SEASONAL ABUNDANCE, COMPOSITION, AND PRODUCTIVITY OF THE LITTORAL FISH ASSEMBLAGE IN UPPER NEWPORT BAY, CALIFORNIA

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ABSTRACT

This study was designed to characterize the littoral fish populations by 1) composition and principal species, 2) diversity and seasonal dynamics, 3) productivity, and 4) important environmental factors.

Monthly samples (January 1978 to January 1979) obtained with four quantitative sampling methods at three stations in upper Newport Bay yielded 55,561 fishes from 32 species which weighed 103.5 kg. The top five species made up over 98% of the total number of individuals. One species, *Atherinops affinis*, predominated in numbers (76.7% of all fishes) and biomass (79.8%). This dominance was reflected in the low overall H' diversity values for numbers ($H'_N = 0.89$) and biomass ($H'_B = 0.84$). Number of species, number of individuals, and biomass were greatest during the spring and summer.

Quantitative clustering of species based on individual samples revealed five species groups which reflected both microhabitat and seasonal differences in the littoral ichthyofauna. Species Group I was made up of five resident species—*A. affinis*, *Fundulus parvipinnis*, *Clevelandia ios*, *Gillichthys mirabilis*, and *Gambusia affinis*. Species Groups II-VI were composed of summer and winter periodics and rare species.

The mean annual production (9.35 g dry weight/m^2 determined by the Ricker production model) of the littoral zone fishes was among the highest of reported values for comparable studies. This high annual production was mainly the result of the rapid growth of large numbers of juveniles that utilized the littoral zone as a nursery ground. Young-of-the-year *Atherinops affinis* contributed 85% of this total production.

Canonical correlation analysis indicated that temperature and salinity together may influence littoral fish abundance. These two abiotic factors accounted for 83% of the variation in the abundances of individual species. Emigration from the littoral zone, therefore, seems to be cued by seasonal fluctuations in temperature and salinity. I propose that this offshore movement forms an important energy link between the highly productive littoral zone and local, nearshore marine environment.

Semienclosed bays and estuaries are among the most productive areas on Earth, ranking with oceanic regions of upwelling, African savannas, coral reefs, and kelp beds (Haedrich and Hall 1976) in terms of animal tissue produced per year. Bays and estuaries harbor large stocks of nearshore fishes and are important feeding and nursery grounds for many species of fish, including commercially important ones. However, the high productivity of fishes is accompanied by low diversity (Allen and Horn 1975) which probably reflects the stressful ecological conditions in bays and estuaries and the high physiological cost of adaptation to them (Haedrich and Hall 1976). The few studies that have dealt with productivity in estuarine fishes were summarized by Wiley et al. (1972) and Adams (1976b).

Utilization of temperate embayments by juvenile and adult fishes is markedly seasonal with high abundances corresponding to the warmer, highly productive months of spring through autumn. Seasonal species typically spend one spring-autumn period in the shallows of a bay growing at an accelerated rate in the warm, highly productive waters (Cronin and Mansueti 1971).

Most studies to date dealing with composition and temporal changes of bay-estuarine fish populations have been conducted on the Gulf of Mexico and Atlantic coasts of the United States where estuaries are larger and more numerous than those on the Pacific coast (e.g., Bechtel and Copeland 1970; Dahlberg and Odum 1970; Derickson and Price 1973; McErlean et al. 1973; Oviatt and Nixon 1973; Recksiek and McCleave

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1973; Haedrich and Haedrich 1974; Targett and McCleave 1974; Livingston 1976; Moore 1978; Shenker and Dean 1979; Orth and Heck 1980). Although quantitative in nature, many of these investigations suffer from the inefficient (Kjelson and Johnson 1978) trawl sampling gear used and the high mobility of most fishes. Adams (1976a, b) used dropnet samples to accurately assess the density and productivity of the fishes of two North Carolina eelgrass beds. Weinstein et al. (1980) used a combination of block nets, seines, and rotenone collections to derive accurate quantitative estimates of fishes in shallow marsh habitats in the Cape Fear River Estuary, N.C.

Previous investigations of fishes in Newport Bay have included a species list (Frey et al. 1970), a general species account (Bane 1968), two individual species accounts (Fronk 1969; Bane and Robinson 1970), and two studies on the population ecology of the fauna based on juveniles and adults (Posejpal 1969; Allen 1976). An assessment of the ichthyoplankton and demersal fish populations during 1974-75 (Allen and White in press) is the most comprehensive work to date.

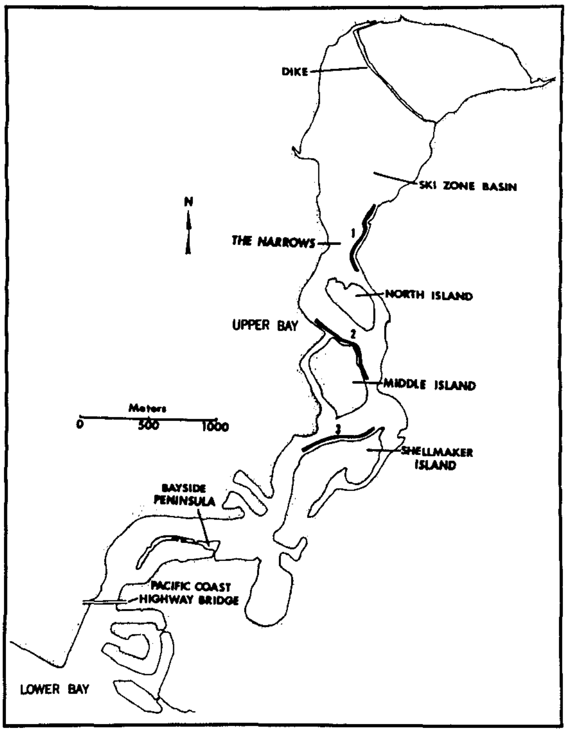

FIGURE 1.—Map of upper Newport Bay, Orange County, Calif., with the locations of the three sampling stations.

Despite these studies, a substantial component of the ichthyofauna, the littoral fishes of the upper bay (0-2 m depth from mean higher high water), had not been adequately sampled. In a study of the demersal ichthyofauna of Newport Bay during 1974-75 (Allen 1976), I found that three—*Atherinops affinis*, *Fundulus parvipinnis*, and *Cymatogaster aggregata*—of the five most numerous species were the ones that occurred in the shallow water over the mudflats which cover about 60-70% of the surface area of the upper bay reserve. Despite their high numerical ranking, the relative abundances of these littoral species were underestimated because sampling was carried out almost exclusively by otter trawls in the deeper channels of the upper bay. The recognition of this gap in our knowledge served as the impetus for the present study.

The main purposes of this study were to characterize the littoral ichthyofauna of upper Newport Bay quantitatively by 1) composition and principal species, 2) diversity and seasonal dynamics, 3) productivity, and 4) key environmental factors that are influencing this fish assemblage.

METHODS AND MATERIALS

Study Area

Newport Bay (lat. 33°37′30″N, long. 117° 54′ 20″W) is located in Orange County, Calif., 56 km southeast of Los Angeles and 140 km north of the Mexican border (Fig. 1). The upper portion is the only large, relatively unaltered bay-estuarine habitat in California south of Morro Bay (lat. 34.5°N). The low to moderately polluted lower portion, commonly called Newport Harbor, has been severely altered by dredging activities, landfills, and bulkheads to accommodate more than 9,000 boats. The study area, the upper two-thirds of the upper bay, is bordered almost completely by marsh vegetation and mudflats. The California Department of Fish and Game purchased and set aside this area as an ecological reserve in 1975.

Three stations, about 0.5 km in length, were spaced evenly along the shore of the upper Newport Bay (Fig. 1). Sampling was stratified based on prior information on the uniqueness of the fish fauna of the three areas (Allen 1976). This design also allowed thorough coverage of the study area. Each station was situated on a littoral (intertidal) mudflat area adjacent to marsh vegetation and was divided into 10 numbered sections of equal size. Selection of the section sampled each month was random in order to satisfy statistical assumptions and minimize the impact of sampling on any particular section from month to month. Each station included a tidal creek or pool (panne) which was sampled on the marsh islands.

Sampling Procedures

Monthly samples were taken at the three stations during the 13-mo period from January 1978 to January 1979 for a total of 39 station samples. Sampling was carried out within ±3 h of daytime neap high tide to minimize tidal level effects. Two days were usually required to sample three stations, stations 1 and 2 the first day and station 3 the second.

Four types of sampling gear were employed at each station as follows:

1) A 15.2 m × 1.8 m bag seine (BS) with 6.4 mm mesh in the wings and 3.2 mm mesh in the 1.8 × 1.8 × 1.8 m bag was used twice at each station. Hauls were made by setting the net parallel to and 15 m off the shore at a depth of 1-2 m. The BS was then hauled to shore using 15 m polypropylene lines attached to 1.8 m brails on each end of the net. Each haul sampled an area of 220 m^2.

2) A 4.6 m × 1.2 m small seine (SS) with 3.2 mm mesh was pulled 10 m along and 2 m from the shore (at a depth to 1 m) and pivoted to shore. Two hauls were made in the inshore area and one haul in the panne at each station. Each haul sampled an area of 62.4 m^2. [One exception to the sampling routine occurred at station 3 panne in April 1978 when no sample was taken due to a dry panne.]

3) A 2.45 × 2.45 × 1.0 m dropnet (DN) with 3.2 mm mesh was used to sample the water column and bottom at 0.5-1.5 m depth. The DN was suspended from a 5.0 × 5.0 × 1.0 m aluminum pipe frame, released by pins at each corner. Two 19 l plastic buckets were attached to each corner of the frame for flotation. The net and frame were maneuvered into position, anchored, and left undisturbed for 10 min. After release the DN was pursed by the chain line and hauled to shore by nylon line. The DN sampled an area of 6.0 m^2.

4) A small, square enclosure (SE) was used in conjunction with an anesthetic (quinaldine mixed 1:5 with isopropyl alcohol) with the intent of sampling small burrow inhabiting fishes, especially gobies. The SE was constructed of heavy duck material mounted on a 1.0 × 1.0 × 1.0 m collapsible frame of 25.0 mm PVC pipe and sampled 1.0 m^2 of bottom. The SE was set at three randomly chosen positions in an undisturbed portion of each station section at a depth of 0.5-1.0 m. The bottom of the SE was forced into the upper few centimeters of substrate and the quinaldine mixture added to the enclosed water column. The enclosed volume and shallow substrate was then thoroughly searched for 10 min using a long-handled dip net of 1.0 mm mesh.

A detailed comparison of the effectiveness of these four methods is the subject of a separate paper (Horn and Allen[2]).

Ten samples were taken at each of the three stations each month (2 BS samples, 3 SS samples, 2 DN samples, 3 SE samples) for a total of 30 samples/mo and 289 samples over the study (minus one SS haul in April 1978 at station 3).

Catches were either frozen on Dry Ice[3] or preserved in 10% buffered Formalin. Specimens >150 mm SL were injected abdominally with 10% buffered Formalin. Subsamples of frozen specimens were oven dried (40°C) for 48-72 h for dry weight determination. Mean dry weights were based on a minimum of 20 individuals/size-class of each common species at each station each month.

Data on six abiotic factors were recorded or determined for each station: temperature, salinity, dissolved oxygen, sediment particle size, depth of capture (by individual samples), and distance into the upper Newport Bay from the Highway 1 bridge (see Fig. 1).

Production Estimation

Production is the total amount of tissue produced during any given time interval including that of individuals which do not survive to the end of that time interval (Ivlev 1966). Productivity is the rate of production of biomass per unit of time (Wiley et al. 1972). Production of a fish stock

[2]Horn, M. H., and L. G. Allen. Comparison of methods for sampling shallow-water estuarine fish populations. Manuscr. in prep. California State University, Fullerton, Fullerton, CA 92634.

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

is the product of the density of fish and the growth of the individuals (Ricker 1946).

An HP9100A program was developed with the aid of Joel Weintraub (California State University, Fullerton) to calculate the production of each recognizable size-class of the common species, those which were collected in at least 2 consecutive months at each station. The model used was that proposed by Ricker (1946) and modified by Allen (1950) and is calculated as follows:

$$P = G\bar{B}$$

where $G = \dfrac{\log_e \bar{w}_2 - \log_e \bar{w}_1}{\Delta t}$ is the instantaneous coefficient of growth;

$\bar{B} = \dfrac{B_1(e^{G-Z}-1)}{G-Z}$ is the average biomass over the time interval;

$Z = \dfrac{-(\log_e N_2 - \log_e N_1)}{\Delta t}$ is the instantaneous coefficient of population change of the immediate sampling area (station) attributable to mortality and migration;

B is the biomass density of fishes at t_1; w_1, w_2 are the mean weights of individuals at time t_1 and t_2; and N_1, N_2 are the numbers of fishes present at t_1 and t_2. $G-Z$ is the net rate of increase in biomass during Δt (1 mo).

The model assumes that production data need not be corrected for immigration and emigration of fishes in and out of the sampling area, provided the density and growth by size-class are estimated frequently enough to accurately assess the abundance and growth of fishes actually in the sampling area (Chapman 1968).

In the present study, growth increments were estimated from length-frequency data for fishes from all three stations each month for each size-class. The length data, therefore, were representative of the entire population of the size-class in the upper Newport Bay and served to minimize the effects which localized movements into and out of a particular station have on monthly growth values. The average weight, $\bar{w}$, of a size-class per month was calculated as follows: 1) Dry weight equivalent for the median length in a size interval (5 mm intervals) was determined using standard length to dry weight curves for each common species; 2) the proportion (range 0-1) of individuals represented in the size interval was multiplied by the dry weight equivalent for the interval; 3) the products were then summed for all size intervals contained within the particular size-class of the species yielding an average weight, $\bar{w}$. This method proved to be more accurate than simply taking the mean length of the entire size-class and determining the dry weight equivalent.

The "best estimate" of biomass density (B) for each discernible size-class was determined in the following manner: 1) The biomass density (wet weight) derived from the method (BS, SS, DN, or SE) shown to be most effective at sampling the particular species was used. Table 1 lists the species with corresponding collecting gear ranked by their effectiveness at capturing the species. This list is based on a comparative study of the sampling methods (Horn and Allen footnote 2); 2) if, as in a few cases, the biomass estimated was inordinately high, due to a large catch in one replicate sample, the estimate defaulted to the next gear type in the rank order; 3) the biomass estimate in wet weight was converted to a dry weight (DW) equivalent by a conversion factor determined for each species and entered into the production model as B_1 (g DW/m^2). Production is the total of all positive values for size-classes during a time period (1 mo in this case) at each station. Negative values were due to sampling error and emigration and were not included in production estimates.

Large individuals (>100 mm SL) of *Mugil cephalus* were not included in production esti-

TABLE 1.—Methods for best estimate of species densities ranked by effectiveness (Horn and Allen text footnote 2). BS = bag seine; SS = small seine; DN = dropnet; SE = square enclosure.

Species	Methods ranked by effectiveness
Atherinops affinis	BS, SS
Fundulus parvipinnis	SS, BS
Clevelandia ios	SE, SS, DN
Anchoa compressa	BS, SS, DN
Gambusia affinis	SS, BS
Cymatogaster aggregata	BS, DN, SS
Gillichthys mirabilis	SS, SE, BS
Anchoa delicatissima	BS, SS
Mugil cephalus	SS, BS
Engraulis mordax	BS, SS
Leuresthes tenuis	BS, SS
Quietula ycauda	DN, SS
Ilypnus gilberti	DN, SS
Syngnathus spp.	SS, DN
Hypsopsetta guttulata	SS, DN
Lepomis macrochirus	BS, SS
Lepomis cyanellus	BS, SS
All other species	BS, SS

mates because quantitative estimates of densities could not be obtained for the large members of this mobile species.

Data Analysis

Cumulative Species Curve

The cumulative number of species in February (low fish density) and June (high fish density) was plotted against the number of samples taken in order to assess the adequacy of sampling. Two random sequences were used for the arrangement of the 30 samples taken each month by the four methods. Each method sampled a unique subhabitat within the littoral zone. Cumulative species curves (reflecting presence/absence) were based on a combination of methods to insure that all possible species occupying the littoral zone at a particular time were represented.

Diversity

Both the Shannon-Wiener information function (Shannon and Weaver 1949) and species richness were used as measures of diversity for pooled station and upper bay samples. The Shannon-Wiener index reflects both species richness and evenness in a sample.

Cluster Analysis and Canonical Correlation

The Ecological Analysis Package (EAP) developed by R. W. Smith was used at the University of Southern California Computer Center to determine species associations (cluster analysis), species abundance correlations to abiotic factors (multiple regression subprogram), and possible effects of abiotic factors on individual species abundance (canonical correlation).

The cluster analysis utilized the Bray-Curtis index of dissimilarity (Clifford and Stephenson 1975). This index allowed quantitative clustering without assuming normality in the sampled population. A square-root transformation of species counts was done to counter the tendency of this index to overemphasize dominant species.

Canonical correlation analysis was used to determine whether and to what extent abiotic factors interacted with individual species abundances in the 39 station samples over the study period. Two separate canonical correlation analyses were made: The first run included six abiotic factors—temperature (TEMP), salinity (SAL), dissolved oxygen (DO), distance into the upper bay from the Highway 1 bridge (DSTUPB), average particle size of the sediment (APRTSZ), and depth of capture (DPTHCAP); the second included only temperature and salinity to determine the amount of variation these two factors accounted for alone.

RESULTS

Temperature and Salinity Patterns

Water temperatures of the littoral zone at all three stations increased steadily during the period January-June from 14°-15°C to 26°-28°C (Fig. 2). The temperatures remained high (>25°C) throughout the summer months and then declined gradually until November. Between November and December the temperature dropped sharply at each station. Temperatures in the pannes were generally higher than the tempera-

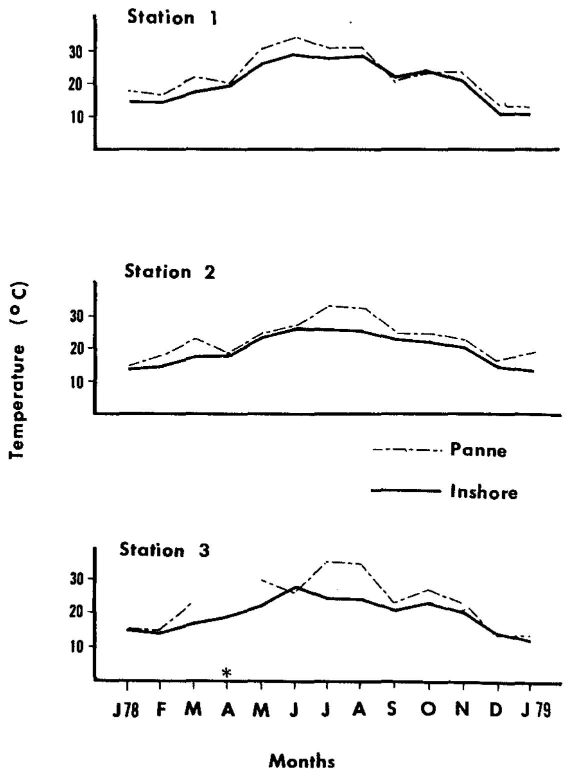

FIGURE 2.—Month-to-month variation (January 1978-January 1979) in water temperature (°C) for the alongshore area and panne at each of the three sampling stations. (* = panne dried-up.)

tures along the shore especially in the summer months (July-September).

Salinity varied more than temperature (Fig. 3) due to rainfall and periodic runoff from surrounding urban areas. In general all stations had low salinities during January through March 1978, a period of heavy rainfall. After May 1978, salinities remained high (between 25 and 32 ppt) with decreases in June 1978 (stations 1 and 3, unknown cause), September 1978 (all stations due to heavy rainfall), and January 1979 (station 3 due to rainfall). Panne salinities at station 1 were consistently low (usually <6 ppt) indicating a constant freshwater input. The pannes at stations 2 and 3, however, usually had salinities equal to or higher than the alongshore area due to evaporation.

Total Catch

Sampling during the 13-mo period yielded 55,561 individuals of 32 species that weighed a total of 103.5 kg (Table 2).

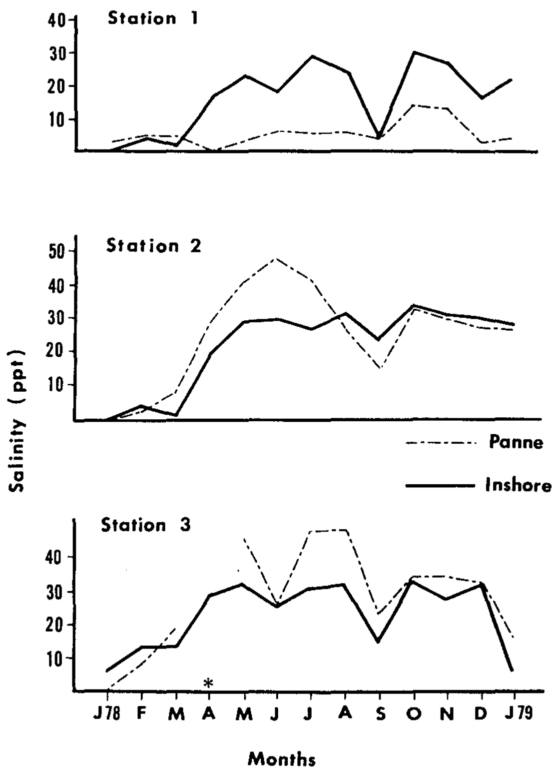

FIGURE 3.—Month-to-month variation (January 1978-January 1979) in salinity (ppt) for the alongshore area and panne at each of the three sampling stations. (* = panne dried-up.)

Atherinops affinis greatly predominated in numbers (76.7%) and biomass (79.9%). *Fundulus parvipinnis* ranked second in both numbers (12.1%) and biomass (7.6%), followed in order by *Gambusia affinis* (5.5% numbers), *Clevelandia ios* (2.4% numbers), and *Anchoa compressa* (1.2% numbers). These five species accounted for 98% of the total number of individuals and 96% of the total biomass (Table 2). The skewed distribution of number of individuals among species was reflected in the relatively low overall H' diversity values of 0.89 for numbers (H'_N) and 0.84 for biomass (H'_B). The vast majority of individuals of most species were either young-of-the-year or juveniles.

Station 1—A total of 13,859 individuals representing 19 species was collected during the year. The catch totaled 22.7 kg. All three of these totals were the lowest of those from the three stations. Overall H' diversity for numbers was 1.17 and for biomass, 0.89. *Atherinops affinis* ranked first in numbers (55.2%) and biomass (76.7%) but was less abundant here than at stations 2 and 3. *Gambusia affinis* (20.6%) and *Fundulus parvipinnis* (19.1%) were common at this station especially in the panne.

Station 2—The greatest number of individuals (24,813) and biomass (42.9 kg) were collected at this site. Although 27 species were captured, over 90% of these individuals were from one species, *Atherinops affinis.* The large number of attached eggs and small (<20 mm) fish caught in July (52% of all *A. affinis*) indicated that this area was a breeding site for *A. affinis. Fundulus parvipinnis* (4.4%) was second in numerical rank. H' for numbers (0.49) and biomass (0.70) were low.

Station 3—A total of 16,889 fishes belonging to 23 species were obtained at this station. *Atherinops affinis* made up 74.4% of the individuals and 78.8% of the 37.9 kg total biomass. Other important species in order of decreasing numerical abundance were *Fundulus parvipinnis* (17.6%), *Clevelandia ios* (3.4%), *Cymatogaster aggregata* (1.3%), and *Anchoa compressa* (1.3%). Overall, H'_N and H'_B were 0.87 and 0.85, respectively.

Cumulative Species Curves

Cumulative species curves from February and June (Fig. 4) reached an asymptote before 20 samples (about 66% of total samples), indicating

TABLE 2.—Monthly abundance and biomass for fish species inhabiting the littoral zone of upper Newport Bay totaled for stations 1-3 (January 1978-January 1979).

Species	January 1978		February		March		April		May		June		July	
	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)
Atherinops affinis	15	70.5	5	158.3	4	92.0	15	59.1	322	1,212.1	6,296	2,377.6	19,817	19,093.3
Fundulus parvipinnis	377	315.7	208	198.3	181	90.4	17	20.7	35	92.2	89	112.3	758	854.8
Gambusia affinis	46	10.3	23	7.1	9	3.2	5	2.8	56	7.1	235	107.4	573	342.9
Clevelandia ios	49	21.4	39	14.3	80	12.9	47	6.1	100	22.4	74	15.8	485	109.0
Anchoa compressa	26	82.9	1	1.2	15	29.4	136	629.3	317	4,393.4	98	1,154.6	77	920.5
Cymatogaster aggregata							11	11.5	141	196.8	4	5.7		
Gillichthys mirabilis	12	2.4	38	5.9	14	3.5	5	10.0	17	39.6	49	127.1	52	141.4
Anchoa delicatissima	10	6.5	1	0.2	28	16.8	47	86.7	17	48.2			1	3.0
Mugil cephalus	41	78.0	11	7.1	1	1.5	1	555.5	1	550.0				
Engraulis mordax													81	89.4
Leuresthes tenuis														
Quietula ycauda	1	1.0							3	1.4	9	3.9	28	14.9
Ilypnus gilberti									3	0.5	10	1.0	24	6.5
Lepomis cyanellus			1	5.2										
Syngnathus auliscus									4	3.6	10	8.7	4	3.3
Hypsopsetta guttulata									10	1.9	4	12.9	2	18.2
Lepomis macrochirus	2	8.1	4	22.2	2	4.1								
Syngnathus leptorhynchus							1	2.1			2	2.6		
Leptocottus armatus					1	1.0			2	4.7	1	1.6		
Acanthogobius flavimanus							2	0.5	1	4.0				
Paralichthys californicus													2	5.4
Pimephales promelas			2	0.2										
Morone saxatilis											1	317.1		
Urolophus halleri														
Mustelus californicus													1	58.0
Seriphus politus														
Cynoscion nobilis													1	6.6
Sphyraena argentea														
Girella nigricans													1	0.4
Symphurus atricauda			1	0.2										
Porichthys myriaster														
Umbrina roncador														
Totals	579	596.8	334	420.2	335	254.8	287	1,384.3	1,029	6,577.9	6,882	4,248.3	21,907	21,667.6
n	10		12		10		11		15		14		16	
H'	1.29	1.46	1.33	1.27	1.37	1.55	1.61	1.22	1.76	1.07	0.44	1.24	0.46	0.56

TABLE 2.—*Continued.*

Species	August		September		October		November		December		January 1979		Totals			
	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	% No.	Wt (g)	% Wt
Atherinops affinis	4,645	13,181.2	4,122	9,606.2	2,902	14,016.0	2,474	12,409.8	1,143	5,738.8	831	4,650.1	42,591	76.67	82,665.0	79.86
Fundulus parvipinnis	312	250.1	1,707	2,323.0	1,023	2,638.8	1,356	738.0	593	259.7	66	26.5	6,722	12.10	7,920.5	7.65
Gambusia affinis	252	42.4	1,029	399.4	680	126.2	149	15.2	20	2.1			3,077	5.54	1,066.1	1.03
Clevelandia ios	68	16.4	151	41.8	66	16.3	142	31.3	28	3.9	5	1.1	1,334	2.40	312.7	0.30
Anchoa compressa	7	104.9	3	53.1	4	104.8							684	1.23	7,474.1	7.22
Cymatogaster aggregata	61	390.9	2	16.6			2	34.1	1	22.6	1	12.4	223	0.40	690.6	0.67
Gillichthys mirabilis	4	27.0	1	20.0	4	37.1	1	12.0			6	0.3	203	0.37	426.3	0.41
Anchoa delicatissima	64	234.4	26	71.7	1	3.5							195	0.35	471.0	0.46
Mugil cephalus									68	13.3	9	1.5	132	0.24	1,206.9	1.17
Engraulis mordax			29	58.6	2	7.2					1	—	113	0.20	155.2	0.15
Leuresthes tenuis	85	57.8	3	2.3									88	0.16	60.1	0.06
Quietula ycauda	5	1.9	4	1.5	2	0.4	1	0.1					53	0.10	25.1	0.02
Ilypnus gilberti							1	0.1					38	0.07	8.1	0.01
Lepomis cyanellus			31	49.3									32	0.06	54.5	0.05
Syngnathus auliscus	1	0.4			1	0.1							20	0.04	16.1	0.02
Hypsopsetta guttulata							1	2.9			2	0.2	19	0.03	36.1	0.03
Lepomis macrochirus													8	0.01	34.4	0.03
Syngnathus leptorhynchus	1	2.8	3	5.2							1	0.3	8	0.01	13.0	0.01
Leptocottus armatus													4	0.01	7.3	0.01
Acanthogobius flavimanus													3	0.01	4.5	<0.01
Paralichthys californicus													2	<0.01	5.4	0.01
Pimephales promelas													2	<0.01	0.2	<0.01
Morone saxatilis													1	<0.01	317.1	0.31
Urolophus halleri	1	430.0											1	<0.01	430.0	0.42
Mustelus californicus													1	<0.01	58.0	0.06
Seriphus politus					1	0.3							1	<0.01	0.3	<0.01
Cynoscion nobilis													1	<0.01	6.6	0.01
Sphyraena argentea							1	4.2					1	<0.01	4.2	<0.01
Girella nigricans													1	<0.01	0.4	<0.01
Symphurus atricauda													1	<0.01	0.2	<0.01
Porichthys myriaster							1	0.1					1	<0.01	0.1	<0.01
Umbrina roncador	1	44.2											1	<0.01	44.2	0.04
Totals	5,507	14,784.4	7,111	12,648.7	4,686	16,950.7	4,129	13,247.8	1,853	6,040.4	922	4,692.4	55,561		103,514.3	
n	14		13		11		11		6		9		32			
H'	0.69	0.55	1.10	0.77	0.99	0.54	0.92	0.27	0.90	0.23	0.42	0.06	0.89		0.84	

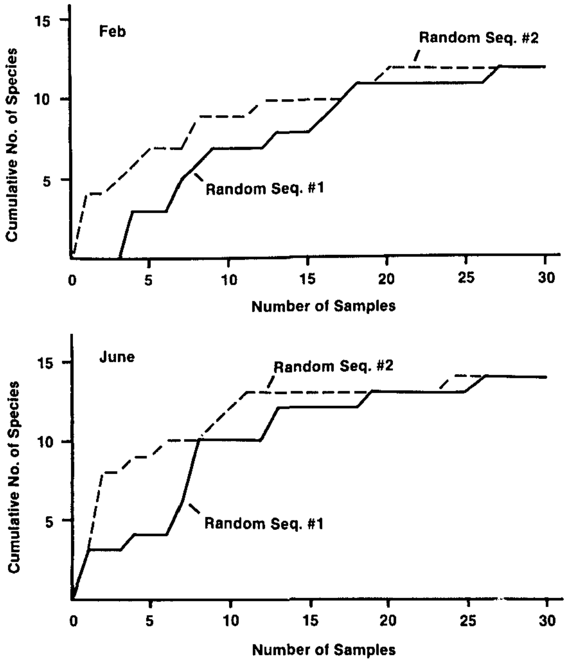

FIGURE 4.—Cumulative number of species as a function of the number of samples of all methods at stations 1-3 combined in upper Newport Bay for two different months (February and June 1978) during the study period. Curves were generated by two random sequences for each month.

that the range of fish species in the area had been adequately sampled by the four methods. Accumulation of species in June, however, was generally more rapid than in February.

Seasonal Abundance and Diversity

Fish abundance and diversity fluctuated markedly during the 13 mo of the study (Fig. 5). As a whole, the ichthyofauna of the littoral zone showed increased species richness from 10 species in January to 16 species in July 1978. The number of species was elevated (>14) for the entire spring-summer period from May to August 1978. Richness then decreased through the fall, reaching its lowest point of six species in December 1978. Diversity H' values fluctuated in a pattern opposite to that of species richness. H'_N decreased during the summer from a high in May of 1.76 to a low in June of 0.44. H'_B also decreased sharply in summer but unlike H'_N continued to decline for the remainder of the study. Both the number of individuals and biomass began to increase dramatically during May 1978 and reached peaks of 21,907 individuals and 21.7 kg in June. Both numbers and biomass decreased in August with number of individuals increasing again in September. Biomass declined once again in September during a period of rainfall and then increased in October. In the months from October 1978 to January 1979 a rapid decline in both numbers and biomass was evident and was especially pronounced from November to December. A greater number of individuals (992-579) and much greater biomass (4,692-597 g) was obtained in January 1979 than in January 1978.

Species Associations

Cluster analysis based on individual samples yielded five species groups which, upon further

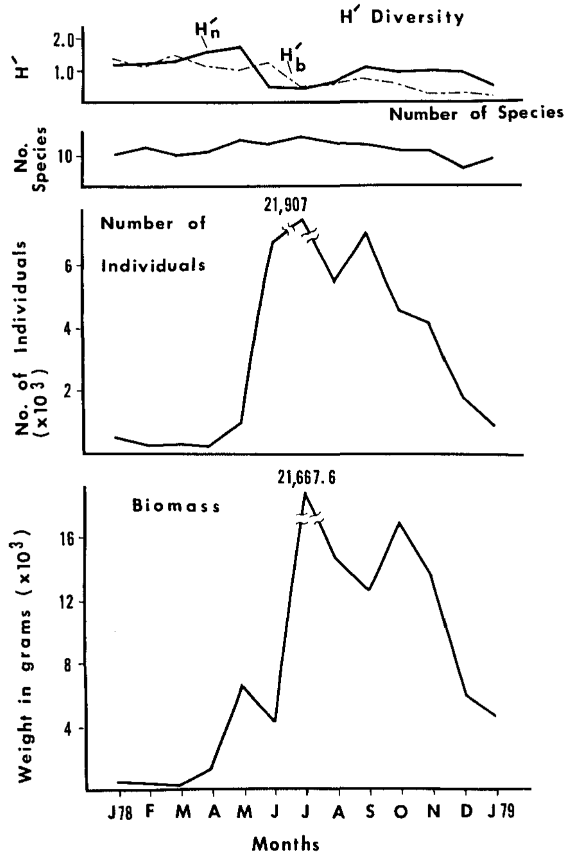

FIGURE 5.—Monthly variation (January 1978-January 1979) in total number of species, diversity H′ (for numbers, H'_N, and biomass, H'_B), number of individuals and biomass (g) for fishes collected by all methods at stations 1-3 combined in the littoral zone of upper Newport Bay.

examination, reflected both spatial (microhabitat) and seasonal differences in the littoral ichthyofauna (Fig. 6).

Group I was a loosely associated group of the five resident species (maintain populations year round in littoral zone) which could be further divided into three subgroups. Subgroup A had only one member, *Atherinops affinis*, an abundant schooling species. *Clevelandia ios* and *Gillichthys mirabilis* which comprised subgroup B are burrow-inhabiting gobiids of the shallows and pannes. Subgroup C included two species, *Fundulus parvipinnis* and *Gambusia affinis*, which inhabited pannes and other high intertidal areas. *Clevelandia ios*, *G. mirabilis*, and *F. parvipinnis* are residents of salt marshes in California and other west coast estuaries and are probably the species most threatened by alterations of these habitats.

Group II consisted of three midwater schooling species—*Anchoa compressa*, *A. delicatissima*, and *Cymatogaster aggregata*—most of which were caught mainly from January to August.

Group III was made up of three distinctly seasonal, benthic species: Two gobiids, *Quietula ycauda* and *Ilypnus gilberti*, and a cottid, *Leptocottus armatus*, which was relatively rare during 1978 compared with previous years (pers. obs.).

Group IV included an engraulid, *Engraulis mordax*; syngnathids, Syngnathus spp. (including *S. auliscus* and *S. leptorhynchus*); and the pleuronectid, *Hypsopsetta guttulata*. These species were seasonally present in mid- to late summer. Members of this group were only loosely associated (> 80% distance).

Group V was composed of four species which were collected at times of low salinities. *Lepomis macrochirus* and juveniles of *Mugil cephalus* were sampled together early in the year (January-March 1978). *Lepomis cyanellus* and *Leuresthes tenuis* were found together only in September.

Group VI included 12 rare species, most of which could be considered summer periodics in the littoral zone in 1978. These were *Umbrina roncador*, *Urolophus halleri*, *Paralichthys californicus*, *Mustelus californicus*, *Cynoscion nobilis*, *Acanthogobius flavimanus*, *Sphyraena argentea*, *Girella nigricans*, *Symphurus atricauda*, *Porichthys myriaster*, *Morone saxatilis*, and *Seriphus politus*.

Members of the species groups identified in the dendrogram (Fig. 6) are illustrated in dia-

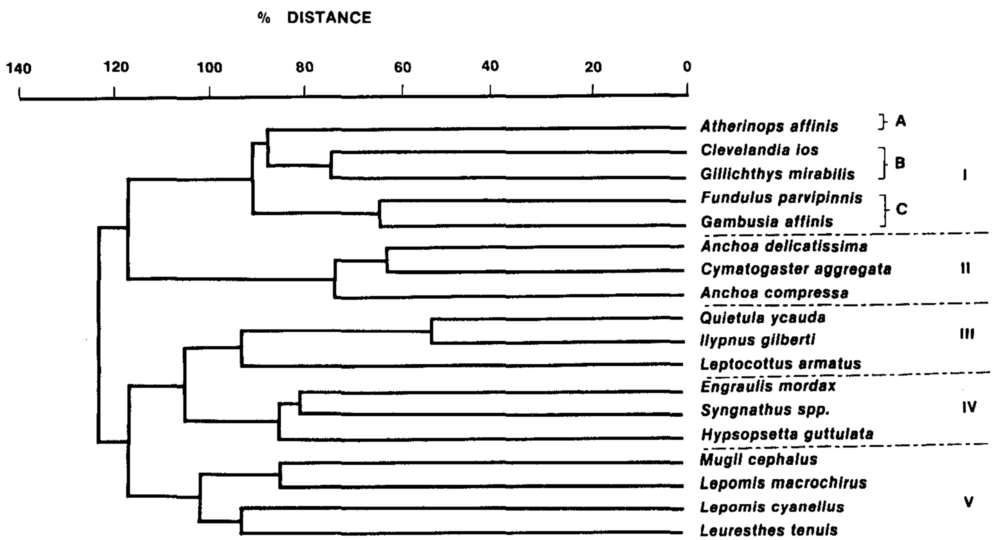

FIGURE 6.—Dendrogram of the clustering of littoral fish species by individual samples taken at stations 1-3 in upper Newport Bay, five species groups (Roman numerals) are recognized according to the Bray-Curtis index of dissimilarity (% distance). A, B, and C are subgroups of species Group I.

grams (Figs. 7-9), depicting occurrences in the alongshore area or panne during three different time periods (January-March 1978, April-September 1978, and October 1978-January 1979). Only species with ≥5 individuals during each time segment were included in the diagrams. These diagrams illustrate the high degree of seasonality within this fish assemblage.

During the January-March 1978 period of heavy rainfall, members of three species groups (I, II, and V) were present in relatively low abundances (Fig. 7). A halocline existed at station 3 during this period, and *Atherinops affinis* was collected only seaward of the halocline at this station. Representatives of group V, *Mugil cephalus* juveniles and *Lepomis macrochirus*, were found associated with very low salinities. Large *M. cephalus* were observed in both the channel and littoral areas during most of the year.

The spring-summer period of April-September 1978 was characterized by increased water temperatures and salinities, accompanied by increased numbers of species and individual fishes (Fig. 8). Green algal beds, composed primarily of *Enteromorpha* sp., *Chaetomorpha linum*, and *Ulva lobata*, developed along the shore of the entire upper bay, and served as a nursery area for large numbers of juvenile fishes. All species groups, except V, were represented during this time. Juveniles of *Atherinops affinis* occurred in large numbers in the shallows with juvenile *Cymatogaster aggregata* also being abundant at station 3. Young-of-the-year *F. parvipinnis* were very abundant in the pannes, especially at stations 1 and 3.

By October the extensive algal beds had disappeared. The October 1978-January 1979 period was marked by decreased number of species and abundance (Fig. 9). The only common species were members of group I (residents) with a few juvenile *M. cephalus* representing group V.

Productivity

Annual production (mean of three stations by month) of the entire upper Newport Bay was 9.35 g DW/m^2 per year (Table 3). Young-of-the-year *Atherinops affinis* contributed 85.1% to total production followed by *Anchoa compressa* (4.9%) and *Fundulus parvipinnis* (4.2%).

Productivity was highly seasonal with the spring-summer period (April-September) accounting for 75.9% of the total annual production (Table 3, Fig. 10). Productivity, which was very

TABLE 3.—Monthly mean production (g DW/m^2) for individual species inhabiting the littoral zone (excluding panne) of upper Newport Bay (February 1978-January 1979).

Species	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Total annual	% total production
Atherinops affinis (adult)				0.0280	0.1049								0.1329	1.42
A. affinis (78 class)					0.0800	0.6764	5.1397		1.2942	0.6428		0.1307	7.9638	85.15
Fundulus parvipinnis	0.0005		0.0007	0.0240	0.0167	0.1323	0.0352	0.0826	0.1033				0.3953	4.23
Clevelandia ios	0.0003			0.0027	0.0051	0.0093	0.0068		0.0431			0.0145	0.0818	0.87
Anchoa compressa	0.0142		0.0045	0.1127	0.2524	0.0485	0.0154		0.0075				0.4552	4.87
Gillichthys mirabilis		0.0001	0.0014		0.0889	0.0361	0.0102	0.0020					0.1387	1.48
Hypsopsetta guttulata					0.0082	0.0020							0.0102	0.11
Mugil cephalus	0.0006	0.0004										0.0003	0.0013	0.01
Anchoa delicatissima	0.0030	0.0002	0.0039	0.0084	0.0013		0.0001	0.0017					0.0186	0.20
Quietula ycauda						0.0011							0.0011	0.01
Engraulis mordax							0.0046	0.0003					0.0049	0.05
Cymatogaster aggregata				0.0074	0.0072	0.0023		0.0101	0.0009				0.0279	0.30
Ilypnus gilberti						0.1197							0.1197	1.28
Lepomis macrochirus	0.0008												0.0008	0.01
Monthly total	0.0194	0.0007	0.0105	0.1832	0.5647	1.0277	5.2120	0.0967	1.4490	0.6428	0	0.1455	9.3522 g DW/m^2/yr	
													April-September 7.0948-75.86%	

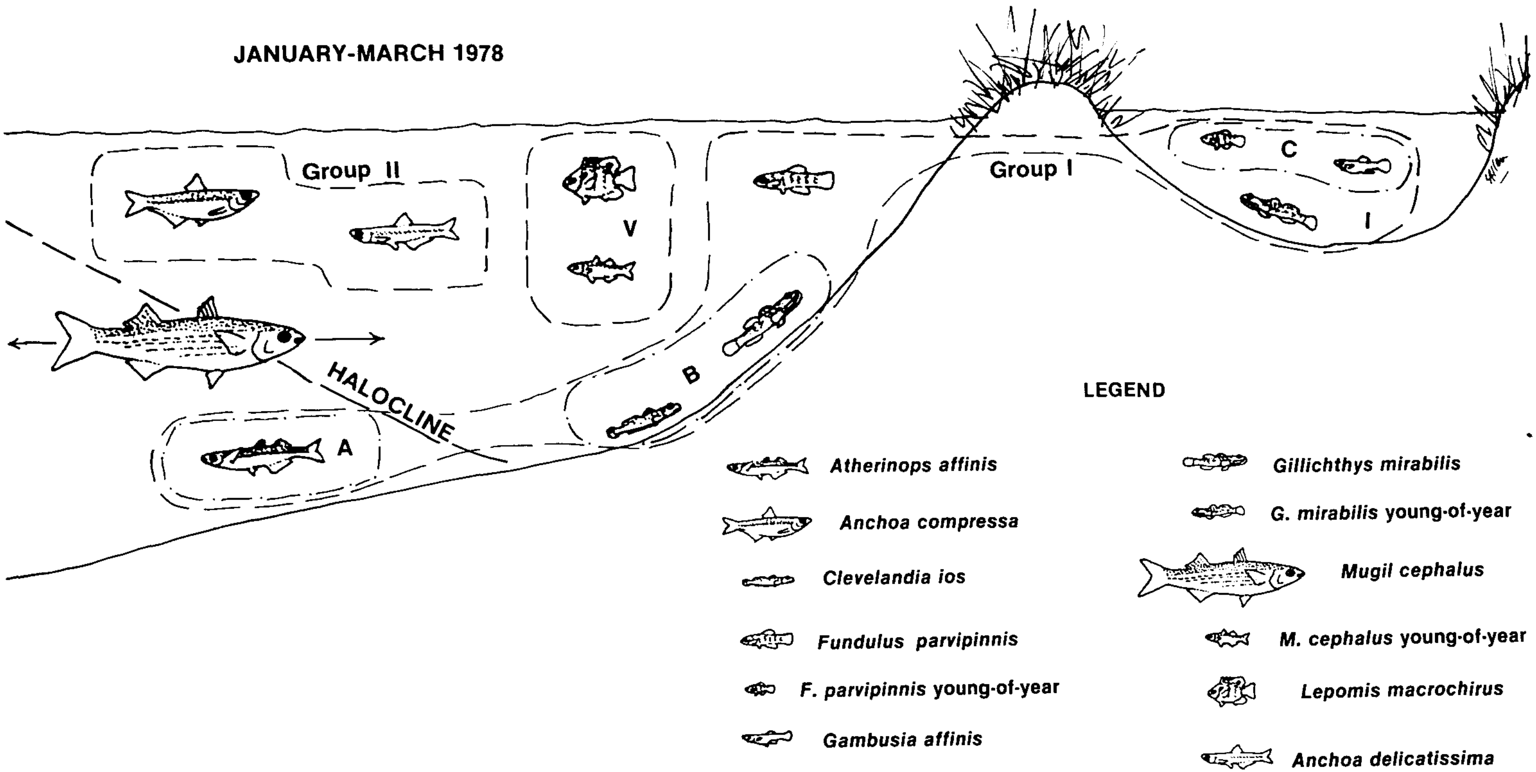

FIGURE 7.— Diagrammatic representation of the principal species inhabiting the littoral zone (alongshore and panne) of upper Newport Bay during January-March 1978. Inclusion level for species was ≥5 individuals in the samples during the period. Dashed lines enclose species from groups derived in the dendrogram of Figure 6. Arrows indicate inshore-offshore occurrence.

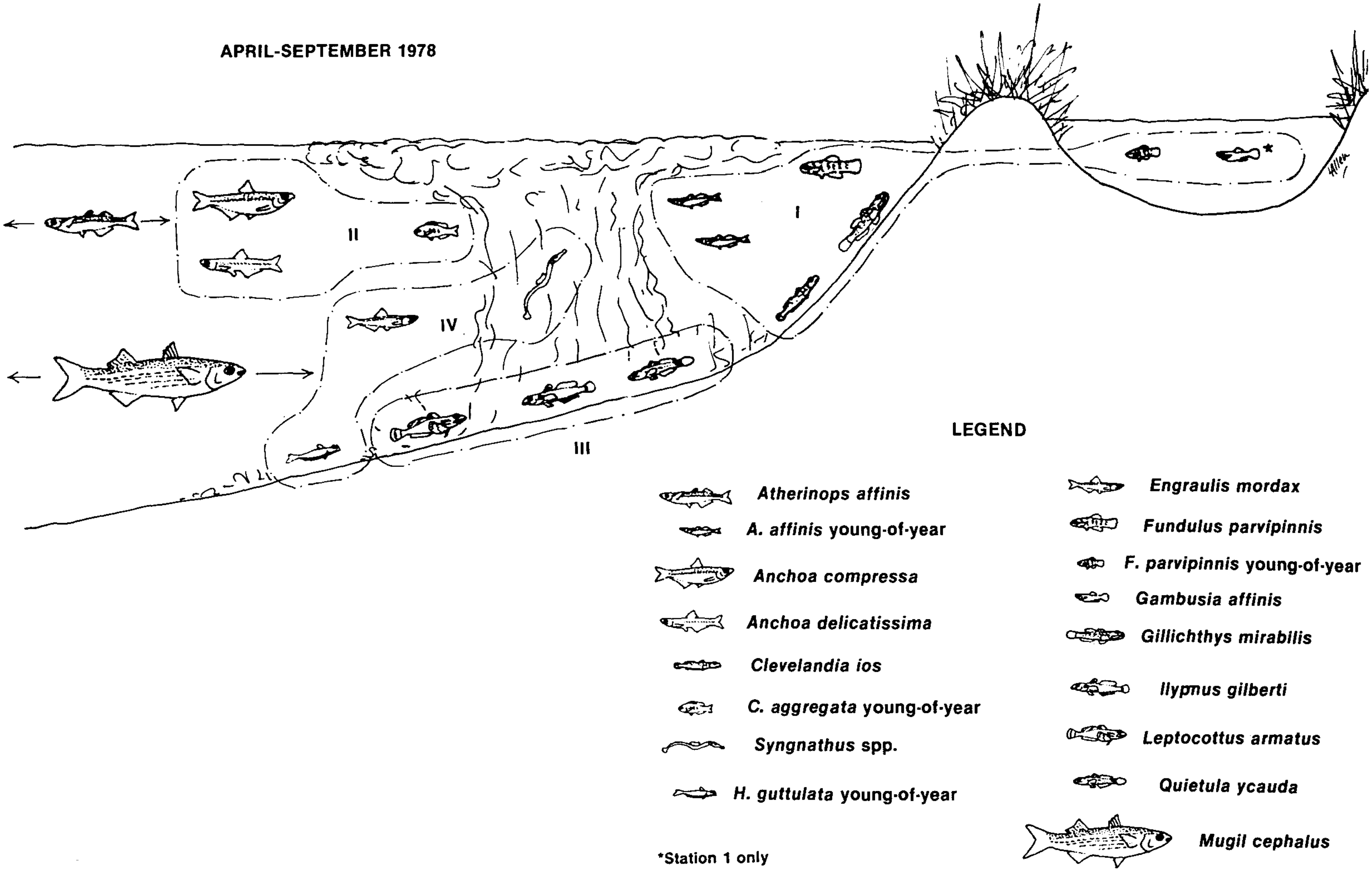

FIGURE 8.—Diagrammatic representation of the principal species inhabiting the littoral zone of upper Newport Bay during April-September 1978. Wavy vertical lines represent the large algal beds present during this period. Other information is the same as in Figure 7. (*Syngnathus* spp. includes *S. leptorhynchus* and *S. auliscus*.)

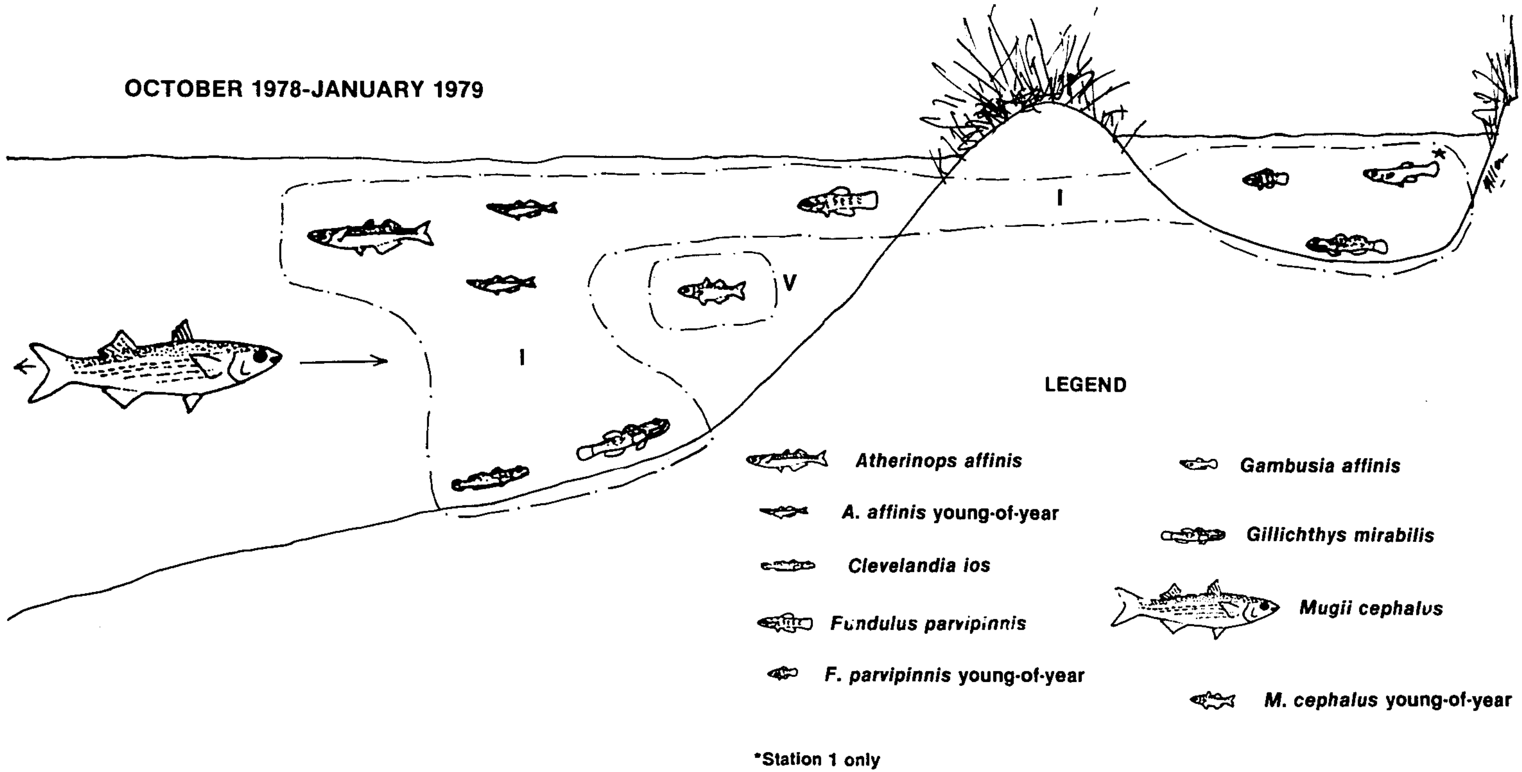

FIGURE 9.—Diagrammatic representation of the principal species inhabiting the littoral zone of upper Newport Bay during October 1978-January 1979. Other information as in Figure 7.

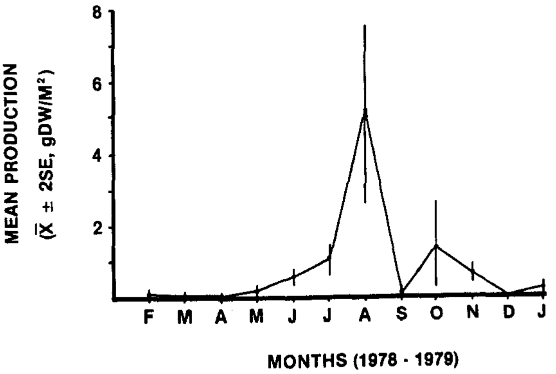

FIGURE 10.—Monthly variation in mean production ($\bar{x} \pm 2$ SE, g DW/m^2) of the littoral fishes from three stations in upper Newport Bay (February 1978-January 1979).

low from February to May 1978, increased rapidly from June to a peak in August (5.2 g DW/m^2). Monthly production then declined drastically in September, a period of heavy rainfall during which many of the larger young-of-the-year *Atherinops affinis* emigrated from the study area. Production increased in October but then showed a steady decline to zero in December, a time of a sharp decrease in mean water temperature in the upper bay.

Relationship of Abiotic Factors to Fish Abundance and Distribution

Temperature was found to have a significant, positive correlation ($P<0.01$, df = 37) with number of species (r = 0.42), number of individuals (r = 0.48), and biomass (r = 0.54) when station totals were considered. Similarly, salinity was significantly correlated with number of individuals (r = 0.36) and biomass (r = 0.64) (Table 4).

Temperature was the factor which yielded the highest number of significant correlations (6) with individual species, followed by salinity, dissolved oxygen, distance into the upper bay, and depth of capture, each with four (Table 4).

An analysis of intercorrelations among abiotic factors yielded three significant ($P<0.05$, df = 37) positive relationships: 1) Temperature and salinity (r = 0.48); 2) temperature and dissolved oxygen (r = 0.53); and 3) dissolved oxygen and distance into the upper bay (r = 0.32).

According to canonical correlation analysis, the six abiotic variables accounted for 93% of the variation in individual species abundances along the first canonical axis (Table 5). A second run indicated that 83% of the variation in species abundances could be accounted for by temperature and salinity alone. This finding strongly implies that interactive effects of temperature

TABLE 4.—Correlation coefficients (r) of individual species numbers and of total number of species, number of individuals, and biomass with six environmental factors. TEMP = temperature, SAL = salinity, DO = dissolved oxygen, DSTUPB = distance into upper Newport Bay from Highway 1 bridge, APRTSZ = average particle size of sediments, DPTHCAP = depth of capture.

Species	Abiotic factors					
	TEMP	SAL	DO	DSTUPB	APRTSZ	DPTHCAP
Atherinops affinis	0.55**	0.57**	0.21	0.00	−0.12	0.23
Fundulus parvipinnis	0.18	0.15	−0.31*	0.00	−0.06	0.03
Anchoa compressa	0.38*	0.21	0.35*	−0.01	0.05	0.24
Clevelandia ios	0.43**	0.22	0.08	−0.09	−0.16	0.23
Mugil cephalus	−0.62**	−0.29	−0.10	0.11	0.26	0.02
Gillichthys mirabilis	0.25	−0.22	0.44**	0.31*	0.01	0.00
Anchoa delicatissima	0.10	0.08	−0.22	−0.22	0.05	−0.02
Gambusia affinis	0.21	−0.25	0.16	0.58**	−0.07	−0.02
Hypsopsetta guttulata	0.30	0.21	0.43**	0.26	−0.10	0.28
Cymatogaster aggregata	0.14	0.28	−0.01	−0.34*	0.01	0.14
Quietula ycauda	0.46**	0.35*	0.19	−0.16	0.01	0.35*
Ilypnus gilberti	0.39*	0.31*	0.23	−0.10	0.11	0.33*
Lepomis macrochirus	−0.29	−0.44*	−0.23	0.10	0.09	0.04
Lepomis cyanellus	0.06	−0.27	−0.29	0.16	−0.20	0.05
Engraulis mordax	0.22	0.16	0.00	0.13	−0.07	0.33*
Leuresthes tenuis	0.16	0.14	−0.09	−0.15	0.10	−0.01
Leptocottus armatus	0.29	0.13	0.38	−0.09	−0.01	0.05
Syngnathus spp.	0.53	0.23	0.35	0.08	−0.07	0.33*
Species totals (by station)						
No. of species	0.42**	0.05	—	—	—	—
No. of individuals	0.48**	0.36*	—	—	—	—
Biomass	0.54**	0.64**	—	—	—	—

* = significant at 0.05 level.
** = significant at 0.01 level.

TABLE 5.—Summary of two canonical correlation runs of individual species abundances against environmental variables.

Axis	R^2	R	X^2	df
Run No. 1 (6 environmental; 18 species)				
1	0.93	0.96	212.9*	126
2	0.84	0.92	144.1*	102
3	0.73	0.85	96.3	80
Run No. 2 (temperature, salinity only, 18 species)				
1	0.83	0.91	77.8*	36
2	0.61	0.78	26.5	17

* = significant at 0.01.

and salinity were important in influencing species abundance.

The 18 most common species were ordinated along temperature and salinity axes using simple correlation values (r) as an index of relative influence of these two factors (Fig. 11). Thirteen of the 18 species were positioned in the upper right quadrant indicating that they were all positively correlated with temperature and salinity. Three species, *Gambusia affinis, Gillichthys mirabilis,* and *Lepomis cyanellus,* located in the upper left quadrant correlated positively with temperature, but negatively with salinity. The lower left quadrant includes two species, *Lepomis macrochirus* and *Mugil cephalus,* with negative temperature and salinity influences. No species were positioned in the negative temperature, positive salinity quadrant probably because this situation rarely occurred in the littoral zone in 1978.

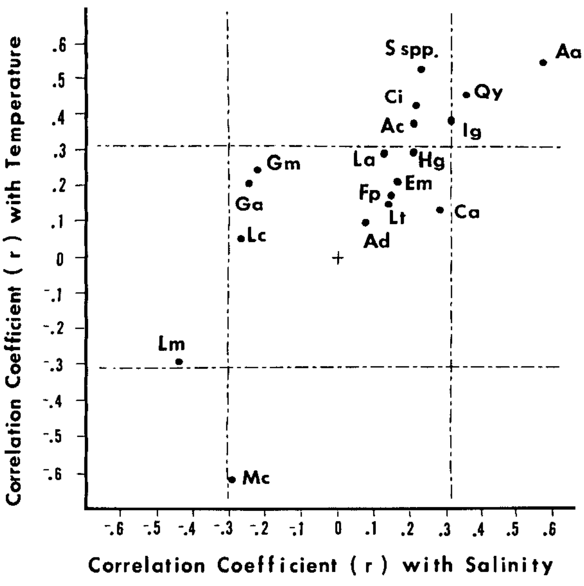

FIGURE 11.—Ordination of 18 common species of the littoral zone of upper Newport Bay on correlation coefficients (r) for temperature (y-axis) and salinity (x-axis). Dashed lines indicate 0.05 significance levels. Aa-*Atherinops affinis*, Ac-*Anchoa compressa*, Ad-*Anchoa delicatissima*, Ca-*Cymatogaster aggregata*, Ci-*Clevelandia ios*, Em-*Engraulis mordax*, Fp-*Fundulus parvipinnis*, Ga-*Gambusia affinis*, Gm-*Gillichthys mirabilis*, Hg-*Hypsopsetta guttulata*, Ig-*Ilypnus gilberti*, La-*Leptocottus armatus*, Lm-*Lepomis macrochirus*, Lt-*Leuresthes tenuis*, Mc-*Mugil cephalus*, Qy-*Quietula ycauda*, Sspp-*Syngnathus* spp.

DISCUSSION

Composition, Diversity, and Seasonal Dynamics

The ichthyofauna of the littoral zone in upper Newport Bay was numerically dominated by a few, low trophic-level species (five species accounted for >98% of all specimens collected), a situation similar to that found in many estuarine fish populations (Allen and Horn 1975). *Atherinops affinis* is an opportunistic feeder and has been characterized as both a herbivore/detritivore (Allen 1980) in upper Newport Bay and a low-level carnivore (Fronk 1969; Quast 1968). The second most abundant fish, *Fundulus parvipinnis,* is a low-level carnivore that feeds on small crustaceans and insects (Allen 1980; Fritz 1975). *Gambusia affinis, Clevelandia ios,* and *Anchoa compressa* are, likewise, low-level carnivores, feeding mainly on insects, benthic microinvertebrates, and zooplankton (Allen 1980).

Large individuals of *Mugil cephalus* were not sampled effectively, but probably constituted a significant proportion of biomass within these fish assemblages. Adult *M. cephalus* fed mainly on detritus and pennate diatoms (Allen 1980). This essentially herbivorous diet closely matches that described by Odum (1970) for *M. cephalus.*

The overall H' diversity values (H'_N range, 0.42-1.76; overall 0.89) for the littoral zone were comparable to values derived from other studies of bay-estuarine fish faunas and to other studies in Newport Bay. Haedrich and Haedrich (1974) derived values of 0.33-1.03 for Mystic River Estuary, Mass.; Stephens et al. (1974) presented indices of 0.65-2.08 for Los Angeles Harbor, Calif.; Allen and Horn (1975) published values of 0.03-1.11 for Colorado Lagoon, Alamitos Bay, Calif.; and Quinn (1980) calculated values of 0.21-2.59 (overall 1.9) for Serpentine Creek in subtropical Queensland. Using otter trawl data, I calculated H'_N values of 0.20-1.96 (overall 0.98) for the upper Newport Bay in 1974-75 (Allen 1976). The concurrent bimonthly portion of this study (Horn and Allen 1981) obtained a bimonthly range for numbers of 0.48-2.17 (overall 1.05) when the deeper channel areas were also sampled. The relatively wide range of H'_N values in all of the above studies reflects the differential utilization of these embayments by fishes on a seasonal basis. At the same time, the low overall diversity reflects dominance both in numbers and biomass by a few species. The seasonal usage has the effect of increasing annual diversity, although only one or two species dominate numerically at any one time. The H' values for biomass (H'_B range 0.23-1.55; overall 0.84) were fairly close to those for numbers and, again, mainly reflected the dominance of *A. affinis* (~80%). In all, 26 of the 32 reported species had young-of-the-year fishes, making up a significant portion of their populations. Fluctuations in juvenile population levels had a substantial effect on the littoral fish populations. Juvenile recruitment plus the immigration of adult fishes presumably for reproduction or for exploitation of high productivity in warmer months were the principal causes for seasonal changes in the ichthyofauna. These activities reflect the widely recognized function of bay-estuarine environments as spawning and nursery grounds (Haedrich and Hall 1976).

The general pattern of increased number of species and numbers of individuals during the late spring through fall period in upper Newport Bay has been observed in many other studies of temperate bay-estuarine fishes (e.g., Pearcy and Richards 1962; Dahlberg and Odum 1970; Allen and Horn 1975; Adams 1976a). Several studies of estuarine fish populations have, in addition, detected summer depressions in abundance between peaks in spring and fall in other estuaries (Livingston 1976; Horn 1980) and in lower Newport Bay (Allen 1976).

Studies of subtropical estuarine fish populations have shown a trend in seasonal abundances that is 6 mo out of phase with the above observations. Fish abundances were highest during the winter months (November-March) in the Huizache-Caimanero Lagoon of Mexico due to increases in members of both demersal and pelagic fishes (Amezcua-Linares 1977; Warburton 1978). This coastal lagoon system is subject to a narrower range of temperatures over the year (18.3°-27.9°C) than most temperate systems. However, the Mexican system undergoes wide variation in salinity, especially during the rainy season from July to October (see section Influence of Abiotic Factors).

Species Associations

Species groupings were subject to strong seasonal influence and bore a striking resemblance to the classification scheme of Atlantic nearshore fish communities proposed by Tyler (1971). According to Tyler's classification the Atlantic nearshore fish communities can be divided into regular and periodic components. Periodic components can be winter seasonals, summer seasonals, or occasionals. The upper Newport Bay fish assemblage had regulars (group I) and periodics (groups II-V). The "anchovy" group (II), the "goby" group (III), and the "*Engraulis-Hypsopsetta*" group (IV) were all summer seasonals. Group V had both winter seasonals in *Mugil cephalus* and *Lepomis macrochirus* and summer seasonals in *Lepomis cyanellus* and *Leuresthes tenuis*. The latter group, however, could best be characterized by the affinity of its components to lower salinities rather than to a particular time of year. The occasional component was represented by the 12 species of group VI which also occurred in the summer. Thus Tyler's classification may have a broader application than he originally proposed, and perhaps holds true for many estuarine ichthyofaunas.

Species Densities and Productivity

Density estimates for some species of littoral fishes are particularly difficult to obtain. Such species include small, burrow-inhabiting fishes of the family Gobiidae and other small benthic fishes such as killifishes, flatfishes, and sculpins which escape under a seine or through the mesh of various nets. This study attempted to obtain density values for all littoral fishes, especially for the elusive species listed above. By setting up the procedure for choosing the "best estimate" of density from among four different sampling methods, actual densities of the species have been more closely approximated.

If the biomass density of *Atherinops affinis* for the entire study is calculated by dividing its total biomass by the total area of coverage by all four sampling gears, a biomass density of 3.3 g/m^2 (or about 0.83 g DW/m^2) is obtained. This density value is lower than the estimate of 1.16 g DW/m^2 derived through the best estimate process (Table 6). In this particular case, most densities were mean values of six bag seines which were very effective (99%) at capturing *A. affinis* (Horn and Allen footnote 2). Biomass density for the gobiid,

TABLE 6.—Grand mean estimate of biomass density (g DW/m²) for common species in the littoral zone (excluding panne) over the 13-mo period (January 1978-January 1979) from the best estimate criteria.

Species	$\bar{X}$ g DW/m²±1 SE
Atherinops affinis (adult)	0.1043±0.0602
A. affinis	1.1590±0.2573
Fundulus parvipinnis	0.1064±0.0223
Gambusia affinis	0.0015±0.0028
Clevelandia ios	0.0261±0.0117
Anchoa compressa	0.1195±0.0493
Cymatogaster aggregata	0.0167±0.0158
Gillichthys mirabilis	0.0131±0.0035
Anchoa delicatissima	0.0077±0.0053
Mugil cephalus	0.0024±0.0018
Quietula ycauda	0.0029±0.0025
Ilypnus gilberti	0.0021±0.0021
Hypsopsetta guttulata	0.0043±0.0035
Engraulis mordax	0.0019±0.0018
Lepomis macrochirus	0.0006±0.0005
Lepomis cyanellus	0.0003±0.0001
	1.5688 g DW/m²

Clevelandia ios, determined by total area coverage was 0.013 g/m² (about 0.003 g DW/m²). The value based on best estimate (using square enclosures and small seine estimates) was about 10 times higher at 0.03 g DW/m². This large discrepancy is due to the low efficiency of the bag seine for capturing this species. Since the bag seine covered the largest area of any of the sampling gears (220 m²), its addition to the density determination for *C. ios* led to the large underestimate. The total biomass density of all species by total area was 4.13 g/m² (or about 1.02 g DW/m²) which again was lower than the best estimate grand mean density of 1.57 g DW/m².

Average standing stock for the upper bay species during 1978 was 784 kg DW, based on an estimate of 50 ha of habitable littoral zone in upper Newport Bay. This is equivalent to 3,136 kg (wet weight) or 6,899 lb of fish. By the same procedure, the average standing stock of *A. affinis* was 631.6 kg DW and that of *C. ios*, 13.1 kg DW.

The annual production of 9.35 g DW/m² for the upper Newport Bay littoral zone in 1978 ranked among the highest values recorded for studies with comparable production determinations of production models (Table 7).

The Newport Bay production estimate in 1978 was surpassed only by the estimate for *Fundulus heteroclitus* (Meredith and Lotrich 1979), an estuarine species of the east coast of the United States. *Fundulus heteroclitus* represented a very efficient energy link between the marsh and the littoral zone in their study. However, as Meredith and Lotrich pointed out, the production value may be an overestimation due to the underestimation of the area of marsh utilized by the fish. The value 4.6 g DW/m² obtained by Adams (1976b) for fishes inhabiting east coast eelgrass beds, which are acknowledged as highly productive areas, is half the estimate for the littoral zone of upper Newport Bay.

Short food chains have been implicated as the primary reason for high production in estuarine fish communities (Adams 1976b), a contention which is supported by the findings of this study. Young-of-the-year *Atherinops affinis* accounted for 85% of the annual production and formed a direct link through their herbivorous/detritivorous diet to the high primary productivity of this estuarine system. The remaining, numerically important species of the littoral zone were low-level carnivores. There is little doubt that this assemblage represents an example of "food chain telescoping" as described by Odum (1970).

Even though the fish production in the littoral zone of upper Newport Bay was high compared with most comparable studies, the value presented here is undoubtedly an underestimate. The largest species of the system, adult *Mugil cephalus*, was not represented in the production estimates due to inadequate sampling. Inclusion of this species would have substantially increased the production value. It is unlikely, however, that productivity of adult *M. cephalus* could approach that of juvenile *Atherinops affinis* which were responsible for 85% of the annual fish production.

Influence of Abiotic Factors

The positive correlations between temperature and total abundance, biomass and number of species, and between salinity and total abundance and biomass indicate the general impor-

TABLE 7.—Comparison of annual fish production (P) for marine or estuarine studies with comparable production determinations. Wet weights were converted by multiplying by 0.25. Values are for all species except where noted.

Locale and habitat	Study	Estimated annual P (g DW/m²)
Delaware salt marsh creek (*Fundulus heteroclitus*)	Meredith and Lotrich (1979)	10.2
Newport Bay littoral zone	present study	9.4
Mexican coastal lagoon	Warburton (1979)	8.6
Cuban freshwater lagoons	Holčík (1970)	6.2
No. Carolina eelgrass beds	Adams (1976b)	4.6
Bermuda Coral Reef	Bardach (1959)	4.3
Texas lagoon (Laguna Madre)	Hellier (1962)	3.8
English Channel pelagic and demersal fishes	Harvey (1951)	1.0
Georges Bank commercial fishes	Clarke (1946)	0.4

tance of these factors to this assemblage. Individual correlations between abiotic factors and species abundances likewise emphasized the importance of temperature and salinity. The correlations between individual species abundances and dissolved oxygen as well as distance into the upper Newport Bay could be due to the intercorrelations of both dissolved oxygen and distance with temperature.

Intercorrelations among factors can confound the interpretation of relationships and introduce redundancy in multivariate analyses. The relationship between dissolved oxygen and distance into the upper Newport Bay is intuitive considering its shallow depths. The positive relationship between temperature and dissolved oxygen was probably due to photosynthesis by green algae during the summer. Winter rainfall in the basically Mediterranean climate of southern California was responsible for the positive correlation between temperature and salinity found in Newport Bay. This relationship is by no means absolute, as evidenced by the low salinities encountered during the tropical rains of September 1978 when temperatures were high.

The results of the second canonical correlation analysis indicate that interaction between temperature and salinity explained most of the variability in species abundance in this system. The correlation between these two abiotic factors probably inflated the R^2 value slightly, but does not negate the overall findings. Ordination of individual species by correlation coefficients with temperature and salinity underscores the influences of these factors on individual species. Furthermore, the substantial decrease in numbers of *A. affinis* at station 1 and the somewhat smaller decrease at station 3 during September rains (low salinity) and relatively high temperatures also illustrate this temperature-salinity interaction.

I propose that an important consequence of temperature-salinity influence found in the present study is the transfer of biomass and, therefore, energy from the littoral zone to the adjacent channel and ultimately to local offshore areas via migration of fishes. This mechanism for energy transfer was best illustrated by the apparent emigration of a large portion of the 0-age class *A. affinis* from the littoral zone from September to December 1978. The transfer also included the biomass produced by essentially all of the periodic species. Weinstein et al. (1980) reached a similar conclusion in their study of the fishes in shallow marsh habitat of a North Carolina estuary. An extensive mark and recapture study should be planned to test this hypothesis in the future.

Seasonal fluctuations of temperate bay-estuarine fish populations may have several causes, but temperature and salinity seem frequently to be the underlying factors. The pattern of increased number of species and individuals with increased temperature in temperate bays and estuaries has been reviewed by Allen and Horn (1975). Recently the large-scale influence of salinity on bay-estuarine fish populations has been demonstrated by Weinstein et al. (1980) for Cape Fear River Estuary, N.C. Unfortunately, any salinity interaction with temperature was not investigated or discussed in the above study.

Studies of subtropical estuaries (Amezcua-Linares 1977; Warburton 1978; Quinn 1980) indicate that salinity may have greater influence on fish populations, since annual temperature ranges are narrower than in temperate bays and estuaries. In each of the above studies on subtropical estuaries, increased abundances corresponded to the season of low rainfall and therefore high salinity. Blaber and Blaber (1981) concluded that turbidity and not temperature and salinity was the single most important factor to the distribution of juvenile fishes in subtropical Moreton Bay, Queensland. However, Blaber and Blaber (1981) did not present statistical evidence to support this contention. The most important environmental factors influencing tropical estuarine (eelgrass) ichthyofaunas are more difficult to identify (Weinstein and Heck 1979; Robertson 1980) and probably include biotic factors such as prey availability, competitors, predators, as well as abiotic factors. Biotic interactions are undoubtedly important in temperate estuarine systems including upper Newport Bay. However, their overall influence on the system is probably swamped by large fluctuations in the physical environment.

Fluctuations in rainfall and temperature regimes during a year and from year to year can have marked effects on the ichthyofauna of estuaries. Moore (1978) has identified long-term (1966-73) fluctuations in summer fish populations in Aransas Bay, Tex. He found that diversity values (H' range of 1.38-2.13) were quite variable from year to year probably as a result of major climatological changes (an unusually wet year; a drought and two hurricanes). These changes in diversity values were probably caused by changes in abundance within a set of resident estuarine species and of periodic species.

In 1978 the ichthyofauna of upper Newport Bay was subjected to rainfall twice that of a "normal" year (70.9 cm for 1978; mean 28.1 cm). The specific effects of this increased precipitation are difficult to assess due to a lack of data from previous years but some guarded comparisons can be made. Population densities of *Atherinops affinis* were lower in 1974-75 than those encountered during 1978 (Allen 1976). Also *Cymatogaster aggregata, Clevelandia ios*, and *Leptocottus armatus* occurred in lower numbers in 1978 than in previous years (Horn and Allen 1981). These discrepancies point out the strong year-to-year fluctuations that occur in the fish populations of upper Newport Bay. This conclusion is in complete agreement with the findings of Moore (1978) and sheds doubt on the possibility of completely characterizing a "normal" year in many estuaries because of unpredictable annual variations in climate.

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