DIEL AND SEASONAL VARIATION IN ABUNDANCE AND DIVERSITY OF SHALLOW-WATER FISH POPULATIONS IN MORRO BAY, CALIFORNIA

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ABSTRACT

More than 11,000 fishes weighing over 197 kg and representing 21 species were caught in bag seine hauls taken at quarterly periods (November 1974, May and August 1975, February 1976) in the southeastern section of Morro Bay. During each sampling period, nine seine hauls were completed, one at each 3-hour interval over a 24-hour cycle. *Atherinops affinis*, *Cymatogaster aggregata*, and *Leptocottus armatus* accounted for 82% of the individuals collected, and *A. affinis*, *C. aggregata*, and *Mustelus californicus* constituted 84% of the biomass obtained. Larger numbers of individuals and greater biomass were collected in night hauls, but nearly equal numbers of species were captured during the day and night. The largest number of species and individuals and greatest biomass were obtained in May, a period of high reproductive activity, whereas the smallest values of these three parameters were recorded in August. Diversity (H') for numbers peaked in May (1.56) but reached a maximum for biomass in November (1.91). Lowest diversity for both numbers (0.86) and biomass (0.79) was recorded in February. Total diversity was 1.63 for numbers and 1.59 for biomass. Wide ranging similarity values (PS) between consecutive sampling periods for numbers (24-64%) and biomass (21-76%) demonstrated the marked seasonality of the shallow-water fish populations of the bay and primarily reflected the fluctuations in numbers or biomass of the four most abundant species (above).

The pattern of total diversity and seasonal similarity for Morro Bay fishes was consistent with a recent model that utilizes diversity and similarity indices together as measures of environmental quality. Analysis of data from three other localities indicated that the model has the potential for application in a variety of temperate bay-estuarine habitats.

Morro Bay (Figure 1), an estuary located on the central California coast (lat. 35°20′ N), is one of the largest and least altered coastal wetlands in California and a critically important aquatic habitat. It supports abundant invertebrate populations and is an integral part of the Pacific flyway for migratory, water-associated birds (Gerdes et al. 1974). The bay is the site of rookeries for two species of herons, and the two endangered bird species, California least tern and peregrine falcon, utilize the resources of the bay. Steelhead occur in the tributary streams and a sizeable sport fishery exists in the bay. Although more than 60 species of fishes are known to occur in Morro Bay (Fierstine et al. 1973), little is known of the dynamics and organization of the fish communities. This lack of information provided the impetus for the present study.

The main purpose of the study was to assess in terms of abundance, diversity, and species composition, the diel (24 h) and seasonal variation of the fish community occurring in the shallow waters of the bay. In addition, the investigation was designed to provide a preliminary test in Morro Bay of the relationship proposed by Haedrich (1975) that indices of diversity (measuring species richness and equitability) and similarity (measuring seasonal composition and succession) as community parameters can be used together as indicators of environmental quality of temperate bays and estuaries. Based on trawl collections of fishes in nine Massachusetts estuaries and embayments, Haedrich (1975) showed that in habitats of low annual (or total) diversity little seasonal change is reflected in high similarity from season to season whereas in locations of high annual diversity lower similarity indicates a greater degree of seasonal change. Low diversities characterized areas of high pollution and higher diversities those of lesser pollution. Because of the reportedly low levels of environmental stress (including human-induced pollution) in Morro Bay (Gerdes et al. 1974), the expected outcome of the present study was that total diversity would be relatively high and similarity between seasons relatively low or show a wide range of values. Comparisons of total diversity and seasonal similarity were made between Morro Bay samples and bag seine collec-

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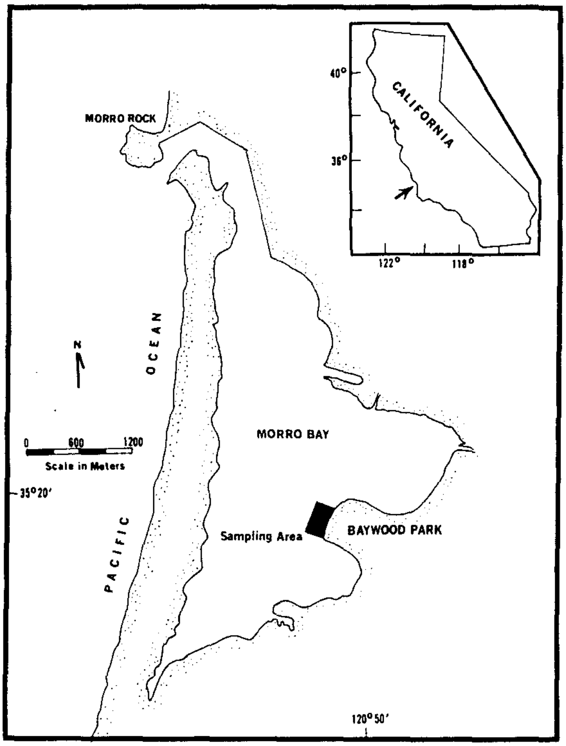

FIGURE 1.—Morro Bay, Calif. Shaded rectangle is the sampling area.

tions taken in three other California bay-estuarine habitats with similar ichthyofaunas.

THE STUDY AREA

Morro Bay is characterized by expansive tidal flats, central channels, and extensive eelgrass beds. During spring low tides, the bay is essentially reduced to a series of channels. Although two creeks empty into the bay, salinities are relatively uniform and approach those of the sea, making the bay more of a marine lagoon than a true estuary.

The study was conducted during quarterly periods (November 1974, May and August 1975, February 1976) in the shallow mudflat and channel area of the southeastern section of Morro Bay adjacent to Baywood Park (Figure 1). The substrate of the area was characterized by a relatively uniform mud-sand material, a large percentage of which was covered mainly by eelgrass, *Zostera marina*, and also a red alga, *Gracilaria* sp., and a green alga, *Ulva* sp. Water depth over the study area was as great as 2 m during high tide periods. Water temperature and salinity were recorded at 30 cm depth at the time each fish sample was taken. Temperatures ($\bar{x} \pm 1$ SD, $n = 9$) were 13.7°±1.4° C in February, 17.9°±0.5° C in May, 19.6°±2.9° C in August, and 11.8°±1.9° C in November. Salinity values were 30.9±0.7‰ in February, 30.0±0.8‰ in May, 31.1±1.0‰ in August, and 31.8±1.7‰ in November. Tidal ranges during the 24-h sampling periods varied from 1.0 m (3.3 ft) in May 1975 to 2.2 m (7.3 ft) in February 1976.

METHODS

Fish sampling was performed with the use of a seine 3 m deep by 29.2 m long with a 2.2 × 2.2 × 2.2 m bag of 6 mm mesh size. The seine was set parallel to the beach from a 3 m skiff and hauled to shore with polypropylene lines. The distance the seine was set from the water's edge was 60 m except at extreme low tides when there was water only in the channels. At these times (the tows at 1500 h and 1800 h in February), successive hauls covering small areas were made until the total area sampled was approximately equal to that of single hauls at higher tide periods. Samples were taken at randomly selected intervals along a 400 m stretch of shore. The total sampling area was approximately 2.4 ha (0.4-0.5% of the total area of the bay) and each seine haul covered about 0.18 ha. Based on visual surveys, this stretch of inshore habitat was typical (in terms of substrate, depth, and position relative to the mouth and main channel) of the rather uniform shallow-water conditions in the bay.

During each of the four sampling periods, seine hauls were made at 3-h intervals over a 24-h cycle for a total of nine samples per visit. For day-night comparisons, the second of the two 0900-h samples was not included each period so that equal numbers of day and night samples (four) were compared. All fishes captured, or aliquots of the largest catches of abundant species, were identified and sorted, and their standard lengths (SL) and weights recorded.

The Shannon-Wiener information function H' was calculated as a measure of diversity in which

$$H' = -\sum_{i=1}^{s} P_i \log P_i$$

where P_i is the proportion of individuals (or biomass) in the ith species. Calculations were based on the use of natural logs ($\log_e$).

The degree of specific change between samples from one period to the next was calculated using the percentage similarity index (PS) developed by Whittaker and Fairbanks (1958). Percentage similarity ranges from 0, when two samples contain no species in common, to 100, when the two samples are identical in both species composition and relative abundance. The index is calculated as

$$PS = 100\,(1.0 - 0.5 \sum \left| P_{ia} - P_{ib} \right|)$$

where P_{ia} is the proportion of individuals (biomass) in the ith species of sample a and P_{ib} the same for sample b. The basic data are the same as are required for the calculation of H', i.e., the number or biomass of individuals in each species of the sample.

RESULTS

A total of 11,627 fishes weighing 197,747 g were captured in 36 seine hauls taken during the four sampling periods (Table 1). Of the 21 species collected, three species, *Atherinops affinis*, *Cymatogaster aggregata*, and *Leptocottus armatus*, composed almost 82% of the total individuals. A fourth species, *Engraulis mordax*, contributed 11.2% of the total. *Mustelus californicus*, *A. affinis*, and *C. aggregata*, accounted for nearly 84% of the biomass collected. *Leptocottus armatus* contributed an additional 7% to the total biomass.

For the four sampling periods taken together,

TABLE 1.—Number of individuals and biomass of fish species collected by beach seine in Morro Bay during four 24-h periods from November 1974 to February 1976. The proportion that each species contributed to total numbers and biomass of each sampling period is expressed as a percentage (%). (Species ranked according to total numbers for the four periods.)

	February 1976				May 1975				August 1975				November 1974				Totals			
	Individuals		Biomass		Individuals		Biomass		Individuals		Biomass		Individuals		Biomass		Individuals		Biomass	
Species	No.	%	g	%	No.	%	g	%	No.	%	g	%	No.	%	g	%	No.	%	g	%
Atherinops affinis	351	16.0	3,996	8.0	998	23.4	40,940	41.2	309	14.2	9,099	41.1	1,960	65.5	7,856	29.7	3,618	31.1	61,891	31.3
Cymatogaster aggregata	—	—	—	—	1,498	35.1	41,049	41.3	1,530	70.4	6,793	30.6	67	2.2	575	2.2	3,095	26.6	48,417	24.5
Leptocottus armatus	1,668	76.2	2,063	4.1	644	15.1	3,649	3.7	272	12.5	3,725	16.8	196	6.5	4,444	16.8	2,780	23.9	13,881	7.0
Engraulis mordax	—	—	—	—	909	21.3	1,532	1.5	2	0.09	3	—	397	13.3	280	1.1	1,308	11.2	1,815	0.9
Fundulus parvipinnis	25	1.1	50	0.1	1	—	10	—	—	—	—	—	229	7.6	728	2.7	255	2.2	788	0.4
Syngnathus leptorhynchus	18	0.8	24	0.05	35	0.8	200	0.2	18	0.8	111	0.5	94	3.1	850	3.2	165	1.4	1,185	0.6
Quietula y-cauda	26	1.2	49	0.1	64	1.5	158	0.2	27	1.2	94	0.4	2	0.1	2	—	119	1.0	303	0.2
Micrometrus minimus	7	0.3	152	0.3	77	1.8	152	0.2	—	—	—	—	6	0.2	149	0.6	90	0.8	453	0.2
Lepidogobius lepidus	43	2.0	6	0.01	—	—	—	—	—	—	—	—	1	—	4	—	44	0.4	10	—
Embiotoca jacksoni	—	—	—	—	11	0.3	171	0.2	9	0.4	340	1.5	17	0.6	1,238	4.7	37	0.3	1,749	0.9
Atherinopsis californiensis	25	1.1	3,659	7.3	1	—	280	0.3	1	0.05	230	1.0	5	0.2	1,296	4.9	32	0.3	5,465	2.8
Mustelus californicus	19	0.9	39,463	79.3	7	0.2	8,322	8.4	—	—	—	—	3	0.1	7,296	27.5	29	0.3	55,081	27.9
Damalichthys vacca	1	0.05	240	0.5	19	0.4	2,390	2.4	—	—	—	—	2	0.1	450	1.7	22	0.2	3,080	1.6
Clupea harengus	1	0.05	88	0.2	—	—	—	—	—	—	—	—	13	0.4	1,276	4.8	14	0.1	1,364	0.7
Clevelandia ios	2	0.1	2	—	2	—	—	—	1	0.05	2	—	1	—	—	—	6	0.1	4	—
Hyperprosopon argenteum	—	—	—	—	3	0.1	121	—	—	—	—	—	1	—	50	0.2	4	—	171	0.1
Myliobatis californica	—	—	—	—	—	—	—	—	3	0.1	1,760	7.9	—	—	—	—	3	—	1,760	0.9
Citharichthys stigmaeus	3	0.1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	1	—
Hypsopsetta guttulata	—	—	—	—	1	—	320	0.3	—	—	—	—	—	—	—	—	1	—	320	0.2
Platichthys stellatus	—	—	—	—	—	—	—	—	1	0.05	8	—	—	—	—	—	1	—	8	—
Sebastes sp.	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	1	—	1	—
Totals	2,189		49,793		4,271		99,295		2,173		22,165		2,994		26,494		11,627		197,747	
Total species	13				16				11				16				21			

nearly equal numbers of species were collected during the day (14) and night (15) (Table 2); however, significantly greater numbers of individuals and biomass were obtained during the night (Table 3). The *PS* value between day and night samples was higher for numbers (68.5%) than for biomass (43.3%). In February, nearly equal numbers of species were collected during the day (9) and night (10). Greater numbers of individuals were collected at night but the difference was not significant. Even though the total biomass obtained during the day in February was greater than that at night, the night samples were more frequently and significantly larger based on paired day-night abundances of each species using the Wilcoxon signed-ranks test (Table 3). The discrepancy was due to the exceptionally large daytime contribution (34,246 g) of *M. californicus* compared with its much smaller contribution (3,402 g) to the night samples. The *PS* value between day and night samples was much higher for numbers (83.3%) than for biomass (40.5%). In May, more species were collected at night (14) than during the day (8). Greater numbers of individuals and biomass were obtained at night but the difference was significant only for numbers. The *PS* value between day and night samples was higher for numbers (60.3%) than for biomass (42.0%). In August, nearly equal numbers of species were collected during the day (eight) and night (seven).

TABLE 2.—Relative numbers and biomass (expressed as percentage) of fish species collected in four daytime (0900-1800 h) and four nighttime (2100-0600 h) seine hauls for each sampling period and the total collection in Morro Bay. (Species ranking as in Table 1.)

	February 1976				May 1975				August 1975			
	No. individuals		Biomass		No. individuals		Biomass		No. individuals		Biomass	
Species	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
Atherinops affinis	19.8	7.6	1.1	31.8	33.1	15.9	78.5	26.2	33.0	19.7	26.6	53.3
Cymatogaster aggregata	—	—	—	—	14.1	49.5	11.2	56.6	50.5	61.2	9.3	28.1
Leptocottus armatus	66.8	88.3	0.7	16.8	14.7	14.5	4.6	3.4	8.0	16.7	7.0	17.9
Engraulis mordax	—	—	—	—	34.7	13.4	3.8	0.8	1.0	—	0.1	—
Fundulus parvipinnis	0.5	0.8	—	0.4	—	—	—	—	—	—	—	—
Syngnathus leptorhynchus	0.8	0.1	—	0.2	1.0	0.8	0.5	0.1	5.0	0.3	2.0	0.1
Quietula y-cauda	1.0	1.4	—	0.4	2.0	1.3	0.3	0.1	1.0	1.9	0.1	0.6
Micrometrus minimus	1.5	0.1	0.4	0.1	0.3	2.8	0.1	0.2	—	—	—	—
Lepidogobius lepidus	—	—	—	—	—	—	—	—	—	—	—	—
Embiotoca jacksoni	—	—	—	—	—	0.5	—	0.3	—	—	—	—
Atherinopsis californiensis	4.5	0.4	5.5	14.0	0.1	—	1.0	—	1.0	—	6.4	—
Mustelus californicus	4.0	0.1	92.3	33.1	—	0.2	—	7.8	—	—	—	—
Damalichthys vacca	—	0.1	—	2.3	—	0.7	—	3.8	—	—	—	—
Clupea harengus	—	0.1	—	0.9	—	—	—	—	—	—	—	—
Clevelandia ios	—	—	—	—	—	0.1	—	—	—	0.1	—	—
Hyperprosopon argenteum	—	—	—	—	—	0.1	—	0.2	—	—	—	—
Myliobatis californica	—	—	—	—	—	—	—	—	2.0	—	48.6	—
Citharichthys stigmaeus	0.8	—	—	—	—	—	—	—	—	—	—	—
Hypsopsetta guttulata	—	—	—	—	—	0.1	—	0.5	—	—	—	—
Platichthys stellatus	—	—	—	—	—	—	—	—	—	0.1	—	0.1
Sebastes sp.	—	—	—	—	—	0.1	—	—	—	—	—	—
Totals	398	1,540	37,120	10,272	1,751	2,209	27,435	62,706	200	1,149	3,622	14,111
Total species	9	10			8	14			8	7		

TABLE 2.—*Continued.*

	November 1974				Totals			
	No. Individuals		Biomass		No. individuals		Biomass	
Species	Day	Night	Day	Night	Day	Night	Day	Night
Atherinops affinis	65.0	66.4	34.4	28.2	44.3	25.3	33.8	30.9
Cymatogaster aggregata	1.0	3.9	1.3	3.8	9.3	29.7	4.4	40.7
Leptocottus armatus	4.2	6.7	14.3	15.2	15.6	31.5	4.5	8.2
Engraulis mordax	25.7	0.2	2.0	0.1	25.8	4.8	1.6	0.5
Fundulus parvipinnis	1.6	14.8	0.6	5.6	0.7	3.4	0.1	0.7
Syngnathus leptorhynchus	1.3	5.6	1.1	6.5	1.3	1.8	0.4	0.8
Quietula y-cauda	—	0.2	—	—	1.0	1.2	0.1	0.2
Micrometrus minimus	0.3	0.1	1.1	—	0.4	1.0	0.4	0.1
Lepidogobius lepidus	—	0.1	—	—	—	—	—	—
Embiotoca jacksoni	0.7	0.5	5.0	5.4	0.3	0.3	0.8	0.8
Atherinopsis californiensis	0.1	0.2	3.3	8.0	0.6	0.1	3.7	2.4
Mustelus californicus	0.1	0.1	35.0	12.7	0.4	0.1	47.8	9.9
Damalichthys vacca	0.1	0.1	1.8	2.0	—	0.3	0.3	2.9
Clupea harengus	—	1.0	—	11.8	—	0.2	—	1.4
Clevelandia ios	0.1	—	—	—	0.1	0.1	—	—
Hyperprosopon argenteum	—	0.1	—	0.5	—	0.1	—	0.2
Myliobatis californica	—	—	—	—	0.1	—	2.2	—
Citharichthys stigmaeus	—	—	—	—	0.1	—	—	—
Hypsopsetta guttulata	—	—	—	—	—	—	—	0.3
Platichthys stellatus	—	—	—	—	—	—	—	—
Sebastes sp.	—	—	—	—	—	—	—	—
Totals	1,535	1,320	13,038	10,791	3,884	6,218	81,215	97,880
Total species	12	15			14	15		

TABLE 3.—Day and night fish samples in terms of numbers of individuals and biomass for each sampling period and the total collection in Morro Bay. Percentage similarity (*PS*) is explained in the text. "Difference" column indicates whether day samples were significantly (S) or not significantly (NS) different from night samples based on paired percentage values for each species (Table 2) (Wilcoxon signed-ranks test for paired values, $P \leq 0.05$, two-tailed).

	No. of individuals				Biomass			
Sampling period	Day	Night	Percentage similarity	Difference	Day	Night	Percentage similarity	Difference
February 1976	398	1,540	83.3	NS	37,120	10,272	40.5	S (night>day)
May 1975	1,751	2,209	60.3	S (night>day)	27,435	62,706	42.0	NS
August 1975	200	1,149	78.8	NS	3,622	14,111	43.0	NS
November 1974	1,535	1,320	74.1	S (night>day)	13,038	10,791	68.5	S (night>day)
Totals	3,884	6,218	68.5	S (night>day)	81,215	97,880	54.3	S (night>day)

Greater numbers and biomass were obtained at night but the difference was not significant in either case. The *PS* value between day and night samples was much higher for numbers (78.8%) than for biomass (43.0%). In November, more species were collected at night (15) than during the day (12). Even though the total number of individuals and total biomass obtained during the day were greater than the totals at night, the night samples in both cases were more frequently and significantly larger based on paired day-night abundances of each species using the Wilcoxon signed-ranks test (Table 3). The discrepancy for individuals was primarily due to a relatively large daytime contribution (394 individuals) of *E. mordax* compared with its much smaller number (3 individuals) in the night samples. The inconsistency for biomass was mainly due to the large daytime contribution (4,560 g) of *M. californicus* compared with its smaller contribution (1,368 g) to the night totals.

Seven species, *A. affinis, C. aggregata, L. armatus, E. mordax, Fundulus parvipinnis, Syngnathus leptorhynchus*, and *Quietula y-cauda*, were captured at least once in each of the 3-h sampling intervals of the four periods. No common species was collected either only during the day or only at night. Among the uncommon species, *Myliobatis californica* and *Citharichthys stigmaeus* were captured only during the day whereas *Clupea harengus, Hyperprosopon argenteum, Hypsopsetta guttulata, Platichthys stellatus*, and *Sebastes* sp. were obtained only at night (Table 2).

Marked changes in numbers, biomass, and diversity occurred between sampling periods although only four species, *A. affinis, Cymatogaster aggregata, L. armatus*, and *Mustelus californicus*, were, in different combinations, the most abundant (numbers or biomass) fishes in the samples (Table 1; Figure 2). Numbers of individuals and biomass both reached highest levels in May and lowest levels in August. Diversity H' on numbers

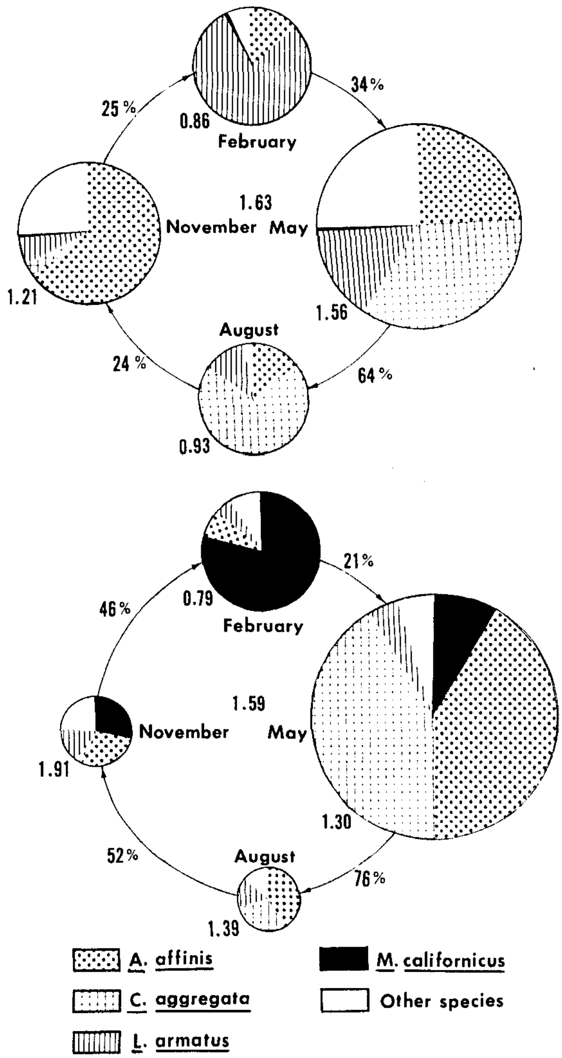

FIGURE 2.—Quarterly data on fish numbers (upper) and biomass (lower) in the Baywood Park section of Morro Bay. Total diversity is given by H' in the center of each cycle. The area of each circle is proportional to the sample size, the number to the lower left of each circle is the quarterly diversity H', and the number on the connecting arrow is the percentage similarity between months. Sampling dates are February 1976, May and August 1975, and November 1974.

was highest in May and lowest in February, whereas H' on biomass was greatest in November but also lowest in February. The *PS* levels for both numbers and biomass were highest between May and August. Lowest *PS* values were obtained for numbers between August and November and for biomass between February and May. Total diversity H' on numbers was similar to that for biomass.

Of the four common species in the samples, *A. affinis* was the most abundant species, composing 31% of both total individuals and biomass (Table 1). For the total collection, significantly more individuals and biomass of *A. affinis* were captured at night than during the day; however, for quarterly periods, a significant day-night difference was recorded only for numbers (night>day) in August (Table 4). Although somewhat larger individuals were commonly obtained in night compared with day samples, the differences were not significant for any collecting period (Table 4). In February, *A. affinis* were bimodal in length frequency (Figure 3), intermediate in mean size (Figure 4), and obtained in small numbers and the smallest biomass. The contribution of *A. affinis* to the total February catch was relatively minor for both numbers (16% of total) and biomass (8%). In May, the largest fish of the four periods were captured and in relatively high numbers. The biomass obtained was the greatest of the study for the species composing >41% of the total May sample. In August, the fish were strongly bimodal in length frequency and smaller in mean size. Numbers reached their lowest level and biomass declined but nevertheless made up >41% of the total August sample. In November, the smallest fish of the study were captured, but they occurred in the greatest numbers and composed >65% of the total November sample. The biomass value, because of the smaller fish, was lower than that for August.

Cymatogaster aggregata, even though absent from February samples, was the second most abundant species composing >26% of total numbers and >24% of total biomass (Table 1). In all sampling periods that *C. aggregata* was captured, larger numbers and greater biomass of the species were collected at night than during the day; however, the differences were significant only in May (Table 4). Although somewhat larger individuals were, in most cases, captured in night compared with day samples, the difference was significant only during May (Table 4). In May, the largest fish of the study were collected (Figure 4) but a wide size range was also represented (Figure 3). Numbers were relatively high and the biomass obtained was the greatest of the study for the species composing >41% of the total May sample. In August, the smallest fish of the study were collected. Biomass declined but numbers increased relative to the previous period and made up >70% of the total August sample. Slightly larger fish were collected in November but numbers and biomass reached low levels, each composing only about 2% of the totals.

Leptocottus armatus was the third most abundant species, composing almost 24% of total numbers but only 7% of total biomass (Table 1). In all sampling periods, larger numbers and greater

TABLE 4.—Number of individuals, biomass, and mean weight of the three most abundant fish species for each sampling period and the total collection in Morro Bay. "Difference" line indicates whether day (D) samples were significantly (S) or not significantly (NS) different from night (N) samples based on four ranked samples from each day and each night period for each species (Mann-Whitney U-test, $P \leq 0.05$, two-tailed).

Item	*Atherinops affinis* Individuals (no.)	*Atherinops affinis* Biomass (g)	*Atherinops affinis* Mean weight (g)	*Cymatogaster aggregata* Individuals (no.)	*Cymatogaster aggregata* Biomass (g)	*Cymatogaster aggregata* Mean weight (g)	*Leptocottus armatus* Individuals (no.)	*Leptocottus armatus* Biomass (g)	*Leptocottus armatus* Mean weight (g)
February 1976:									
Day	79	412	5.2	—	—	—	266	265	1.0
Night	118	3,264	27.7	—	—	—	1,360	1,728	1.3
Difference	NS	NS	NS				S (N>D)	S (N>D)	NS
May 1975:									
Day	580	21,548	37.2	247	3,069	12.4	258	1,259	4.9
Night	351	16,441	46.8	1,094	35,480	32.4	321	2,155	6.7
Difference	NS	NS	NS	S (N>D)	S (N>D)	S (N>D)	NS	NS	NS
August 1975:									
Day	66	964	14.6	101	337	3.3	16	255	15.9
Night	226	7,520	33.3	703	3,959	5.6	192	2,520	13.1
Difference	S (N>D)	NS	NS	NS	NS	NS	NS	NS	NS
November 1974:									
Day	997	4,489	4.5	15	163	10.9	65	1,869	28.8
Night	877	3,045	3.5	52	412	7.9	88	1,645	18.7
Difference	NS	NS	NS	NS	NS	NS	NS	NS	NS
Totals:									
Day	1,722	27,413	15.9	363	3,569	9.8	605	3,648	6.0
Night	1,572	30,270	19.3	1,849	39,851	21.6	1,961	8,048	4.1
Difference	S (N>D)	S (N>D)	NS	NS	NS	NS	S (N>D)	S (N>D)	NS

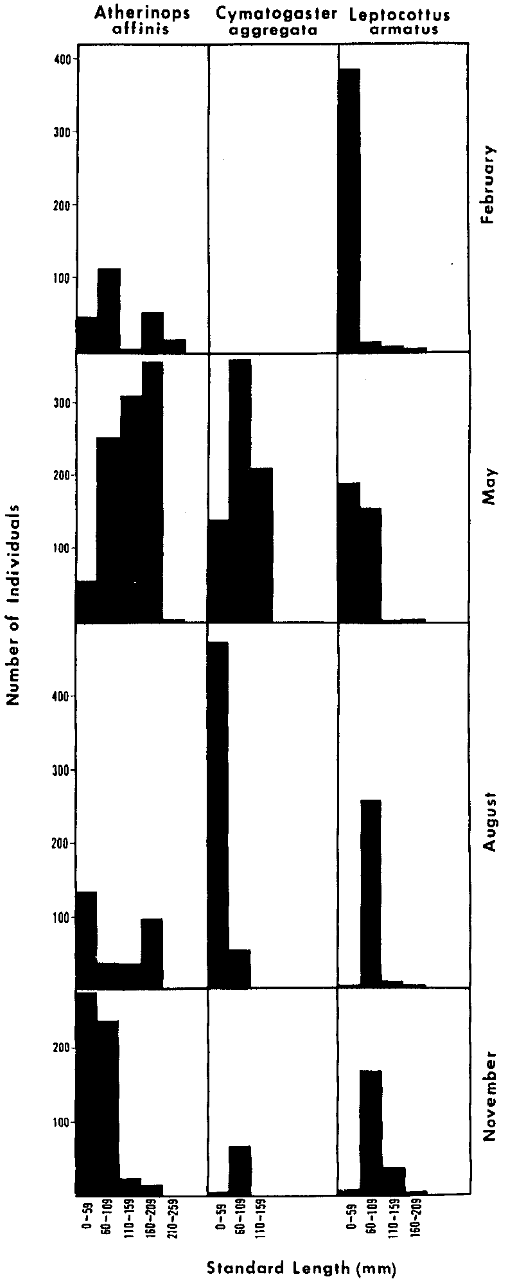

FIGURE 3.—Length frequencies of the three most abundant fish species for the quarters sampled in Morro Bay. Sampling dates are February 1976, May and August 1975, and November 1974.

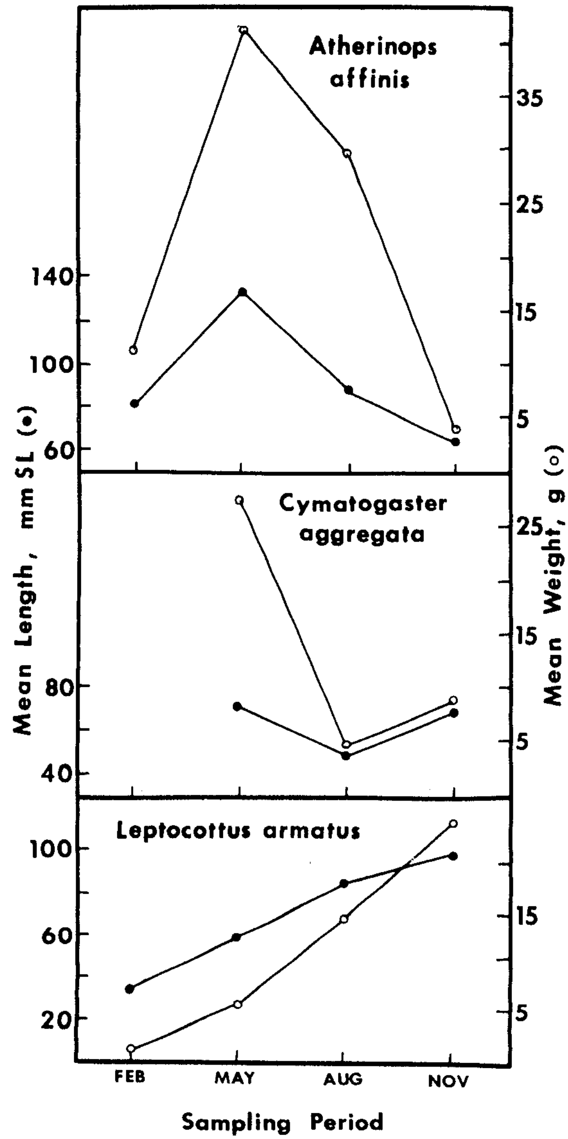

FIGURE 4.—Mean lengths (dots) and weights (circles) of the three most abundant fish species for the quarterly sampling periods in Morro Bay. Sampling dates are February 1976, May and August 1975, and November 1974.

biomass of *L. armatus* were collected at night than during the day; the differences were significant for the February sample and the total collection (Table 4). No significant differences in mean size were found between day and night samples; slightly larger individuals were captured at night in February and May whereas somewhat larger fish were collected during the day in August and November (Table 4). In February, the smallest fish of the study (Figures 3, 4) were collected in large numbers. The number of individuals composed >76% of the total sample; however, biomass contributed only about 4% of the total. In May, fish size and biomass increased whereas numbers decreased. This pattern continued through the August and November sampling periods and was in sharp contrast to that recorded for either *A. affinis* or *C. aggregata*. In August, a small number of relatively large *L. armatus* were collected. The corresponding biomass accounted for more than 16% of the total sample. In November, a small number of larger individuals were captured. The corresponding biomass made up >16% of the total sample.

Although only 29 individuals of a fourth species, *M. californicus*, were captured during the study, the fish ranked second in biomass and accounted for almost 28% of the weight of the total collection (Table 1). The largest number of *M. californicus* were caught in February when they were concentrated in the channels as a result of the spring low tide. The corresponding biomass accounted for >79% of the total February sample (Figure 2). Mean size was 834 mm total length and mean weight was 2,077 g. Too few specimens were collected to compare the abundance and mean size of individuals in day and night samples.

DISCUSSION

The results of this study indicate that the shallow-water fish populations of Morro Bay undergo both diel and seasonal variations in abundance (numbers and biomass), diversity, and species composition. A relatively small number of species (three) accounted for a large proportion (82%) of the total number of individuals collected. These findings are consistent with the results of several other studies of temperate bay-estuarine fish populations that have been reviewed by Allen and Horn (1975). A pattern that emerged from these studies was that at least 75% of the sampled fishes belonged to five or fewer species even though many more species were collected.

In terms of overall diel variation, more individuals and greater biomass were obtained in night samples but nearly equal numbers of species were collected during the day and night. Very few species, usually the rarer forms, were captured either only during the day or only at night.

Although surprisingly little is known concerning day-night differences in utilization of various habitats by fishes (McCleave and Fried 1975), most of the information that is available on trawl or seine samples in inshore waters indicate that greater catches, either of species, individuals, or biomass, are obtained at night (e.g., Hoese et al. 1968; Allen 1976; Livingston 1976). McCleave and Fried (1975) collected fewer total individuals at night and equal numbers of species day and night with a beach seine in a Maine tidal cove; however, they found that four numerically important species were either present only at night or more abundant at night.

Diurnal-nocturnal activity patterns and daytime gear avoidance, particularly by larger fish, are two factors among a complexity of circumstances that produce day-night differences in abundance and composition of net-caught fishes. Little is known about the first factor for bay-estuarine fishes although McCleave and Fried (1975) reviewed the diel patterns of a few inshore species. They and Hoese et al. (1968) both considered the second factor to be of importance in their respective studies. In my study, gear avoidance probably was one of the factors causing the generally smaller (numerically) daytime catches. However, size differences of day vs. night captured individuals of the three most abundant species were insignificant in almost all cases thus casting doubt on the assumption that the larger fish avoid the seine in the daytime. This reasoning is perhaps most relevant for *L. armatus*, the only nonschooling member of the three-species group.

Quarterly fluctuations in biomass (totals, diversity H', and *PS* values) were of greater magnitude than those for numbers, but both parameters expressed the seasonal dynamics of fish populations in the shallow waters of the bay. In February low numbers and biomass diversity but relatively high total biomass represented an early influx of prereproductive adults. The peak numbers and biomass reached in May corresponded to an abundance of *A. affinis* and *C. aggregata* of mature size (see species accounts below) as well as the presence of several other species in wide size ranges. Reduced numbers and biomass in August but high *PS* values for both numbers and biomass between May and August indicated that young-of-the-year fishes remained in the shallow waters while larger individuals migrated out of the sampling area. The large number of individuals and high biomass diversity recorded for November was the result of a relatively even distribution of biomass among juvenile fishes which continued to utilize the inshore areas late in the year.

Seasonal abundance and diversity were only partly attributable to variations in physical factors. Salinity was not an important factor because values were relatively high and varied little in the sampling area, an indication of the marine character of the bay. Tidal ranges were smallest in May, the period of highest fish abundance, and largest in February, the month of lowest diversity. Temperature, the environmental factor most frequently recognized as having a major influence on temperate, shallow-water fish populations (e.g., Allen and Horn 1975; Subrahmanyam and Drake 1975; Wallace 1975; Hoff and Ibara 1977), did not consistently correspond to changes in abundance and diversity of Morro Bay fish populations: The largest increase in mean temperature (4° C) occurred between February and May, the transition period marked by the greatest increase in abundance and diversity. In contrast, the greatest decline in temperature between sampling periods (8° C from August to November) was accompanied by a substantial increase in abundance and diversity.

The life history patterns of the three most abundant species, *A. affinis, C. aggregata*, and *L. armatus*, serve not only to help clarify the seemingly conflicting responses to temperature of the fish populations but to illustrate the strategies of utilization of a bay-estuarine environment by inshore fishes. These patterns, recognized in previous studies, are discussed in turn below for each of the three species and related to the data I recorded in Morro Bay.

In his study of *A. affinis* in Newport Bay in southern California, Fronk (1969) recognized 3 age classes based on length frequencies (80-90 mm fork length in the first year; 120-130 mm by the second year; 150 mm after the third year) and found that spawning occurred from February to August (peak in May) when the fish were in their second and third years of life. These findings correspond to the seasonal length frequencies and abundance I recorded for *A. affinis* in Morrow Bay. In February, the bimodal size distribution included small numbers of both immature and larger individuals, some of which had mature gonads. May was marked by a high abundance of large fish, many of which released eggs and milt upon capture. The substrate of the sampling area apparently is an optimal spawning site since it is known (Frey 1971) that *A. affinis* attaches its eggs to eelgrass and low-growing algae such as *Gracilaria* sp. The egg masses were frequently found on the vegetation that was obtained in the seine hauls. By August, the number of small juveniles had increased but adult numbers had decreased. The overwhelming domination of the November catch by first (mainly) and second year fish is consistent with the apparent movement of postreproductive adults out of the shallow spawning areas that become nursery grounds for the juvenile fish.

In his study of *C. aggregata* in Anaheim Bay in southern California, Odenweller (1975) identified three age classes based on otolith rings and length frequencies. Fish in their first year ranged between 31 and 87 mm SL ($\bar{x}$ 57 mm), in their second year between 68 and 115 mm ($\bar{x}$ 88 mm) and in their third year between 81 and 117 mm ($\bar{x}$ 101 mm). *Cymatogaster aggregata* gives birth in the spring, primarily in May, according to Bane and Robinson (1970) and Odenweller (1975). Both Bane and Robinson (1970) and Allen (1976) found that in Newport Bay (southern California) the majority of adults migrate out of the bay after breeding in the spring leaving juveniles to utilize the area as a nursery ground. These adults apparently return to the bay to bear young the following spring. The seasonal abundance and size frequencies of *C. aggregata* in Morro Bay are in accord with the patterns found in the southern California bays and estuaries. The absence of the fish in February, its abundance in a wide size range in May and the presence of almost only small juveniles in August are indicative of the existence of the migratory breeding pattern in Morro Bay. The November catch, consisting of a small number of juveniles slightly larger than the August individuals, is further support for the existence of the pattern. Most of the young-of-the-year, which mature at or soon after birth (Bane and Robinson 1970), apparently moved out of the shallows after mating in the late summer or early fall.

According to studies carried out by Jones (1962) in Tomales Bay (near San Francisco) and San Francisco Bay and Tasto (1975) in Anaheim Bay (near Los Angeles), *L. armatus* is a winter spawner with the peak in January and February. Sexual maturity is reached near the end of the first year of life at approximately 120-150 mm SL for females and 110-120 mm SL for males. Tasto (1975) found that the Anaheim Bay population consisted almost entirely of juvenile fish and that postspawning mortality was apparently high, based on the absence of the older fish in the population, a sharp reduction in the catch per unit effort of adults during the breeding season and the capture of only two spent females. The data I obtained on *L. armatus* in Morro Bay are generally consistent with those of the two studies cited. Following the February sample, which was composed almost entirely of small juveniles, the frequency of larger fish progressively increased through the successive quarterly periods so that in November the catch was made up of primarily large juveniles and secondarily of fish in the reported mature size range. Winter spawning was evident even though few adults were collected. The rarity of adults could have been due to at least four factors: 1) net avoidance by adults, 2) postspawning mortality by adults, 3) migration of adults out of the area after spawning, or 4) migration of young individuals into the area after spawning occurred elsewhere. Although the third factor has been discounted by Tasto (1975), all four possible causes deserve further investigation.

In terms of Haedrich's (1975) model for assessing the environmental quality of estuaries and embayments, Morro Bay can be classified as a relatively unspoiled habitat in that relatively high total diversity and a wide range of seasonal similarity values were recorded. It is instructive, however, to compare the Morro Bay data with those available for three southern California bay-estuarine habitats with similar ichthyofaunas: 1) Mugu Lagoon (lat. 34.1° N), 2) Colorado Lagoon (lat. 33.8° N), and 3) upper Newport Bay (lat. 33.6° N). Mugu Lagoon is a relatively unaltered habitat with diversity and similarity values comparable to those for Morro Bay whereas Colorado Lagoon and upper Newport Bay, two more highly perturbated sites, have lower diversity values yet wider ranging season-to-season similarity indices than Morro Bay or Mugu Lagoon (Table 5).

All four habitats are largely marine in character with salinities usually approaching those of the ocean. Upper Newport Bay is the most frequent exception in that during occasional years of heavy winter rainfall salinities are greatly reduced in the extreme upper portions of the habitat. Although generally considered to be a relatively unaltered estuary in southern California (Frey et al. 1970), upper Newport Bay, unlike Morro Bay, is subject to pollutant inflow from both urban and agricultural runoff and a high rate of sedimentation (with accompanying increased turbidity) during years of increased rainfall (e.g., Horn and Allen in press). Colorado Lagoon, the partially isolated upper arm of Alamitos Bay, receives pollutants and nutrients from street runoff and heavy recreational use especially during the summer months when eutrophic conditions usually develop (Allen and Horn 1975). The lower reaches of both Newport Bay and Alamitos Bay have been altered by extensive marina development and by modification of their openings to the sea. Mugu Lagoon is in a relatively undisturbed condition primarily because it has been for more than 30 yr under ownership of the U.S. Navy which restricts access to the area (MacDonald 1976). The fish faunas of these three environments are basically similar to that of Morro Bay with three of the five most abundant species in upper Newport Bay and Mugu Lagoon and four of the five most abundant species in Colorado Lagoon also in the top five in Morro Bay.

The sampling procedure (bag seine deployed from shore) and substrate conditions (varying mud to sand) were similar for the four habitats. Collections were made monthly in the locations other than Morro Bay; quarterly data were extracted for comparison with the Morro Bay values. The main difference in the collection of data among the four locations was the type of beach seine used. In Colorado Lagoon, as in Morro Bay, a 29.2 m seine with 6 mm mesh in the bag was used, whereas in Mugu Lagoon and upper Newport Bay a 15.2 m seine with 3 mm mesh in the bag was employed. The difference in effectiveness of the two types of seines is incompletely known but considered to be slight (M. H. Horn and L. G. Allen unpubl. data); moreover, the discrepancy is judged to be of minor importance since it does not parallel the diversity-similarity differences among the four ichthyofaunas (Table 5).

Quarterly data (February-November 1977) from bag seine samples of 29 species in Mugu Lagoon (Quammen[2]) yielded a total H' value of 1.52 and PS values ranging from 30 to 62% (Table 5). Thus,

TABLE 5.—Number of species (S), Shannon-Weiner diversity (H'), and season-to-season percentage similarity values (PS) based on quarterly bag seine collections of fishes in four bay-estuarine habitats in California. Environmental status is a qualitative assessment (see discussion section).

Bay-estuary	Location (latitude)	S	H'	PS	Environmental status	Data source
Morro Bay	Central California (35.3° N)	21	1.63	24-64	Relatively unaltered	This study
Mugu Lagoon	Southern California (34.1° N)	29	1.52	30-62	Relatively unaltered	M. L. Quammen (unpubl. data)
Colorado Lagoon	Southern California (33.8° N)	16	0.75	2-57	Highly altered	Allen and Horn (1975)
Upper Newport Bay	Southern California (33.6° N)	23	0.66	13-96	Moderately altered	Horn and Allen (in press)

the diversity and similarity pattern for Mugu Lagoon is close to that for Morro Bay as would be expected for an unspoiled habitat. Data obtained during quarterly periods (February-November 1978) from bag seine collections of 23 species in upper Newport Bay (Horn and Allen in press) resulted in a total H' value of 0.66 and *PS* indices ranging from 13 to 96% (Table 5). Quarterly bag seine data (February-November 1973) for 16 species in Colorado Lagoon (Allen and Horn 1975) produced a total H' value of 0.75 and *PS* measures ranging from 2 to 57% (Table 5). According to the Haedrich (1975) model, the relatively low diversity values for upper Newport Bay and Colorado Lagoon should be accompanied by high similarity values and dominance of the community by one or a few species. However, a combination not explicitly recognized by Haedrich, that of low diversity and wide ranging seasonal similarity, is evident in these two habitats. Low H' values combined with variable *PS* values indicate a high seasonal abundance of one or a few species. This condition is realized in that in each case there was an extreme summer abundance of only one species—*A. affinis* in upper Newport Bay and *E. mordax* in Colorado Lagoon. In the most highly stressed habitat, low diversity, and a high relative abundance of a single species over the entire year (i.e., high seasonal similarity) would be predicted by the model. Thus, upper Newport Bay and Colorado Lagoon would be rated as intermediate in environmental quality. In general, Colorado Lagoon could be considered as the more highly perturbated of the two habitats (Table 5). The heavy rainfall of 1978, the year in which the upper Newport Bay data were collected, probably was a primary factor in producing the low diversity and divergent similarity values (Horn and Allen in press).

The use of the two indices in combination appears to have greater resolution and predictive strength than the use of only species diversity as an indicator of pollution, as has been proposed by Bechtel and Copeland (1970). Diversity H' provides information on species richness and equitability but not on species composition. The absolute replacement of one species by another, possibly a result of environmental alteration, would not be detected by a diversity measure nor would the seasonal succession of individual species. An index of similarity provides an indication of the magnitude and direction of seasonal dynamics.

The diversity-similarity approach holds promise as one of the procedures for distinguishing the relative quality of bay-estuarine habitats and deserves to be tested in additional localities. The results for Morro Bay also underscore the need for a more thorough knowledge of its fish communities since it is a relatively pristine habitat that may be subject to a number of alterations in the future (Gerdes et al. 1974).

[2]Millicent L. Quammen, graduate student, Department of Biological Science, University of California, Santa Barbara, CA 93106, pers. commun. August 1979.

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