

# LONG-TERM FLUCTUATIONS OF EPIBENTHIC FISH AND INVERTEBRATE POPULATIONS IN APALACHICOLA BAY, FLORIDA

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## ABSTRACT

A 3-yr study was made concerning seasonal changes in the biota of Apalachicola Bay. The Apalachicola River causes a temporal progression of changes of various environmental parameters in the bay such as salinity, turbidity, nutrients, and detritus levels. Fishes were more widespread in their distribution throughout the bay than invertebrates. This was thought to be related to trophic response and habitat preference. High levels of relative dominance prevailed for both groups with the top three species of each group accounting for more than 80% of the total number of individuals taken.

Peak levels of monthly abundance of various dominant fish species tended not to overlap through a given 12-mo period. Invertebrate species abundance usually reached peak levels during summer and fall periods. The seasonal appearance and distribution of organisms in the Apalachicola Bay system was comparable to that found in other estuaries in the northern Gulf of Mexico. The temporal and spatial distribution of estuarine fishes and invertebrates was associated with species-specific reproductive cycles, trophic relationships, and habitat preferences. The Apalachicola estuary was viewed as a seasonally stable system, with regular temporal fluctuations of the biota through each annual cycle.

There is a rapidly growing literature concerning fluctuations of populations of epibenthic estuarine organisms (Dahlberg and Odum 1970; Bechtel and Copeland 1970; Copeland and Bechtel 1971; McErlean et al. 1973; Oviatt and Nixon 1973; Copeland and Bechtel 1974; Gallaway and Strawn 1974; Livingston 1975). Haedrich and Haedrich (1974) noted that seasonal changes of fish populations in a Massachusetts estuary allow more species to utilize the estuary than if there were constant direct competition. Staggered reproductive cycles were postulated as a partial explanation for this "dynamic situation." Trophic variability was also considered a mechanism for reduced competition. Copeland and Bechtel (1974) identified key environmental requirements for six Gulf coast species, and considered such limits as potential criteria for estuarine management programs. Oviatt and Nixon (1973) noted that although fish biomass remained constant throughout the year, individual species abundance varied seasonally. They found that biomass and numbers of individuals could not be accounted for on the basis of physical

parameters alone, and it was considered that biological functions such as competition and predation could be more important determinants of species distribution in estuarine systems.

The present study is part of a comprehensive field program in Apalachicola Bay, Fla. (Livingston et al. 1974). This is a relatively unpolluted, shallow coastal estuary bounded by barrier islands. The bay is physically dominated by the Apalachicola River (Estabrook 1973; Livingston et al. 1974). This paper is concerned with long-term, seasonal fluctuations of epibenthic fish and invertebrate populations, and the possible interrelationships of the physicochemical and biological elements of the Apalachicola Bay system.

## MATERIALS AND METHODS

### Field Operations

A detailed description of the sampling methodology is already available (Estabrook 1973; Livingston et al. 1974). Physicochemical and biological samples were taken monthly from March 1972 to February 1975 at a series of stations in East Bay and Apalachicola Bay (Figure 1). Water samples were taken at the surface and

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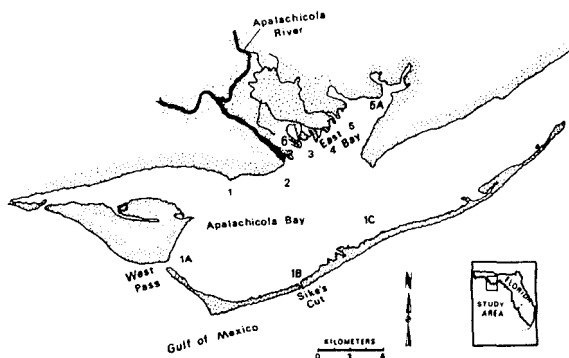


FIGURE 1.—The Apalachicola Bay system with permanent sampling stations for long-term studies concerning fluctuations of populations of epibenthic fishes and invertebrates.

bottom with a 1-liter Kemmerer bottle. Temperature was measured with a stick thermometer and/or a YSI<sup>2</sup> dissolved oxygen meter. Salinity was determined with a temperature-compensated refractometer periodically calibrated with standard seawater. Color was measured with a (Hach) American Public Health Association platinum-cobalt standard test while turbidity was determined with a Hach model 2100A turbidimeter. Light penetration readings were taken with a standard Secchi disk. River flow data were provided by the U.S. Army Corps of Engineers (Mobile, Ala.) while local climatological information was provided by the Environmental Data Service, NOAA, U.S. Department of Commerce.

Biological collections were made with 5-m (16-foot) otter trawls (¾-inch mesh wing and body; ¼-inch mesh liner). Repetitive, 2-min trawl tows were taken at each station at speeds of 2-3 knots. Seven subsamples were taken at stations 1, 2, 4, 5, and 6 while two samples were taken at stations 1A, 1B, 1C, 3, and 5A. All organisms were preserved in 10% Formalin, sorted and identified to species, measured and/or counted (standard length for fishes; total length for shrimps; carapace width for blue crab, *Callinectes sapidus*). Stations 1 and 4 were also sampled at night, approximately 1-2 h after sunset for the first 2 yr of the study.

All statistical analysis was carried out using an interactive computer program designed for the study of extensive data collections. The extent of

interstation community similarity was tested using the  $C_\lambda$  index of overlap (Morisita 1959; Horn 1966). This index determines the probability that two randomly drawn samples from populations  $X$  and  $Y$  will be the same species relative to the probability that two individuals of the same species will be drawn from population  $X$  or  $Y$  alone.

$$\lambda_x = \frac{\sum_{i=1}^S x_i^2}{X^2} \quad \lambda_y = \frac{\sum_{i=1}^S y_i^2}{Y^2}$$

$$C_\lambda = \frac{2 \sum_{i=1}^S x_i y_i}{(\lambda_x + \lambda_y) XY}$$

where

- $S$  = number of species
- $x_i$  and  $y_i$  = number of individuals of the  $i$ th species in populations  $X$  and  $Y$
- $X$  and  $Y$  = total number of individuals in the two communities
- $\lambda_x$  and  $\lambda_y$  = measures of diversity (Simpson 1949) as modified for sampling with replacement (Horn 1966).

Values for this index range from 0 (no species in common) to 1. A hierarchical (stepwise) multiple regression analysis was carried out using monthly population size as the dependent variable. Various physicochemical and biological parameters (temperature, salinity, chlorophyll  $a$ , turbidity, color, Secchi disk depth, total depth, local rainfall, wind speed and direction, tidal stage, river flow, and dissolved oxygen) were used as the independent variables. All such functions were tested in the same month of collection and with a 1-mo lag in the physicochemical parameters. Due to the relatively high number of independent variables, the stepwise regression was used whereby one variable at a time was systematically introduced into the equation, and, at each step, the variable added was the one giving the greatest increase in the multiple correlation coefficient. While not necessarily giving the "best" equation, this method is computationally feasible, and frequently gives results comparable to methods that would determine all possible regressions. Since the salinity, color, and turbidity

<sup>2</sup>Yellow Springs Instrument Co. Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

data had skewed distributions, logarithmic transformations were used for such variables to approximate normality.

## RESULTS

### Physicochemical Parameters

Depths of the various stations ranged from 1 to 2.5 m. With the exception of shallow areas, such as station 6, which are characterized by periodically moderate concentrations of widgeon grass, *Ruppia maritima*, East Bay has a silty-sand bottom with little benthic macrophyte development. Stations proximal to river drainage (stations 2-4) are marked by strong currents and seasonally high deposits of allochthonous detritus (leaf litter, branches, etc.). Except for shallow fringing areas, Apalachicola Bay (stations 1, 1A-1C) has little benthic macrophyte development; it is dominated by silty-sand bottom with interspersed oyster bars.

The Apalachicola River is a major determinant of the physical environment of the bay system. There is a seasonal fluctuation in flow with peak levels occurring during winter and spring months. Local rainfall, with peaks during late summer and early fall, is out of phase with this pattern. During the present period of study, river flow determined salinity throughout the bay. Mean salinity in East Bay was lower than that in Apalachicola Bay; oligohaline areas (stations 5A, 6) were without measureable salinity from mid-winter to early summer. Outer bay stations had higher salinities; at station 1B, the salinity did not go below 15‰ during the 3-yr study. During periods of increased salinity, the shallow bay system was vertically stratified (Estabrook 1973; Livingston et al. 1974). However, there was little

horizontal or vertical variability in water temperature at any given time. Low temperatures occurred during the winter months. Turbidity levels were relatively high throughout the bay, and were directly related to river flow rates. Color levels reflected both river flow and proximity to land runoff, with elevated levels in East Bay areas during the summer. Although there were various complex physical changes in different areas of the bay due to basin physiography, local runoff, tidal currents, depth, etc., the major habitat features of the Apalachicola Bay system were determined by river conditions.

### Distribution of Fishes and Invertebrates

Similarity coefficients (cumulative, by station) are shown in Table 1. Species such as bay anchovy, *Anchoa mitchilli*; Atlantic croaker, *Micropogon undulatus*; and sand seatrout, *Cynoscion arenarius*, were dominant throughout the sampling area. Others such as scaled sardine, *Harengula pensacolatae*, and Gulf menhaden, *Brevoortia patronus*, were taken primarily in East Bay. High interstation similarity of species assemblages of fishes was noted, although grass bed areas such as station 6 were characterized by higher numbers of species than other (mud-flat) stations. There was increased spatial variability among the invertebrate assemblages. Species such as the blue crab and the penaeid shrimps (*Penaeus setiferus*, *P. duorarum*) were more evenly distributed throughout the system than others. Grass shrimps (*Palaemonetes pugio*, *P. vulgaris*, *P. intermedius*) were more frequently taken in the grass beds of East Bay while the brief squid, *Loliguncula brevis*, was a dominant species in Apalachicola Bay. High levels of species similar-

TABLE 1.— $C_{\lambda}$  values (by station) for invertebrates and fishes taken in the Apalachicola Bay system (March 1972-February 1975).

Station	Station 1			1A	1B	1C	2	3	4		5	5A	6
	Day	Night	Day						Night				
	Invertebrates												
1 day		0.96	0.94	0.79	0.95	0.97	0.80	0.92	0.99	0.94	0.95	0.93	
night	0.63		0.76	0.52	0.95	0.87	0.58	0.77	0.95	0.79	0.83	0.85	
1A	0.85	0.54		0.93	0.84	0.95	0.93	0.96	0.69	0.96	0.97	0.80	
1B	0.36	0.29	0.22		0.65	0.84	0.94	0.88	0.73	0.98	0.87	0.91	
1C	0.57	0.46	0.86	0.91		0.94	0.67	0.84	0.95	0.89	0.90	0.78	
2	0.82	0.34	0.58	0.22	0.23		0.85	0.94	0.96	0.95	0.97	0.94	
3	0.68	0.53	0.50	0.15	0.31	0.49		0.95	0.78	0.95	0.91	0.84	
4 day	0.96	0.54	0.73	0.20	0.38	0.92	0.68		0.91	0.99	0.98	0.92	
night	0.87	0.90	0.69	0.24	0.69	0.62	0.69	0.82		0.93	0.94	0.93	
5	0.74	0.25	0.53	0.10	0.19	0.98	0.41	0.85	0.50		0.98	0.92	
5A	0.84	0.36	0.58	0.09	0.58	0.97	0.54	0.94	0.64	0.97			
6	0.23	0.20	0.16	0.06	0.09	0.16	0.79	0.28	0.25	0.17	0.21		

ity were noted among river-dominated and East Bay stations (1, 2, 4, 5, 5A); outer bay stations (1A, 1B, 1C) also were somewhat alike according to the  $C_{\lambda}$  similarity analysis. Station 6, as a grass-bed area, differed from most of the other collections. Station 1B, with consistently higher salinity than the other stations, differed in terms of invertebrate species composition. These data indicate that fishes are more widespread in their distribution throughout the bay system than the invertebrates, which were more habitat-specific with respect to substrate, salinity, etc.

### Seasonal Fluctuations of Dominant Species

Comparative dominance figures for the 10 most numerous fish and invertebrate species are given in Table 2. Relative dominance is high in both groups with the top three species of fishes and invertebrates constituting 77.0 and 80.7% of the respective combined totals. Some species such as *H. pensacolae*, *B. patronus*, and Atlantic threadfin, *Polydactylus octonemus*, were found during limited periods (April 1973, April 1974, and May-August 1973, respectively). Seasonal variations in the six dominant species are shown in Figure 2. The most conspicuous species was *A. mitchilli*, which was particularly abundant during the first year of study. Peaks of numbers usually occurred during fall or early winter (October-January). With *M. undulatus*, peak levels usually were noted during late winter or early spring (February-March) whereas *C. arenarius* reached abundance during late spring and summer months (usually around August). The sea catfish, *Arius felis*, usually peaked by midsummer (July) while Atlantic bumper, *Chloroscombrus chrysurus*, and southern kingfish, *Menticirrhus americanus*, were prevalent

TABLE 2.—The 10 dominant species of fishes and invertebrates taken in the Apalachicola Bay system from March 1972 to February 1975. Figures are expressed in percentages of total numbers of individuals.

Fish	%	Invertebrate	%
<i>Anchoa mitchilli</i>	42.3	<i>Penaeus setiferus</i>	40.1
<i>Micropogon undulatus</i>	26.0	<i>Palaemonetes pugio</i>	20.4
<i>Cynoscion arenarius</i>	8.7	<i>Callinectes sapidus</i>	20.2
<i>Leiostomus xanthurus</i>	5.4	<i>Penaeus duorarum</i>	5.3
<i>Harengula pensacolae</i>	2.6	<i>Lolliguncula brevis</i>	4.3
<i>Bairdiella chrysura</i>	1.6	<i>Penaeus aztecus</i>	2.6
<i>Chloroscombrus chrysurus</i>	1.5	<i>Neritina reclinata</i>	1.5
<i>Polydactylus octonemus</i>	1.4	<i>Portunus gibbesii</i>	1.1
<i>Arius felis</i>	1.3	<i>Palaemonetes vulgaris</i>	0.8
<i>Brevoortia patronus</i>	1.2	<i>Rhithropanopeus harrisi</i>	0.5

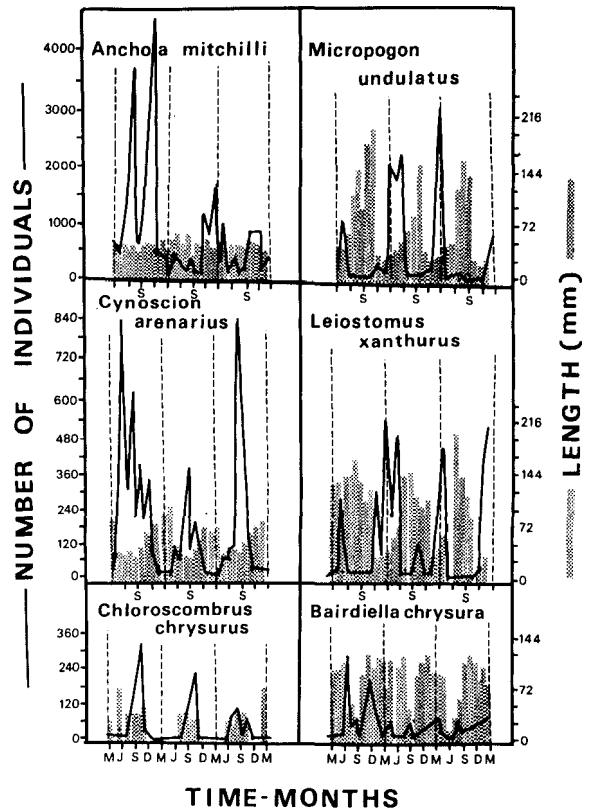


FIGURE 2.—Seasonal changes of numbers of individuals and mean size of six dominant species of fishes taken in the Apalachicola Bay system from March 1972 to February 1975.

during late summer or early fall (August-October). The spot, *Leiostomus xanthurus*, usually peaked during winter and spring months; silver perch, *Bairdiella chrysura*, had a variable abundance curve. Overall, there was considerable regularity in the appearance of the dominant bay fishes even though there was often a marked within-species variation in total numbers from year to year.

Annual fluctuations of the dominant invertebrate species are shown in Figure 3. The white shrimp, *Penaeus setiferus*, was prevalent from August to November with autumn peaks of abundance; the other penaeids usually reached high numbers in the late spring (*P. aztecus*) or late summer (*P. duorarum*). *Palaemonetes pugio* was usually found in the bay during spring months (March-May) while *P. vulgaris* reached high numbers in November. The blue crab peaked during summer and winter periods. Early summer and fall peaks were noted for *Lolliguncula*

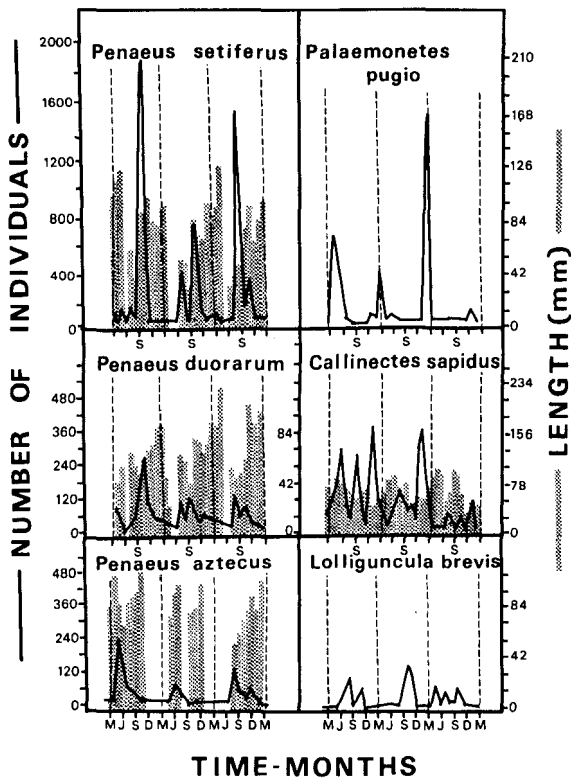


FIGURE 3.—Seasonal changes of numbers of individuals and mean size of six dominant species of invertebrates taken in the Apalachicola Bay system from March 1972 to February 1975 (*Palaemonetes pugio* and *Lolliguncula brevis* were not measured).

*brevis*. Unlike the fishes which usually reached peak levels during different months of the year, the invertebrates tended to increase in numbers during spring and fall periods.

Annual peaks of abundance often coincided with influxes of juvenile fishes and invertebrates. A more detailed analysis of this is shown for two representative species of fishes (Figure 4) and invertebrates (Figure 5). The young stages of *Micropogon undulatus* entered the bay during the winter at which time there was a continuous recruitment for several months. Decreased numbers coincided with gradual increases in size during spring and summer months. With *Cynoscion arenarius*, recruitment of young occurred during spring and summer, with subsequent increases in size during fall and winter months. The blue crab had peaks of young individuals during summer and winter periods although an almost continuous succession of young crabs entered the bay during the year. Young stages of *Penaeus*

*setiferus* were found during the summer with growth occurring through fall and winter. The other penaeid shrimps had similar growth patterns with recruitment of the young during summer and fall periods. The data indicate that various patterns of recruitment and growth occur among the different estuarine species, although the inverse relationship of numbers and size appears to hold for most of the dominants.

Results of the regression analysis are shown in Table 3. Factors such as chlorophyll *a*, Secchi disk readings, and color repeatedly accounted for some of the variability associated with fluctuations of estuarine populations. Often such associations were made with a 1-mo lag in the independent variable. In most cases, the given independent variables accounted for less than 50% of the variability of the population data. There was a distinct correlation with factors related to trophic phenomena such as chlorophyll *a* and Secchi disk readings; this would indicate that biological functions such as feeding behavior and reproduction could play an important role in the determination of population shifts in the Apalachicola Bay system. These data indicate that no single set of forcing functions can account for the population changes of various estuarine species. Species abundance is dependent on complexes of interactions and possibly can be accounted for more adequately by relating such processes to dynamic changes in physical variables as well as important biological parameters. It is obvious that regression analysis cannot account for changes in

TABLE 3.—Results of the stepwise regression analysis of various independent parameters and species (population) occurrence in the Apalachicola Bay system from March 1972 to February 1975. Independent variables are listed by order of importance with  $R^2$  expressed as a cumulative function of the given parameters.

Species	Independent variables	$R^2$
<i>Anchoa mitchilli</i>	Chlorophyll <i>a</i> , Secchi	0.38
<i>Micropogon undulatus</i>	River flow (lag), Secchi (lag)	0.46
<i>Cynoscion arenarius</i>	Chlorophyll <i>a</i> , wind, Secchi (lag), temp	0.83
<i>Polydactylus octonemus</i>	Chlorophyll <i>a</i> (lag), salinity, Secchi	0.58
<i>Arius felis</i>	Temp, wind	0.30
<i>Leiostomus xanthurus</i>	Turbidity (lag), Secchi, salinity, temp	0.85
<i>Chloroscombrus chrysurus</i>	Temp (lag), temp, salinity	0.44
<i>Menticirrhus americanus</i>	Temp (lag)	0.19
<i>Symphurus plagiatus</i>	Color (lag), color, Secchi	0.63
<i>Bairdiella chrysura</i>	Wind, temp, color	0.40
<i>Penaeus setiferus</i>	Wind, chlorophyll <i>a</i> , incoming tide, color	0.48
<i>Palaemonetes pugio</i>	Turbidity	0.36
<i>Callinectes sapidus</i>	Secchi, incoming tide	0.49
<i>Penaeus duorarum</i>	Chlorophyll <i>a</i> , Secchi	0.41
<i>Lolliguncula brevis</i>	Chlorophyll <i>a</i> (lag), temp	0.43
<i>Portunus gibbesii</i>	Chlorophyll <i>a</i> (lag), Secchi	0.39
<i>Palaemonetes vulgaris</i>	Turbidity	0.32
<i>Rhithropanopeus harrisi</i>	Wind	0.18
<i>Callinectes similis</i>	Chlorophyll <i>a</i> , temp	0.34

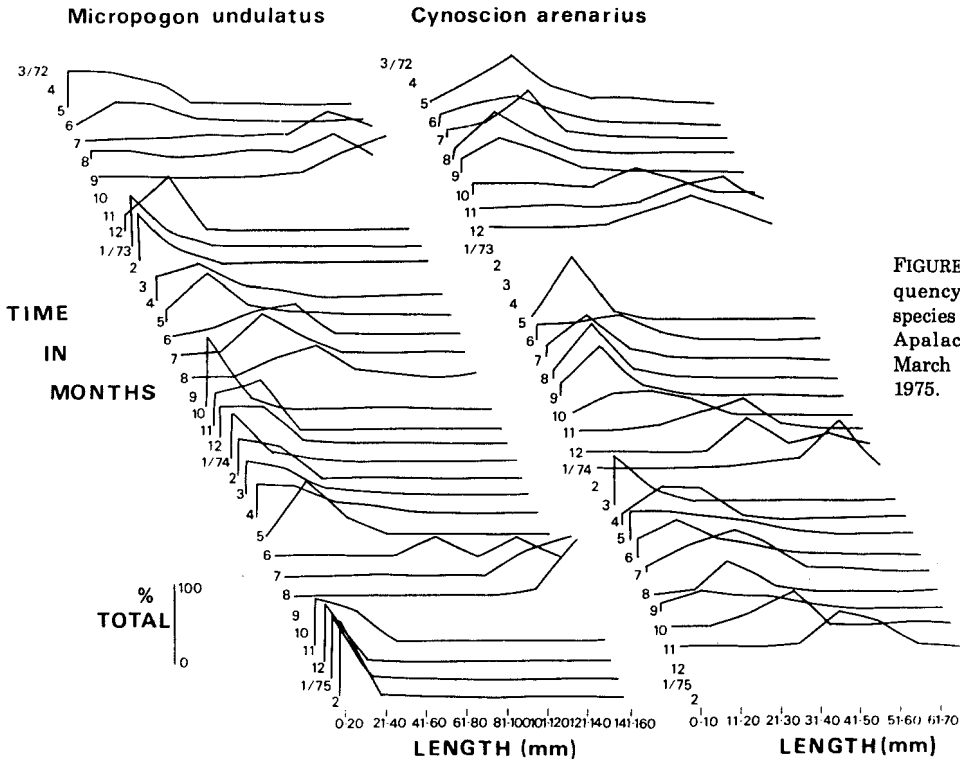


FIGURE 4.—Monthly size-frequency distribution of two species of fishes taken in the Apalachicola estuary from March 1972 through February 1975.

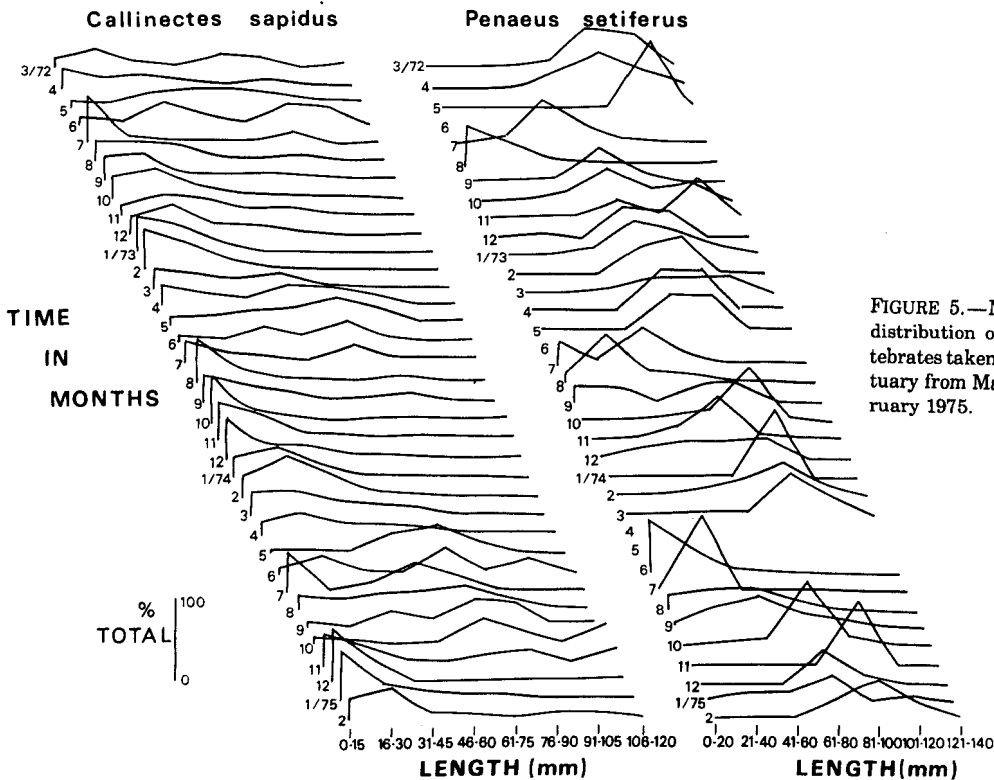


FIGURE 5.—Monthly size-frequency distribution of two species of invertebrates taken in the Apalachicola estuary from March 1972 through February 1975.

the adaptive response of populations to the extremely complex environment of the estuary. The data indicate that, in this case, temperature and salinity might not be as critical in the determination of seasonal fluctuations of estuarine populations as biological functions such as trophic response and possibly reproduction.

## DISCUSSION

A review of the literature (Gunter 1945, 1950; Daugherty 1952; Reid 1955; Van Engel 1958; Gunter and Hall 1965; Williams 1965; Tagatz 1968; More 1969; Pérez Farfante 1969; King 1971; Lyons et al. 1971; Swingle 1971; Perret and Caillouet 1974; Stokes 1974; Swingle and Bland 1974) confirms that although minor variations were evident (notably among the fishes), there was a generally high level of conformity concerning the time of appearance of various dominants in the Apalachicola estuary with previously recorded data from other northern Gulf areas. Although such timing was essentially stable from year to year, there was considerable within-species variability in annual abundance. For example, the bay anchovy was particularly dominant during the summer and fall of 1972, while fewer individuals were taken during the succeeding 2 yr. The Atlantic bumper, although not considered a common Gulf species (Perret and Caillouet 1974), was relatively common in the Apalachicola estuary, especially during the first year of collection. Some species reflected particular habitat preferences: *Palaemonetes pugio* was located primarily in grass-bed areas of East Bay during periods of low salinity while *L. brevis* was found in outer bay areas during summer and fall periods of increased salinity. Although generalized temperature and salinity preferences have been shown for various estuarine species (Copeland and Bechtel 1974), as a whole these organisms show a wide tolerance for short-term changes in these parameters. This could help to explain the general lack of importance of temperature and salinity as critical variables in the multiple regression analysis; quite obviously, other functions such as acclimatization would tend to complicate such a direct approach to determination of causative agents. The multiple regression technique was limited in its application to causal relationships since various biological functions are probably involved in the determination of a given population curve.

It is possible that trophic relationships and reproductive cycles are of critical importance in the spatial and temporal distribution of estuarine populations. As in other Gulf estuaries, the Apalachicola Bay system is dominated by juvenile stages of a small number of species. The bay anchovy, abundant in a size range of 35-50 mm, is considered to be a generalized zooplanktivore at this stage, feeding in the water column on copepods, amphipods, mysids, larval and juvenile shrimps and fishes, etc. (Darnell 1958; Odum and Heald 1972; Carr and Adams 1973). Various studies (Roelofs 1954; Darnell 1958; Fontenot and Rogillio 1970) indicate that *M. undulatus* (juveniles, 10-50 mm) feeds primarily on zooplankton (copepods and amphipods) while *C. arenarius* (juveniles, 40-99 mm) consumes larger zooplanktors such as mysids, shrimp, and larval or juvenile fishes (Darnell 1958; Springer and Woodburn 1960). Juvenile (up to 40 mm) spot also feed on zooplankton; more mature fish of this species (40-200 mm) become benthic omnivores (Roelofs 1954; Darnell 1958; Springer and Woodburn 1960). Juvenile *B. chrysura* (16-160 mm) feed on copepods, mysids, shrimp, and small fishes (Darnell 1958; Carr and Adams 1973). Thus, the dominant fishes in the Apalachicola Bay system are primarily planktivorous although possible differences could exist in vertical feeding distribution and the size and species composition of the prey organisms. Previous work has shown that *Anchoa mitchilli* feeds on small crustaceans and *C. arenarius* eats the larger, more motile crustaceans. Both *Leiostomus xanthurus* and *B. chrysura* feed on small mid-water planktors (mainly copepods) as early juveniles, with later stages becoming benthic omnivores feeding largely on mysids and shrimp. Increased concentrations of zooplankton occur in Apalachicola Bay during the spring and summer while palaemonetid shrimp are abundant during winter and early spring (H. L. Edmiston pers. commun.). Thus, diversity in feeding behavior would contribute to the observed vertical partitioning of prey organisms among various planktivorous species; such data are consistent with the observed distribution of fishes in Apalachicola Bay at any given period of time.

Of the six most prevalent invertebrates in the Apalachicola estuary, five are benthic omnivores and one is a probable planktivore. Juvenile blue crabs consume detritus while larger individuals (20-200 mm) are omnivorous, feeding on detritus

and plant material, mollusks, polychaetes, crustaceans, and fishes (Darnell 1959; Tagatz 1968; Odum and Heald 1972). Penaeid shrimp are also omnivores, feeding on similar forms (Williams 1965; Darnell 1958; Eldred et al. 1961; Odum and Heald 1972). *Palaemonetes pugio* feeds primarily on detritus (Adams and Angelovic 1970; Oviatt and Nixon 1973; Welch 1975). Qualitative observations indicate that *Lolliguncula brevis* is a planktivore (Dragovitch and Kelly 1967). Thus, most of the epibenthic invertebrates utilize detritus and are more closely associated with sediment type, benthic macrophyte distribution, and placement of allochthonous forms of detritus than the planktivorous fishes; this, together with certain (species-specific) temperature and salinity tolerances, could provide a partial explanation for the observed differences in the spatial distribution of the fishes and invertebrates.

Another important evolutionary mechanism for the partitioning of the energy resources of an estuary is the temporal succession of species over an annual cycle. Abundance interrelationships expressed as percentage of total catch are shown in Figure 6. There was a certain regularity of percent representation of dominant species of fishes and invertebrates in the Apalachicola system. For example, relative occurrence of *P. pugio* was high during spring months while *Penaeus setiferus* was dominant during late summer and fall. The blue crab was abundant during winter periods. Among the fishes, *C. arenarius* was dominant during the spring and summer while *A. mitchilli* (after the first year of sampling) predominated in the fall and *M. undulatus* prevailed during the late winter and spring. When a comparison was made among the 10 most dominant species of fishes for peaks of abundance, such increases were evenly distributed over a 12-month period. However, of the top 10 species of invertebrates, most peaks of abundance occurred during fall periods (September-November) with secondary concentrations of peaks during early summer (May-June). Livingston (in press), describing patterns of species richness and diversity in Apalachicola Bay, noted that there was an annual double peak in fish and invertebrate diversity although there was far more seasonal variability in *N* (numbers of individuals) and *S* (numbers of species) among fishes than invertebrates. These data would tend to corroborate and elucidate such findings. Thus, although the top dominants in both groups showed distinct temporal

sequences in relative peak abundance, there was a tendency for increased numbers of invertebrate species during summer and fall periods whereas peaks of *N* and *S* for fishes were more continuously distributed throughout the year. Major dominants for both fishes and invertebrates thus showed temporal partitioning through an annual cycle. The noted differences in temporal distributional patterns of fishes and invertebrates could be related to trophic response, with the planktivorous fishes competing for a more limited resource than the omnivorous (detritivore and omnivore) invertebrate species.

Several conclusions can be made with regard to the biotic component in the Apalachicola estuary. Various independent ecological factors operate to determine the spatial and temporal distributions of such organisms. Biological functions, as adaptive responses to the physical and trophic environment, determine such distributional patterns, allowing a somewhat orderly temporal succession of dominant forms within certain broad trophic spectra. Patterns of reproduction of various dominant estuarine species have evolved in such a way as to permit such long-term partitioning of the estuarine environment. Superimposed on this are certain in situ mechanisms whereby further resource division occurs due to vertical and horizontal distribution of the component species. This is largely determined by various microhabitat phenomena such as salinity, bottom type, currents, availability of detritus, etc. In addition, biological determinants such as intraspecific competition and predation further modify the individual component populations. Thus, no single parameter prevails in the determination of the community structure of an estuary which undergoes predictable seasonal changes even though it is a physically forced system. Although there is considerable short-term fluctuation in the numbers of individuals of various populations, the system maintains a certain temporal constancy which, according to a traditional view of such phenomena, could be termed stability. This does not mean that such a system is not in a constantly transient state; on the contrary, through various natural and unnatural mechanisms such as habitat alteration and destruction, hurricanes, etc., the various population equilibria can be shifted so that the system is no longer characterized by a stable temporal succession of energy utilization. Each population fluctuates around a certain point of equilibrium; such fluctuations are



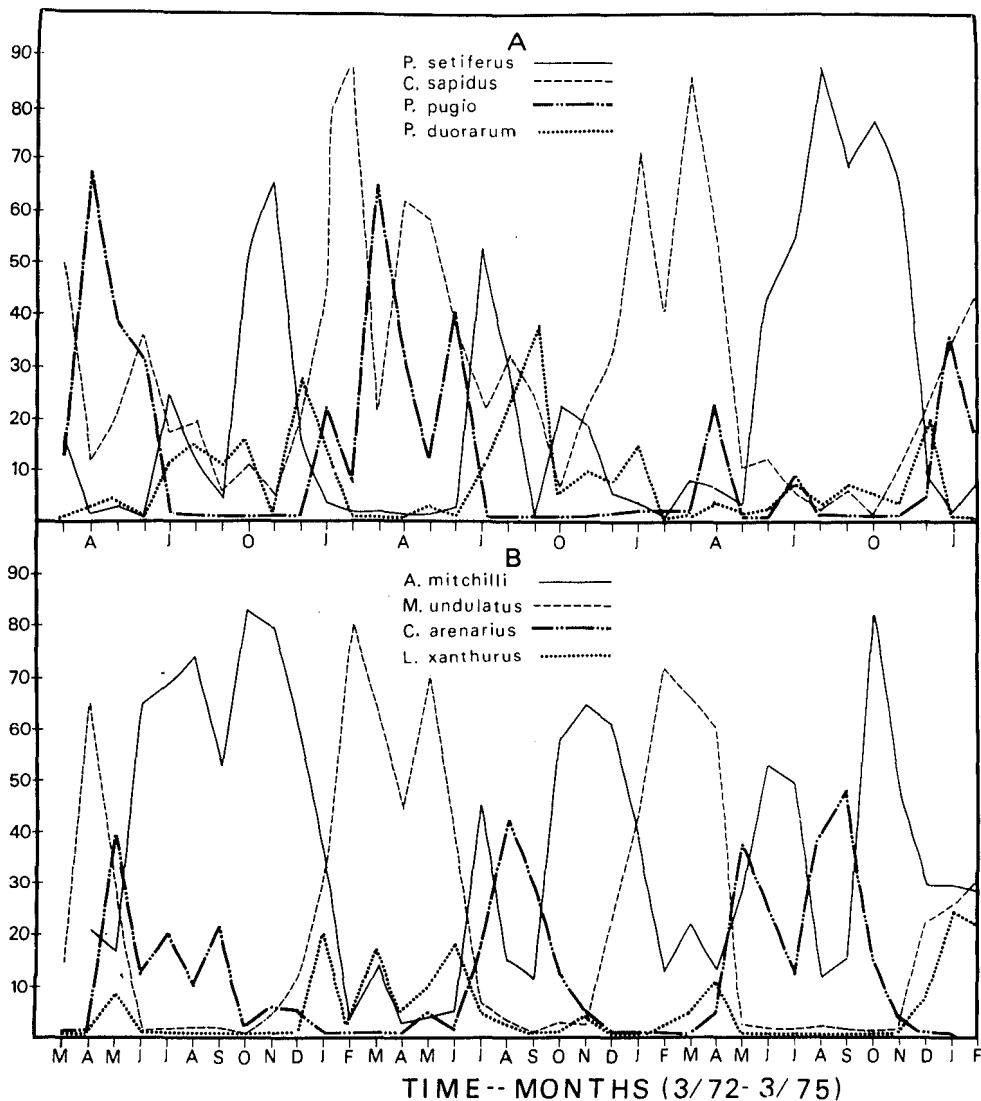


FIGURE 6.—Relative importance (% of total) of four dominant species of invertebrates and fishes taken in the Apalachicola Bay system from March 1972 through February 1975. Such species represent 82.4 and 86.0% of the respective 3-yr totals.

determined by various natural and man-induced phenomena such as overfishing and pollution. The stability of the system depends on the maintenance of various populations within certain limits of fluctuation. This has serious implications for any estuarine management program. Holling (1973) pointed out that instability (in the sense of large fluctuations) of individual populations may actually introduce a capacity for persistence or resilience. Such resilience can be attributed not only to component populations but to

the system as a whole. Stability thus is seen as the "ability of a system to return to an equilibrium state after a temporary disturbance," (Holling 1973). Resilience, however, is a measure of the ability of a given system to absorb changes of primary forcing functions and still persist. By this measure, an estuarine system such as Apalachicola Bay comprises various populations which undergo considerable annual fluctuations but nevertheless are maintained within a relatively stable temporal succession.

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