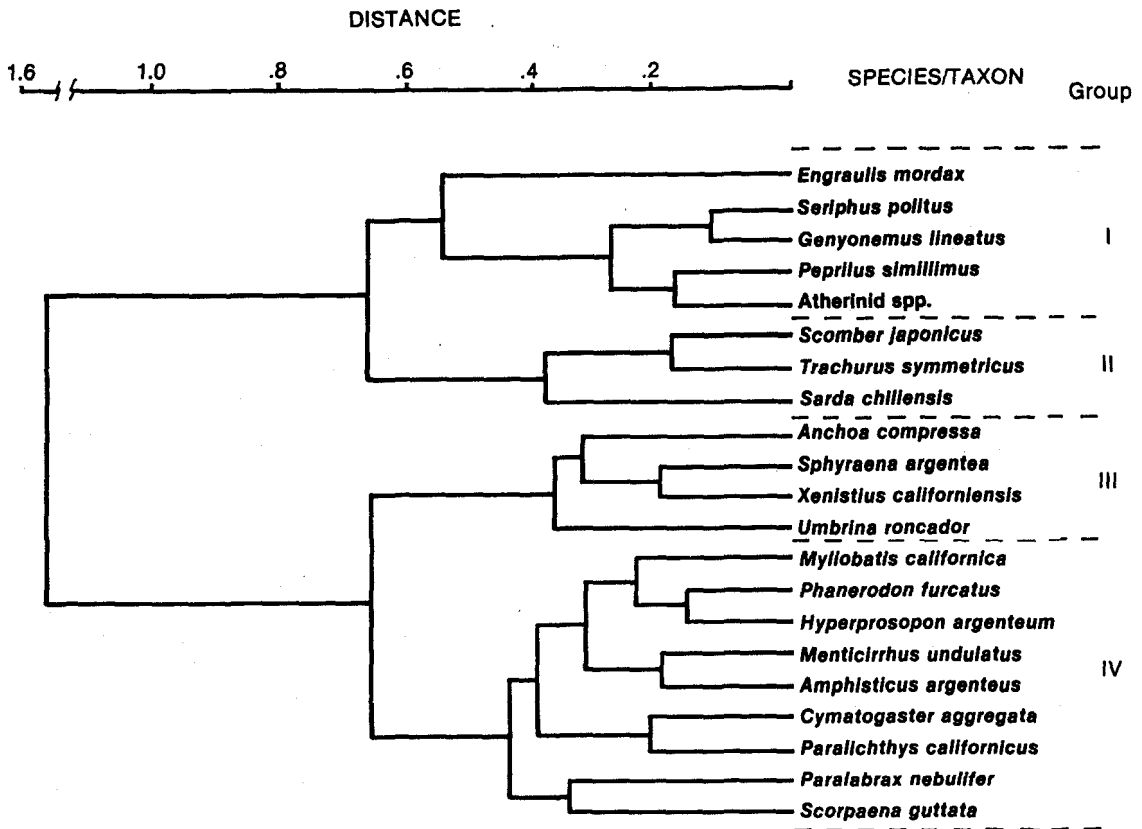
FIGURE 5.—Dendrogram depicting the clustering of 20 species and 1 taxon based on abundance within lampara samples. Four species groups (Roman numerals) are recognized according to the Bray-Curtis index of dissimilarity (ecological distance).

shallow depths during the night. More individuals were collected during the warmer months, although this relationship was highly dependent on the catches of *E. mordax*.

The catches of all the members of species Group I were correlated with time of collection and depth (negative) (Table 4). Only the abundances of *E. mordax* (positive) and atherinid spp. (negative) were correlated with temperature. *Scomber japonicus* and *T. symmetricus* of Group II were usually found farther offshore in the study area (positive with depth). The catches of *S. japonicus* and *Sarda chiliensis* were positively correlated with temperature. However, *T. symmetricus*, like many of the other species, was collected in greater numbers at night, while *S. chiliensis* was captured almost exclusively during the day. The catches of all members of species Group III were negatively correlated with depth and temperature, although the temperature correlation for *X. californiensis* was not significant. Six of the eight species in species Group IV were negatively correlated with

depth, although no other consistent pattern was apparent.

The occurrence and distribution of the 21 abundant species are displayed graphically in relation to diel period and depth in Figures 6 and 7. Species are presented in the species groups derived for the dendrogram of species associations (Fig. 5). Only species with >10% occurrence during the particular diel period are included in the illustrations.

During daylight periods, species Groups I, III, and IV were distributed close to shore, mostly within the 5-11 m depth block (Fig. 6). The high variance of catches during the day indicated that the species are highly clumped in distribution and are probably schooling at this time (especially members of Groups I and III). Species of Group II were primarily found offshore within the 12-16 m and 18-27 m depth blocks and occurred mainly during the warmer months. Group III on the other hand occurred during the colder months.
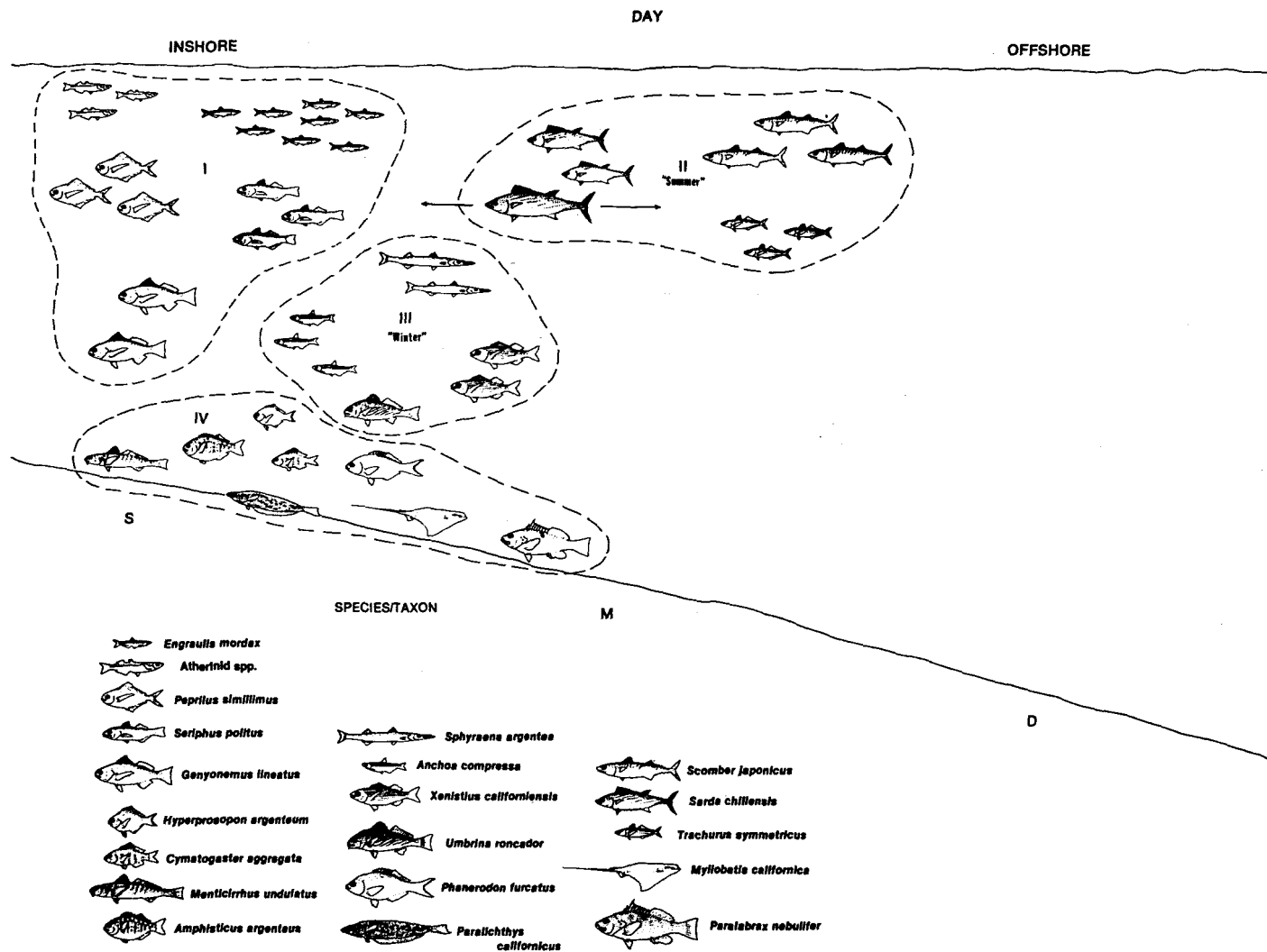
At night the distribution of species was quite dif-

DAY

INSHORE

OFFSHORE

I

II
"Summer"

III
"Winter"

IV

S

M

D

SPECIES/TAXON

Engraulis mordax

Atherinid spp.

Peprilus simillimus

Seriphus politus

Genyonemus lineatus

Hyperprosopon argenteum

Cymatogaster aggregata

Menticirrhus undulatus

Amphistichus argenteus

Sphyraena argentea

Anchoa compressa

Xenistius californiensis

Umbrina roncador

Phanerodon furcatus

Paralichthys
californicus

Scomber japonicus

Sarda chiliensis

Trachurus symmetricus

Myliobatis californica

Paralabrax nebulifer

FIGURE 6.—Generalized illustration of the principal fish species (and taxon) present in the nearshore waters off San Onofre-Oceanside, Calif., during daylight hours. Dashed lines enclose species groups derived from the Figure 5 dendrogram. Inclusion of species is limited to those that were caught on >20 cruises. Arrows indicate onshore-offshore movement. Fishes are not drawn strictly to scale. S, M, and D represent shallow, middepth, and deep blocks, respectively.
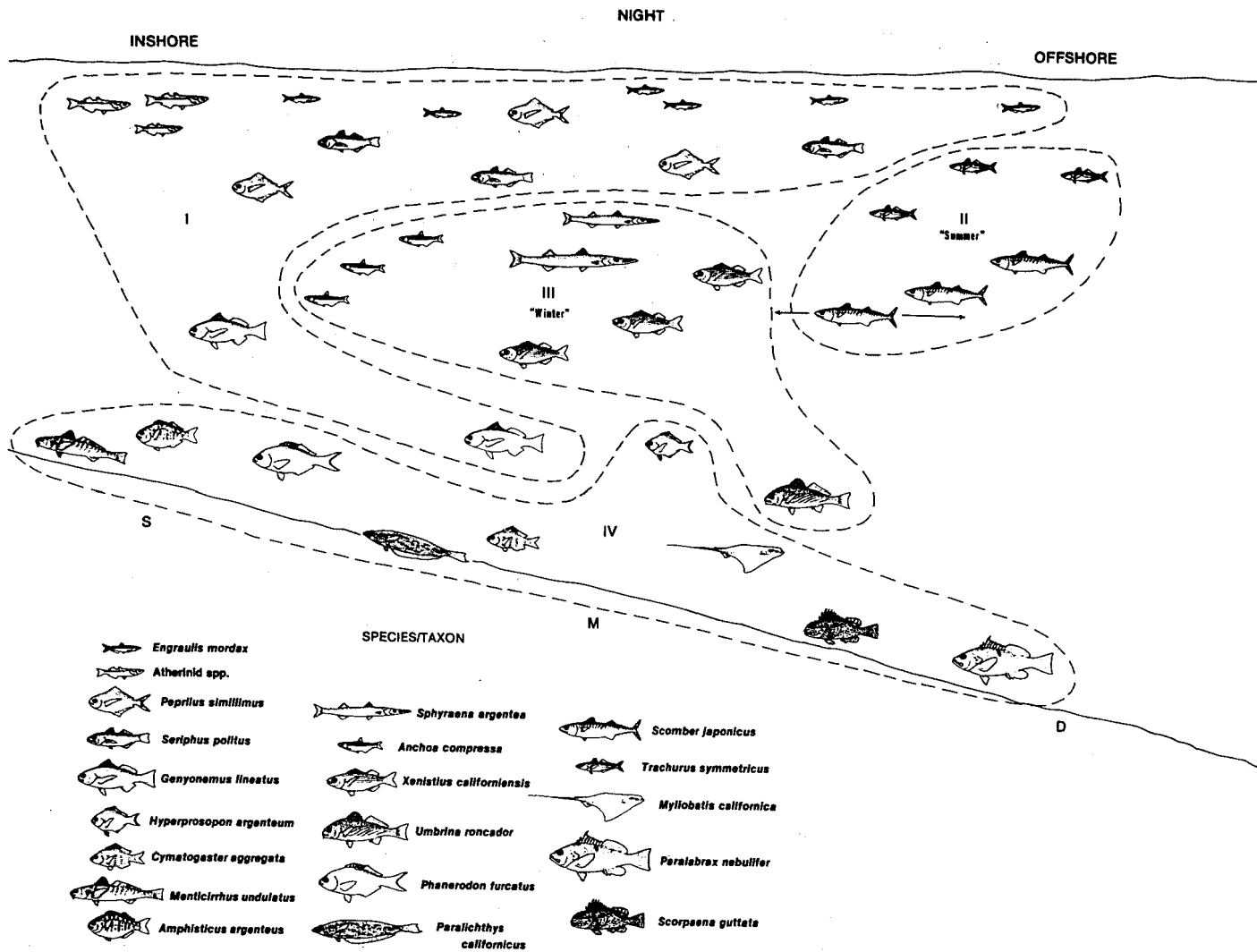
FIGURE 7.—Generalized illustration of the principal fish species (and taxon) present in the nearshore waters off San Onofre-Oceanside, Calif., at night. Other information as in Figure 6.

ferent (Fig. 7). Members of Group I (especially *E. mordax, Seriphus politus,* and *G. lineatus*) dispersed offshore, resulting in a much more even distribution of individuals among net-hauls. Certain species in Groups III and IV also moved offshore at night. Group II persisted over the deeper portions of the study area, with *Sarda chiliensis* absent at night.

Interrelations of Depth Block, Water Clarity, and CPUE

The relations between CPUE and water clarity were significantly negative for five of seven major taxa in one or more depth blocks during the day (Table 5). Water clarity differed significantly among depths (Shallow block: $\bar{x} = 4.4$ m; middepth block: 6.8 m; deep block: 9.6 m; Kruskall-Wallis $H = 33.8$, df $= 2$, $P < 0.001$). ANCOVA results, however, indicated that, although water clarity in addition to depth block were in general negatively related to daytime catches, there were no depth by water clarity interactions (all $P > 0.10$). On average, only an estimated 12-16% of the total variation in the CPUE of major taxa was attributable to variations in water clarity with any depth block (Table 5).

Diel Effects on Catch Efficiency

The percentage recapture of fin-clipped *Seriphus politus* on average was significantly ($P < 0.05$) greater ($\bar{x} \pm SE = 13 \pm 3\%, N = 40$ net-hauls) during the day versus night ($25 \pm 3\%$, $N = 24$ hauls). Parametric estimators for the percentage recapture versus water clarity relation were not possible for daytime tests due to the nonnormality of these data; however, about 30% of the variation in the ranks of daytime recapture data was attributable to water clarity ($r_s = -0.54$, $P < 0.001$). Queenfish recaptures at night were insignificantly (Pearson's $r = -0.31, P = 0.14$) related to water clarity.

Day-Night Feeding Comparison

No significant differences in stomach fullness (CI) were found between day- and night-caught specimens of *E. mordax, G. lineatus,* and *P. simillimus* (Table 6). Specimens of *Seriphus politus,* however, had significantly greater foregut fullness at night, while those of *Atherinopsis californiensis* had significantly greater fullness during the day (Table 6).

TABLE 5.—Summary of Spearman's rank correlation (r_s) values and significance levels for comparisons of CPUE and water clarity within depth blocks for two categories and four major species plus one taxon (* $= P < 0.05$; ** $= P < 0.001$). Dashes indicate insignificant ($P > 0.05$) results. Also indicated is the estimated percentage of total variation (R^2) of daytime CPUE explained by variation in water clarity in each depth block. R^2 approximations reflect results of parametric regressions performed in an ANCOVA with water clarity as covariate and depth block as treatment.

Category or species/taxon	Rank correlation (Spearman's r_s)			Estimated % variance ($= R^2$)		
	5-11 m	12-16 m	18-27 m	5-11 m	12-16 m	18-27 m
Total individuals	−0.36*	−0.61**	—	20	37	24
Total individuals minus *Engraulis mordax*	—	−0.58**	−0.60*	13	32	33
Engraulis mordax	—	−0.34*	—	15	11	8
Seriphus politus	−0.31*	−0.34*	—	18	9	9
Genyonemus lineatus	—	—	—	8	2	—
Peprilus simillimus	—	—	—	6	7	6
Atherinid spp.	—	−0.45*	—`	3	17	12

TABLE 6.—Summary of results of day versus night comparisons of the contents index (CI) of foregut samples of the five most abundant fishes present in lampara collections (* denotes statistical significance).

TEST—Wilcoxon signed-rank test of median CI for paired day-night samples

Species	N (day-night)	Paired N	Ts	P	
Engraulis mordax	40/36	8	14	0.29	NS
Seriphus politus	49/49	9	4	0.02	(night>day)*
Genyonemus lineatus	42/44	9	18	0.30	NS

TEST—Wilcoxon two-sample test

Species	N (day-night)	Z	P	
Peprilus simillimus	26/16	0.13	0.90	NS
Atherinopsis californiensis	29/33	5.42	<0.001	(day>night)*

DISCUSSION

The nearshore pelagic ichthyofauna between San Onofre and Oceanside, Calif., was dominated by silvery-sided, schooling fishes. *Engraulis mordax*, the dominant pelagic species offshore (Mais 1974), was also the most abundant species nearshore. *Seriphus politus* and *G. lineatus*, the two abundant sciaenids in this assemblage, are best characterized as bottom associated fishes which rise into the water column. Both of these species are well represented in bottom-trawls in the area.[5] *Genyonemus lineatus* is generally more abundant in trawls, indicating that it is more closely associated with the bottom than *S. politus*. The three species above, together with *P. simillimus* and atherinid spp., constituted species Group I. Members of this group were abundant and ubiquitous within the area and accounted for >98% of the total individuals collected. Species Groups II and III represented periodic components (Tyler 1971) within the assemblage. Group II comprised three species of higher carnivores that generally occurred in the offshore portion of the study area during the warmer months (spring-summer). Group III, on the other hand, contained four species that were more abundant at shallow depths during the colder water months (fall-winter). Two of these species, *Anchoa compressa* and the sciaenid *Umbrina roncador*, are known to occur in bay-estuarine habitats such as Newport Bay during the summer months (Horn and Allen 1981). Both *A. compressa* and *U. roncador* belong to primarily tropical families. The presence of these two species in the study area during fall-winter suggests that they may seasonally migrate out of embayments and into shallow coastal waters in response to cool-water temperatures. The bottom-associated species of Group IV were relatively rare in catches with the exception of the bat ray, *Myliobatis californica* (California bat ray). *Myliobatis californica* occurred in about one-third of all net-hauls and ranked sixth in number of total occurrences. Its relatively large size ($\bar{x} \simeq 2$ kg) and high frequency of occurrence make *M. californica* a more important component of this nearshore assemblage than numerical abundance alone would indicate.

Upcoast and downcoast locations were generally similar in terms of total individuals, species counts, and in the abundances of most common species. The few exceptions (atherinids, *Sphyraena argentea*,

Trachurus symmetricus, *Xenistius californiensis*) that were more abundant at the upcoast location probably reflect the proximity of the San Onofre kelp bed. All of these species are known to associate with kelp beds or rocky reefs at some time during the year (Feder et al. 1974; Hobson and Chess 1976; Mais 1974).

Significant date effects found by Wilson's ANOVA's reflected a certain amount of temporal variation within this assemblage of fishes. Some of these date effects can be attributed to spatial patchiness and sampling error; other date effects undoubtedly reflect short-term, temporal changes in the environment. Upwelling is probably a major factor contributing to short-term variation in the abundance and distribution of these fishes. The waters within the Southern California Bight can be subjected to bouts of upwelling anytime during the year, although upwelling is most likely to occur during March-July (Parrish et al. 1981). Both short-term temperature variations due to upwelling and long-term seasonal warming and cooling of coastal waters probably influenced the 10 observed correlations between sea surface temperature and the abundance of individual taxa. The abundances of only two of the top five taxa however were significantly correlated to sea temperature (*Engraulis mordax*, positive; atherinids, negative). *Peprilus simillimus*, the fourth most abundant species, varied significantly between dates (ANOVA results), but showed no significant relationship to temperature. Extremely patchy distributions and high vagility might account for the observed short-term variations in the abundance of *P. simillimus*. Neither *Seriphus politus* nor *Genyonemus lineatus* varied greatly in seasonal abundance although *S. politus* did show a significant date effect (ANOVA) that was apparently unrelated to temperature. These two sciaenids were largely responsible for the uniformity of catch seen when *Engraulis mordax* was excluded from the catch totals. The only major change in catches of *S. politus* and *G. lineatus* occurred during the October-December periods of 1979 and 1980 when CPUE was depressed. During this time of year the adults of both species presumably migrated out of our sampling area into deeper water.

Temporal distributions differed for *Scomber japonicus*, *Sarda chiliensis*, and *Sphyraena argentea*, the major higher carnivores of the assemblage. The observed temporal differences probably reflect differences in general longshore migratory patterns and residence of juveniles within the study area (e.g., presence of juvenile *S. argentea* near San Onofre kelp bed during fall-winter, authors' pers. obs.). A pos-

sible explanation for the virtual absence of *Sarda chiliensis* from night collections is that they may migrate offshore of 30 m depth before or at dusk on a daily basis. Net avoidance can be effectively discounted, since this fast swimming scombrid can presumably see the net better during the day than at night.

Although location differences and temporal changes were evident for some species within this assemblage, the dominant pattern shown by the most abundant species was one of a general dispersal offshore at night from nearshore diurnal schools. Diel interactions with depth were found for total individuals, total individuals minus *Engraulis mordax*, species counts, numbers of *E. mordax*, and numbers of *Seriphus politus*. Various diel and/or depth effects were also found for other taxa, including *Peprilus simillimus*, *Genyonemus lineatus*, atherinid spp., and *Scomber japonicus*. These results plus the significant correlations between species abundances and time of collection and depth underscore the general importance of diel and depth factors to the abundance and distributions of fishes in this assemblage.

Greater net avoidance under conditions of increasing water clarities, such as occur at greater distances offshore, potentially confounds our evaluation of depth (onshore/offshore) patterns. Correlations between the CPUE of major taxa and water clarity indicate persistent, negative relationships (Table 5). Variations in water clarity, however, were never observed to explain >16% of the variance in catch; and among the major taxa analyzed in detail for CPUE-water clarity relations, mean CPUE differed by more than a factor of 10 to over four orders of magnitude between the 5-11 m and 18-27 m depth blocks during the day. For this reason, we strongly feel that the potentially greater net avoidance in clearer waters farther offshore is insufficient to explain the observed daytime onshore/offshore stratification of these fishes.

Net avoidance also is a possible complicating factor to our interpretation of day-night differences in catch (i.e., higher night catches). Our test results in fact indicate an approximately twofold greater average catch efficiency for *Seriphus politus* at night versus during the day. However, CPUE of *S. politus* differed by a factor of four and by over three orders of magnitude between diel periods at the 12-16 m and 18-27 m depths, respectively. As above for the potential confounding of daytime depth patterns, we feel that diel differences in catch efficiencies alone cannot explain the marked diel patterns that we have observed.

Dispersal of schooling (especially pelagic) fishes under low light conditions has been noted repeatedly in the literature (Shaw 1961; Loukashkin and Grant 1965; Woodhead 1966; Hobson 1968). Four possible hypotheses (or a combination thereof) can be proposed to explain the phenomenon of nocturnal dispersal.

1. Schools disperse because light levels are insufficient for fish to maintain visual contact. Vision is an important factor in the maintenance of a polarized state and parallel swimming in schooling fishes (Shaw 1978). Some fishes can maintain polarized schools in light intensities as low as 0.5-0.01 footcandle (Shaw 1961), but disperse in total darkness (Shaw 1961; Loukashkin and Grant 1959, 1965). Some species have the ability to form polarized schools by the light of the full moon alone (Shaw 1961, 1978). The acousticolateralis system may also play an important role in polarization and spacing within schools (Shaw 1978) and is not dependent on light levels. Highly sensitive visual and acoustic systems may allow nearshore pelagic fishes to school even under minimal light intensities. If the visual and acoustic systems of these fishes prove to be sufficiently sensitive, an explanation for the observed nocturnal dispersal probably lies elsewhere.

2. Schools disperse because predation pressure is less intense at night. Hobson (1978) has argued that the threat from predators is a major force behind aggregating (i.e., schooling) behavior in fishes. At low light intensities pressure from visual predators such as those found in this nearshore habitat should be less. However, for this hypothesis to be valid there must be some disadvantage to schooling at night. Theoretically (Eggers 1976) and empirically (Koslow 1981), schooling occurs at the expense of prey consumption. With the threat from predators diminished at night, dispersal of fishes within a school may allow greater food consumption by lessening visual-field overlap (Eggers 1976). Dispersal under these conditions, however, would only be advantageous if the species feeds at night (see hypothesis 4 below).

3. Schools disperse offshore at night to facilitate reproduction among members. DeMartini and Fountain (1981) presented evidence for dusk spawning in *Seriphus politus* during March-August along the same stretch of southern California coastline. Crepuscular spawning probably helps conceal adults and planktonic eggs from visual predators. Unbalanced, day-night sex ratios at shallow depths[6] and egg

hydration rates (DeMartini and Fountain 1981) indicate that most male *S. politus* migrate offshore to spawn each night while individual females on average move offshore only once every week.

Engraulis mordax spawns exclusively at night (Hunter and Macewicz 1980) during its peak (January-April) spawning period. Spawning activity may be partially responsible for nocturnal dispersal in this species during this period of year. However, since most *E. mordax* in our catches were juveniles, its offshore dispersal at night is probably unrelated to spawning.

We believe that at least part of the general nocturnal dispersal pattern may be explained by the reproductive behavior of *Seriphus politus*. However, not enough is known about the reproductive habits of the other abundant fishes of this assemblage to assess the overall importance of spawning behavior to nocturnal dispersal.

4. Schools disperse at night for individuals to feed on nocturnally active prey. Hobson (1968) stated that some authors have greatly underestimated the extent to which vision can be used at night by predatory fishes. Many species of California nearshore fishes possess scotopic visual pigments which have spectral sensitivities best suited for twilight and night vision (Hobson et al. 1981). Five species that were important in our study (*Hyperprosopon argenteum*; spotted scorpionfish, *Scorpaena guttata*; *Seriphus politus*; *Xenistius californiensis*; and *Umbrina roncador*) were included in Hobson et al.'s (1981) list of fishes that forage at night. Hobson and his colleagues were able to characterize the feeding behavior of these nocturnal species through extensive field observations. Midwater planktivores oriented in a tail-down attitude in the water column at night. This presumably allowed them to feed on organisms overhead which were silhouetted against back-lighted surface waters.

Our comparison of day versus night gut fullness has assumed that most planktonic prey are evacuated from foreguts in <12 h at 14°-24°C and that any remaining contents would be in a highly digested state and, therefore, weigh less during nonfeeding periods. These assumptions seem reasonable in light of a recent determination of gastric evacuation rates in *Engraulis mordax*. At 15°C, foregut excavation rates were <30 min for small *E. mordax* larvae and about 2 h for the egg yolks and embryos of *E. mordax*

(Hunter and Kimbrell 1980). Our interpretations of day-night CI's are based on the further reasonable assumption that gut evacuation rates are not seriously confounded by different digestabilities of planktonic prey eaten during the day versus at night.

Engraulis mordax has been described as a diurnal planktivore by Loukashkin (1970). However, a great deal of indirect evidence including 1) the predicted inadequacy of diurnal ration (Leong and O'Connell 1969); 2) eye and retinal morphology (O'Connell 1972); 3) size selective biting and filtering behavior (Leong and O'Connell 1969; Koslow 1981); and 4) the ability to capture and consume large copepods and euphausids (Loukashkin 1970, cited in O'Connell 1972) suggest that *E. mordax* feeds at night as well as during the day. The results of our gut fullness analysis lend support to the hypothesis of nocturnal feeding in *E. mordax*. Day-collected fishes did not contain greater amounts of food in the foregut than night specimens, which would be expected if *E. mordax* was strictly a diurnal feeder. Thus, the observed nocturnal dispersal of this species is likely due in large part to feeding behavior. It is also possible that predation pressure interacts with feeding to influence the diel behavior of *E. mordax*.

Hobson and Chess (1976) determined that *Seriphus politus* was primarily a nocturnal feeder. Schools of *S. politus* migrated offshore at night from shallow water where they had formed resting schools during the day; and specimens collected at night in open water contained large, nocturnally active zooplankters (Hobson and Chess 1976). Our analysis of gut fullness corroborates these findings. Night-captured specimens of *S. politus* contained a greater amount of (primarily mysid) prey than those of day-captured specimens. Hence we conclude that dispersal at night facilitates feeding in *S. politus*. Differential offshore dispersal of juvenile, female, and male *Seriphus politus* at night is undoubtedly related to the aforementioned breeding as well as feeding behavior.

Genyonemus lineatus probably feeds day and night as evidenced by gut fullness during both diel periods. A trend toward more food in the foregut was evident in night-collected specimens, but the difference was not statistically significant. Gut contents of *G. lineatus* collected at dawn and dusk from Long Beach Harbor have also suggested a greater amount of food in dawn-captured specimens, but, as with our study, the difference was not statistically significant at the 0.05 level (Richard N. Bray[7]). *Genyonemus lineatus*

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depth distributions of immature versus adult queenfish (*Seriphus politus*). Manuscr. in prep. Marine Science Institute, University of California, Santa Barbara, CA 93106.

[7]Richard N. Bray, California State University, Long Beach, CA 90840, pers. commun. April 1982.

can be characterized as an opportunistic feeder that forages both day and night (M. J. Allen[8]). Nighttime dispersal in this species as in *Seriphus politus* could be related to feeding activity.

Results of day-night comparisons of foregut fullness in *Peprilus simillimus* were inconclusive due to the limited time period over which samples were available (June and July 1980 only). Our data nonetheless indicate that, at least during this time period, *P. simillimus* fed both day and night.

Atherinopsis californiensis appears to be strictly diurnal in its feeding activities. The observed dispersal within the inshore section of the study area probably has some other cause(s) than feeding behavior.

In summary, feeding behavior is probably an important factor related to nocturnal dispersal in *Seriphus politus*, *Engraulis mordax*, and *Genyonemus lineatus* but not in *Atherinopsis californiensis*. Crepuscular spawning may also be important in determining diel movements in *S. politus* during March through August. The cause of school dispersal in atherinids (represented by *A. californiensis*) is unknown, but deprivation of visual schooling cues and relaxed predation pressures remain as two possibilities.

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