

# LIFE HISTORY, FEEDING HABITS, AND FUNCTIONAL MORPHOLOGY OF JUVENILE SCIAENID FISHES IN THE YORK RIVER ESTUARY, VIRGINIA<sup>1,2</sup>

LABBISH N. CHAO<sup>3</sup> AND JOHN A. MUSICK<sup>4</sup>

## ABSTRACT

Four abundant sciaenid fishes, *Cynoscion regalis*, *Bairdiella chrysoura*, *Micropogonias undulatus*, and *Leiostomus xanthurus*, use the York River, Va., as a nursery ground and as an adult seasonal feeding ground. In addition, six species of sciaenids, *Menticirrhus saxatilis*, *M. americanus*, *Sciaenops ocellata*, *Cynoscion nebulosus*, *Pogonias cromis*, and *Larimus fasciatus*, are present in the estuary occasionally. Yearling *C. regalis* were first caught in April and young-of-the-year in July or August. Yearling *B. chrysoura* were first caught in March or April and young-of-the-year in July or August. Juvenile *Micropogonias undulatus* and *Leiostomus xanthurus* may be present in the York River all year-round. Young-of-the-year *L. xanthurus* were first caught in April and *M. undulatus* were first caught in August. Small *M. undulatus* (<20 mm TL) were caught from August to June, which may indicate a prolonged spawning season (or a late spawning stock). Emigration to the ocean was found in all the four species during late fall or early winter. Water temperature and dissolved oxygen seemed to be the most important factors in the spatial and temporal distributions of these four species in the York River.

Mouth position, dentition, gill rakers, digestive tract, pores and barbels, nares, and body shape of six sciaenid species, *Larimus fasciatus*, *C. regalis*, *B. chrysoura*, *M. undulatus*, *Menticirrhus saxatilis*, and *Leiostomus xanthurus*, were found to be important in locating and ingesting prey in the water column. Stomach contents indicated that the food partitioning of these six species was closely correlated with the species and their prey habitat. *Larimus fasciatus*, *C. regalis*, and *B. chrysoura* fed mainly above the bottom, whereas *Micropogonias undulatus*, *Menticirrhus saxatilis*, and *L. xanthurus* fed on epifauna, infauna, or both. Juvenile sciaenids are able to coexist in the same area because of differences in spatial and temporal distribution, relative abundance, and food habits.

Sciaenid fishes are among the most important in-shore bottom fishery resources of the Atlantic and Gulf of Mexico coasts of the United States (Roithmayr 1965; Joseph 1972; Gutherz et al. 1975). Sciaenid fishes usually use the estuary as a nursery ground and seasonal feeding ground. Among the 14 species of sciaenids recorded from Chesapeake Bay proper (Musick 1972), young-of-the-year of 10 species were caught in the York River system during this study. *Leiostomus xanthurus*, *Micropogonias undulatus*, *Bairdiella chrysoura*, and *Cynoscion regalis* were the most abundant species. *Menticirrhus saxatilis*, *M. americanus*, *Sciaenops ocellata*, *C. nebulosus*,

*Pogonias cromis*, and *Larimus fasciatus* were caught only occasionally.

Juvenile sciaenids, except the Atlantic croaker, *Micropogonias undulatus*, usually entered the York River in late spring and left in late fall. During this period, sciaenid fishes dominated bottom trawl catches in the York River (Colvocoresses 1975; Markle 1976). By yearly average, they composed more than 50% of the total catch by weight and 18 to 28% by number of individuals. The purpose of this study is to describe the coexistence of the four most abundant juvenile sciaenids in the York River system, Va., based upon relative abundance, temporal and spatial distribution, length frequency, apparent movements, and feeding habits. Morphological structures related to feeding habits and habitats were also studied. Specimens of the banded drum, *Larimus fasciatus*, and the northern kingfish, *Menticirrhus saxatilis*, were included to show the range of variability in the feeding habits of juvenile sciaenids. Bottom trawl surveys conducted by the Virginia Institute of Marine Science (VIMS) from January 1972 to

<sup>1</sup>A portion of a dissertation submitted to the School of Marine Science, College of William and Mary, Williamsburg, Va., in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Marine Science, by the first author, May 1976.

<sup>2</sup>Contribution No. 816, Virginia Institute of Marine Science, Gloucester Point, Va.

<sup>3</sup>Ichthyology Unit, Vertebrate Zoology Division, National Museum of Natural Sciences, Ottawa, Ontario, Canada K1A 0M8.

<sup>4</sup>Virginia Institute of Marine Science, Gloucester Point, VA 23062.

December 1974 provided the data for analyses of distribution and food habits. An analysis of fish community structure based on this data has been reported by Colvocoresses (1975).

The York River and its major tributaries (Pamunkey and Mattaponi rivers) represent an estuarine system which is relatively well known biologically and is relatively undisturbed (Boesch 1971). The general trend of geomorphology, hydrography (salinity, dissolved oxygen, and temperature), ecology, and alteration by man of the area were described by McHugh (1967), Boesch (1971), and Brehmer.<sup>5</sup>

## MATERIALS AND METHODS

### Survey Programs

Seven longitudinal strata (A, B, C, D, E, F, and G) and three cross-sectional substrata (north shoal, channel, and south shoal) within each stratum were sampled monthly (Figure 1). Shoal hauls were usually in water <4 m and channel hauls in water >5 m deep. Randomly numbered square grids (540 m on a side) were assigned as trawl stations. In the lower 16 km (10 miles) of the York River, strata A, B, C, and D were sampled from March 1972 to December 1974. The upper part of the York River was sampled from January 1972 to March 1974, but the random method was not used until June 1972 and strata E, F, and G were not designated until January 1973. Before the random sampling program, fixed sampling stations in the channel were assigned at 8-km (5-mi) intervals from the mouth of the York River (mile zero) up to 45 km (mile 28, also see Haven 1957; Markle 1976). Data from fixed station samples (January–May 1972) were combined within the strata for analyses. Lower portions of the Mattaponi and Pamunkey rivers (strata: M and P) were sampled after January 1973. Three substrata (1, 2, and 3) were set at 8-km (5-mi) intervals for the lower 24 km (15 mi) upstream from their confluence with the York River (about 45 km from the York River mouth). Each sampling stratum was divided into station grids, each measuring 540 m on a side; four to six grid stations were sampled randomly from each stratum monthly.

<sup>5</sup>Brehmer, M. L. 1970. Biological and chemical studies of Virginia's estuaries. Unpubl. manusc., 120 p. Va. Inst. Mar. Sci., Gloucester Point.

## Gear

Bottom trawl tows were against the current, of 5-min duration on the bottom with a 4.9-m (16-ft) semiballoon otter trawl (7-m rope, 1.9-cm bar mesh, 0.63-cm bar mesh cod end liner), 7-m bridle, and 0.6-m weighted otter doors at a speed of approximately 90 m/min. Nine stations were sampled monthly with beach seines along the shores of lower parts (strata A–D) of the York River (Figure 1) and three replicate hauls were made with a 15.25-m (50-ft) bag seine (1.8 m deep with a square bag, 0.64-cm bar mesh in the wing and 0.48-cm bar mesh in the bag). Thirteen beach seine stations were selected along the shores of the upper part of the York River (strata E–G, Figure 1). These stations were only sampled from July to October in 1972 and 1973 with a 30.5-m (100-ft) bag seine. Beach seine data were used only for length frequency analysis in the present study. Hydrographic (salinity, temperature, and dissolved oxygen) data were collected from both surface and bottom water.

### Sampling Procedure

All fishes were identified, counted, and weighed in the field or laboratory. Total length (TL), measured from snout to the posterior tip of the caudal fin (on the midline), was taken to the nearest millimeter. All individuals of each species were measured from each trawl haul. For very large catches, at least 25 individuals were subsampled. Specimens were randomly selected for stomach analyses and preserved in 10% Formalin;<sup>6</sup> stomachs were dissected out and transferred to 40% isopropanol or 70% ethanol. Stomach contents were identified to the lowest practical taxon and frequency of occurrence of each item was recorded.

The standard methods of Hubbs and Lagler (1964) were used for all counts and measurements, if applicable. Upper and lower jaw lengths were measured from tips of the premaxilla and dentary, respectively, to the symphysis at the posterior corner of the mouth gape. Digestive tracts were removed from the fish. The intestine was straightened and measured from its junction with the stomach to the anus. Osteological observations

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

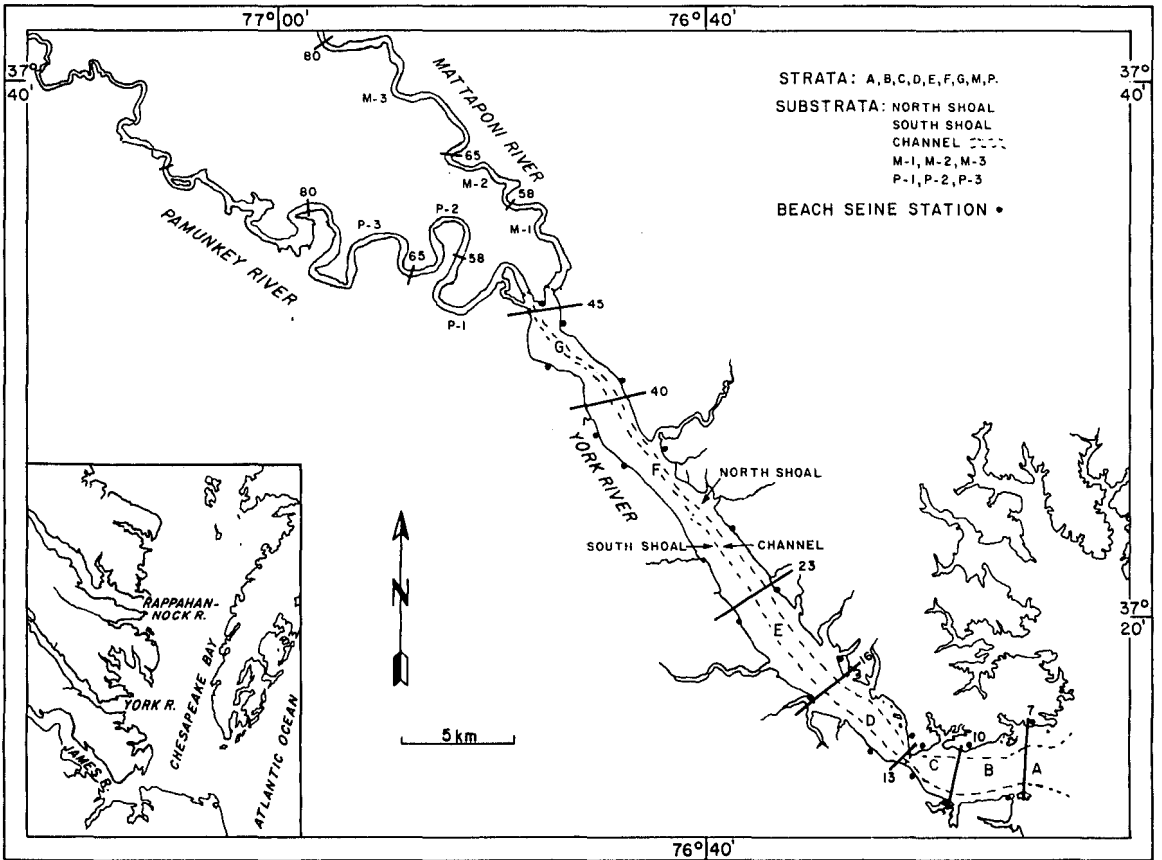


FIGURE 1.—The trawl strata, substrata, and beach seine stations in the York River estuary, Va. Strata: A–G, M, and P. Substrata: north shoal, channel, and south shoal. Substrata in Mattaponi River expressed as M-1, M-2, and M-3, in Pamunkey River as P-1, P-2, and P-3. River distances from the mouth of York River (0 km) are indicated in kilometers.

were made on cleared and stained specimens, according to the methodology of Taylor (1967).

The nomenclature used for the study fishes follows Chao (in press). *Micropogonias* must replace *Micropogon* because the generic name *Micropogon* was preoccupied by Boie (1826 in Aves). The specific name *chrysoura* is used instead of *chrysur* for *Bairdiella* because the spelling *chrysurus* was used by the original author (Lacepède 1803:166).

## RESULTS AND DISCUSSION

### Hydrographic Description

Water depth, temperature, salinity, and dissolved oxygen were measured with each sample and are listed in the appendix section of Chao (1976). The benthic environment was of particular

importance to the present study. Mean values for bottom temperature, salinity, and dissolved oxygen in each stratum from May 1972 to August 1973 are summarized in Figure 2, to show seasonal patterns in the York River estuary.

### Temperature

The bottom water temperature of the York River (Figure 2) was lowest in January and highest in July (1973) or August (1972). The gradual increase of temperature from April to June and the decrease from October to December are most important to migratory fishes in the York River (Markle 1976). In winter months (December–February), the bottom temperature of the upper portion of the York River was lower than that of the lower portion. No apparent differences in temperature were found among the shoal and the

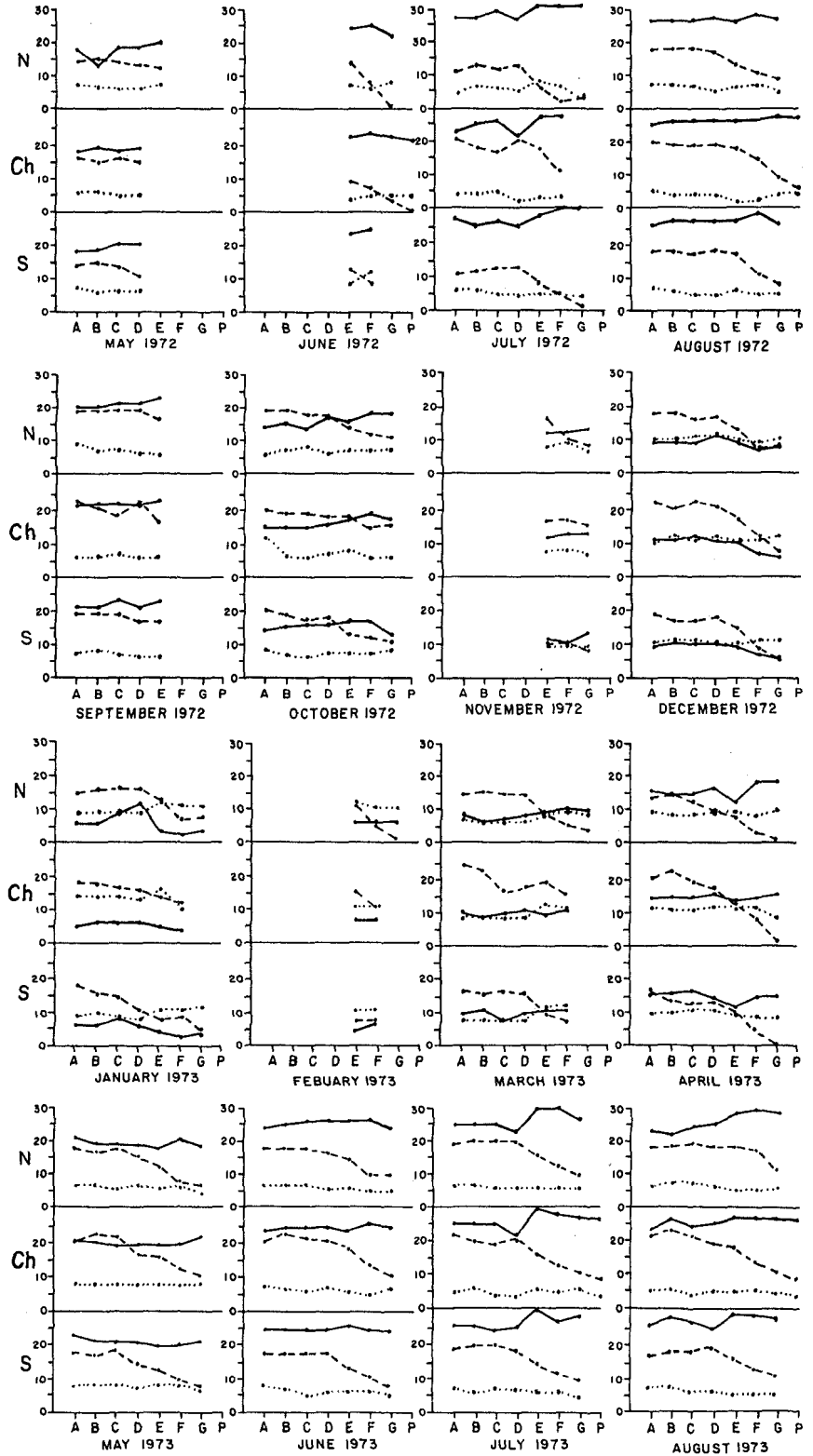


FIGURE 2.—Monthly means of the bottom temperature ( $^{\circ}\text{C}$ —solid line), salinity ( $\text{‰}$ —dashed line), and dissolved oxygen (milligrams/liter—dotted line) in the York River estuary from May 1972 to August 1973. Strata: A–G in York River and P in Pamunkey River. Substrata: N = north shoal, Ch = channel and S = south shoal.

channel stations. In spring months (March–May), bottom temperatures increased rapidly, and the upper portion of the York River had slightly higher temperatures than the lower portion. The shoal stations also showed a slightly higher mean bottom temperature than the channel stations. In summer months (June–August), the bottom temperature of the upper portion of the river was higher than the lower portion. The shoal stations also showed a higher mean bottom temperature than the channel stations. In fall months (September–November), bottom temperature decreased rapidly. The upper portion of the river had slightly higher temperatures than the lower portion in the early fall (September–October). In early winter (December), bottom water temperature was slightly higher in the lower portion of the river (Figure 2). No apparent differences were found among the shoal and channel stations.

#### Dissolved Oxygen

Dissolved oxygen in the York River (Figure 2) was generally lower in warmer months (May–October) and higher in colder months (November–April). In the warmer months, dissolved oxygen was lowest at the deeper channel stations. There was no apparent difference between the upper and lower portions of the York River. In colder months, dissolved oxygen was slightly higher in the upper portion of the river and no apparent difference was found among shoal and channel stations.

#### Salinity

Salinity decreased toward the upper portion of the York River (Figure 2). Lower salinities usually were found in spring (March–May) and winter (December–February). The extremely low salinities of June to August 1972, were caused by hurricane Agnes (Anderson et al. 1973). Salinity at channel stations was usually higher than at shoal stations, especially in the lower portion of the river from March to June.

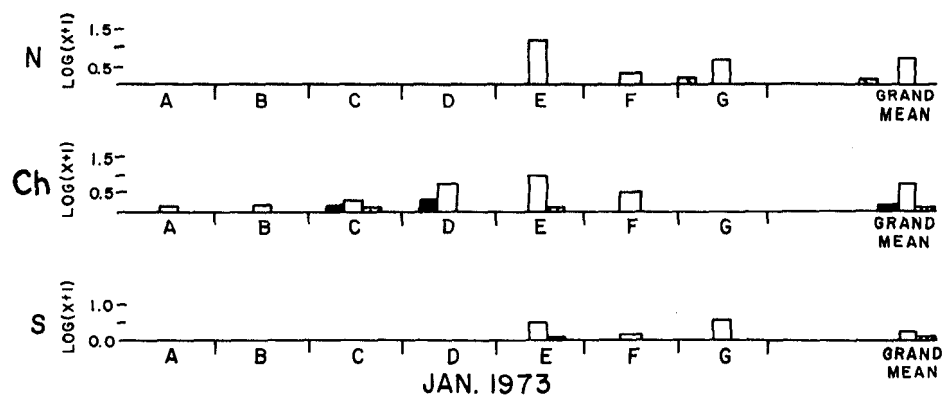
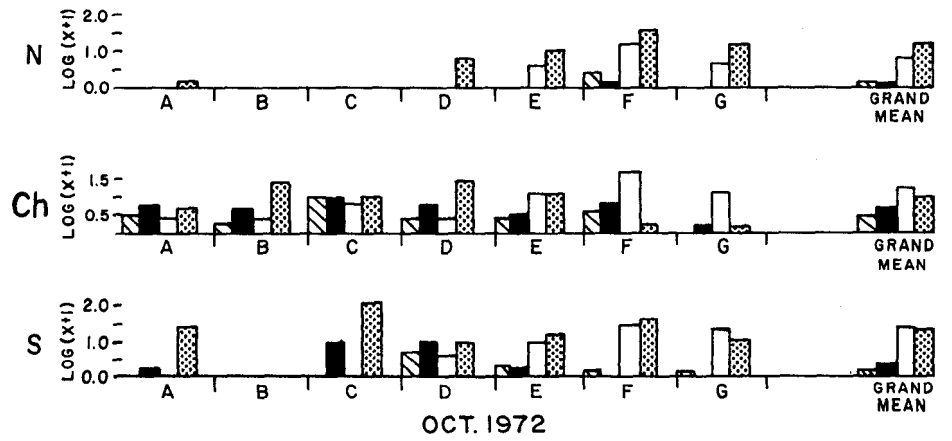
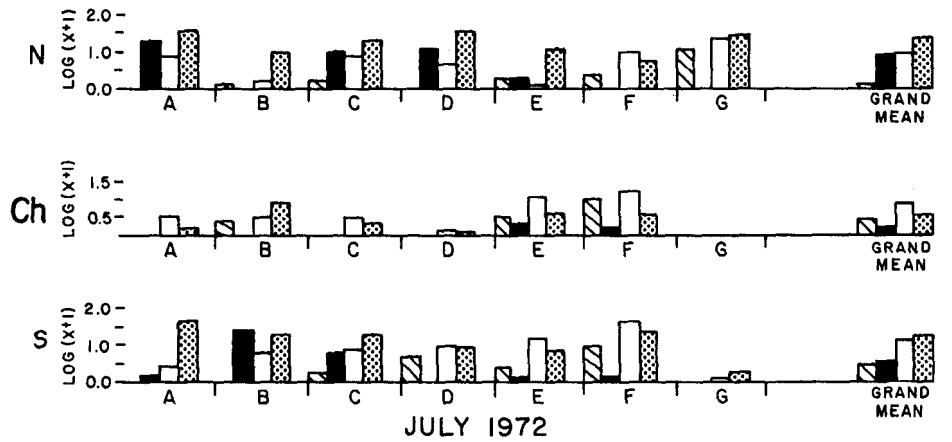
### Temporal and Spatial Distributions

Young sciaenids are among the most abundant migratory finfishes in the York River (Massmann 1962; Colvocoresses 1975; Markle 1976). Temporal and spatial distributions of juveniles of the four most abundant sciaenids, *Cynoscion regalis*,

*Bairdiella chrysoura*, *Micropogonias undulatus*, and *Leiostomus xanthurus*, are compared (Figures 3–5) to determine ecological partitioning during their estuarine life. The relative abundance of each species is expressed by the geometric mean,  $\log_{10}(x + 1)$ , of the individual catches per tow within the substrata, where  $x$  is the mean number of individuals per tow. Four months (July, October, January, and April) were selected to represent the seasonal abundances from different parts of the York River (Figure 3). Monthly mean catches per tow by river distance (stratum) and depth (substratum) were compared (Figures 3–5). Fishes caught in the Mattaponi and Pamunkey rivers were compared only by river distance (Figure 4).

In July 1972 and 1973, all four species of juvenile sciaenids were present in all parts of the estuary except the upper part (Figures 3–5). Relative abundance varied among species (Figure 3). *Bairdiella chrysoura* was more abundant in the lower and middle part of the river, while *C. regalis* and *M. undulatus* were more abundant in the upper part of the river (Figure 5). *Leiostomus xanthurus* was ubiquitous. *Micropogonias undulatus* gradually declined in abundance upstream in both the Mattaponi and Pamunkey rivers (Figures 4, 5). *Leiostomus xanthurus* catches were quite variable in the Pamunkey River. This may have been caused by the contagious distribution of this species. Sciaenids were more abundant in shoal stations (Figure 3) than channel stations, especially in July 1972. Colvocoresses (1975) and Markle (1976) noted a general decline in the mean number of species and individuals of fishes caught per month in the summer from channel stations. This may be attributed to a reduction in the dissolved oxygen concentration, usually below 5 mg/l at the bottom of the channel (Markle 1976; Brehmer see footnote 5), and was apparently the case in the present study (Figure 2). Catches of *C. regalis* did not decline in channel stations, but this species is the best adapted for pelagic life of the four species studied (see "Correlation of Feeding Structures and Food Habits" section), and may have been captured in midwater where dissolved oxygen values did not decline.

In October (1972, 1973) juveniles of all four species of sciaenids were present in all parts of the estuary (Figure 3) and all reached their highest total abundance (Markle 1976). *Cynoscion regalis* was more abundant in the lower parts of the York River; *B. chrysoura* and *L. xanthurus* were more



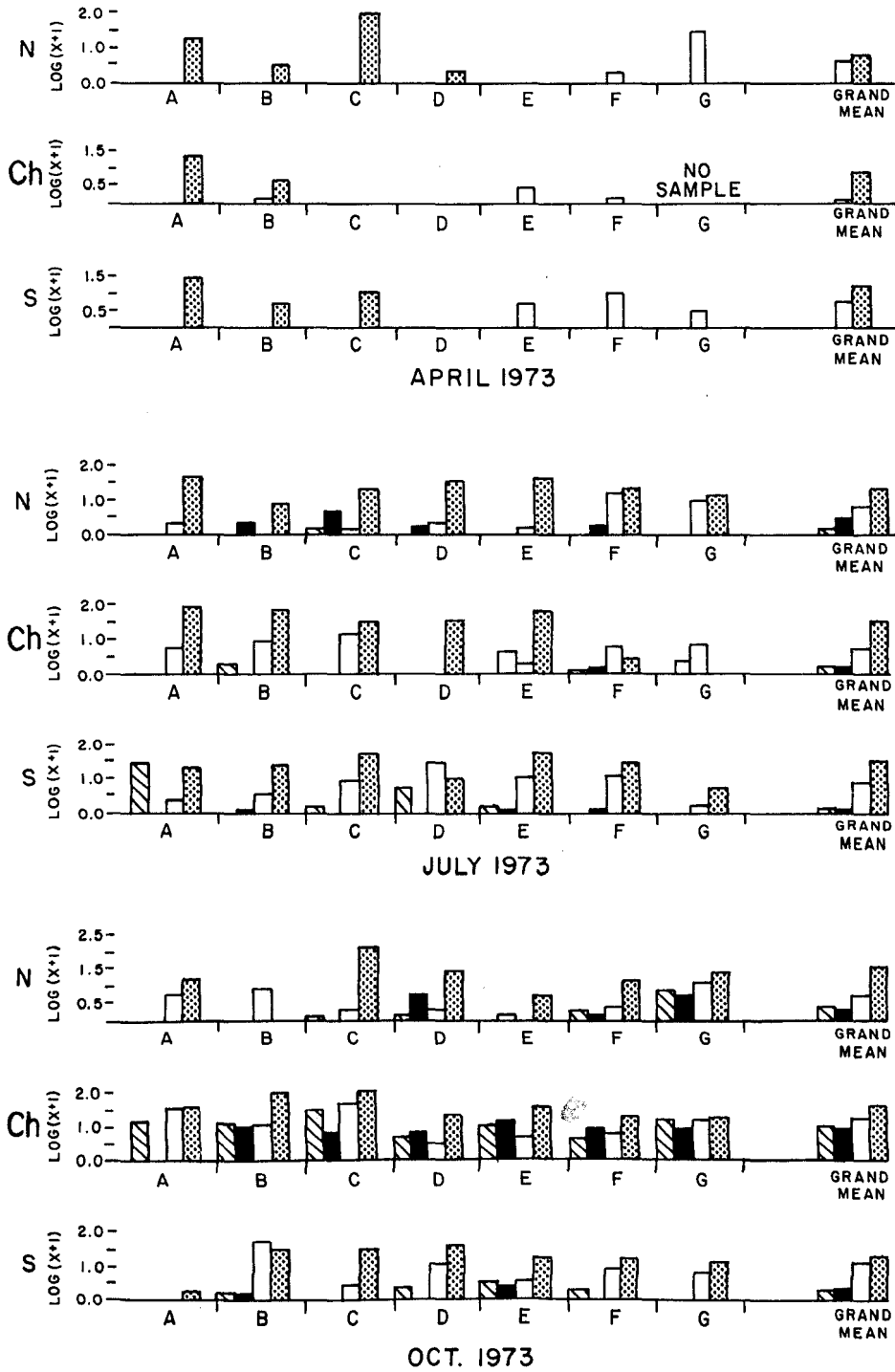


FIGURE 3.—Seasonal abundance of four juvenile sciaenids with depth and distance upstream in the York River. Mean numerical catch per tow of each substratum expressed as  $\log(x + 1)$ . Strata: A-G; substrata: N = north shoal, Ch = channel, and S = south shoal.

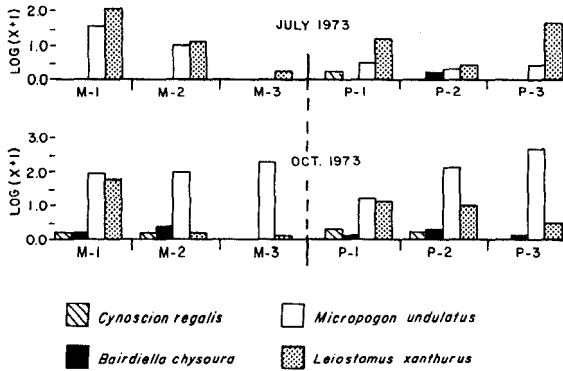


FIGURE 4.—Seasonal abundance of four juvenile sciaenids in the Mattaponi and Pamunkey rivers. Mean numerical catch per tow of each substratum expressed as  $\log(x + 1)$ . Strata: M = Mattaponi River, P = Pamunkey River. Substrata: 1, 2, and 3 designated by river distance upstream.

abundant in the middle part of the river. *Micropogonias undulatus* was more abundant in the upper part of the river, and especially in the Mattaponi and Pamunkey rivers (Figures 4, 5). Mean catch per tow increased up the estuary. Depth distribution of these four species of sciaenids indicated that they were more abundant in the channel stations (Figure 3). The relative abundance at south shoal stations was higher than at north shoal stations. The area was larger and the sampling depth was greater in the south shoal than the north shoal area (Colvocreases 1975; Chao 1976). Also, the average size of young sciaenids, especially the young-of-the-year groups, was larger in the channel than in the shoal stations (see section on "Distribution and Size"). Larger size juvenile sciaenids might use deeper areas to seek food and shelter.

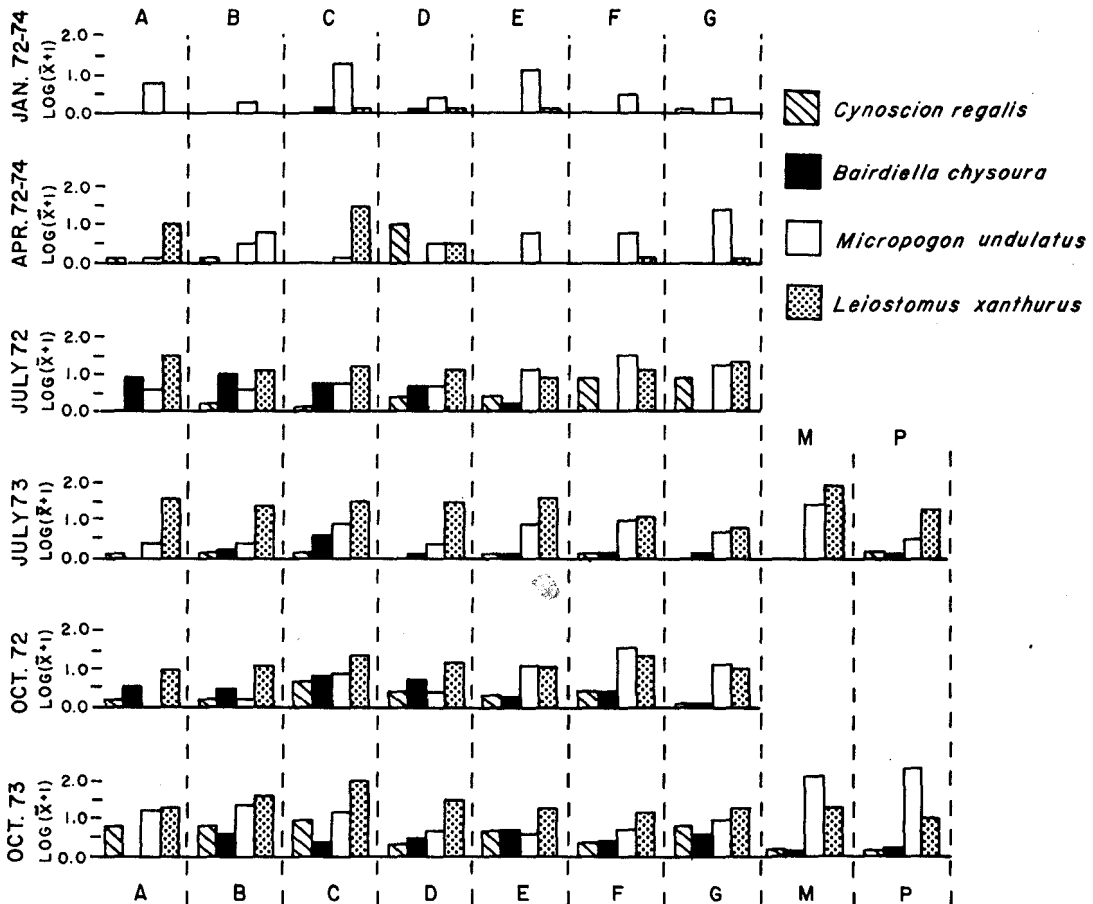


FIGURE 5.—Seasonal mean abundance of four juvenile sciaenids along the salinity gradient (strata) in the York River estuary. Grand mean numerical catch of four juvenile sciaenids per tow of stratum expressed as  $\log(x + 1)$ . Strata: A-G in York River, M = Mattaponi River, P = Pamunkey River. Grand means of January and April represent the average of 3 yr. (1972 to 1974).



In January 1972–74, the numbers of individual sciaenid fishes were considerably reduced, except for *M. undulatus* (Figures 3, 5). *Cynoscion regalis*, *B. chrysoura*, and *L. xanthurus* were caught only occasionally. During the winter months, resident fish species were more abundant than transients, especially in the upper tributaries of the York River (Markle 1976). *Micropogonias undulatus* was the most abundant sciaenid fish in the middle part of the York River (Figure 5). Depth distribution in January 1973 (Figure 3), indicated that most fish were caught in the channel. Bottom temperatures of the channel stations were higher than shoal stations (Figure 2), which might have been the major factor causing the concentration of young sciaenids in the channel.

In April 1972–74, *C. regalis*, *M. undulatus*, and *L. xanthurus* were caught (Figures 3, 5). *Cynoscion regalis* was absent in 1973 (Figure 3) but sparse in 1972 and 1974 (Figure 5). *Micropogonias undulatus* was more abundant in the upper part of the river and *L. xanthurus* was more abundant in the lower reaches (Figures 4, 5), apparently because the young-of-the-year *L. xanthurus* had just entered the estuary (see section on "Distribution and Size"). Depth distribution of these two species (Figure 3) showed that they were more abundant in shoal areas, especially *M. undulatus*. *Bairdiella chrysoura* was completely absent.

### Life History and Size

Length-frequency distributions (Figures 6–19) indicate that juvenile *Leiostomus xanthurus*, *Bairdiella chrysoura*, *Cynoscion regalis*, and *Micropogonias undulatus* enter the York River consecutively from April on, and all but *M. undulatus* leave the York River by December. Seasonal size distributions of these four species in the York River will be discussed individually and compared with studies from other areas. Modes I and II in Figures 6 and 10 and the following discussions represent young-of-the-year (mode I) and yearlings (or older fishes, mode II), respectively, except in *M. undulatus* and Figure 16, where modes I and II represent young-of-the-year and mode III the yearlings (or older fishes).

#### *Leiostomus xanthurus* Lacepède—Spot

**EARLY LIFE HISTORY IN THE YORK RIVER.**—Young-of-the-year spot, entered the

trawl and beach seine catches in early April and most left by December (Figure 6, mode I). A few smaller fish stayed in the estuary over winter. Yearling spot usually entered the study area from March to May and left the area in September (Figure 6, mode II). The intermediate mode (between modes I and II) on Figure 6, April and May 1972, was not found in the 1973 and 1974 samples. This may indicate late spawning in the previous year (1971). The length frequencies of young spot from May to July during 1972–74 were pooled and grouped by river strata (Figure 7). Young-of-the-year spot moved up to the confluence of the Pamunkey and Mattaponi rivers (Figure 1); most yearling spot stayed in the lower parts of the York River. During the same periods, no differences were found between the length frequency distributions in shoal and channel stations (Figure 8) of either young-of-the-year or yearling spot.

Spot caught in the beach seine (Figure 8) were obviously smaller than those taken by trawls. Spot was the most abundant sciaenid in the beach seine zone (depth <1.5 m) for collections with the 15.25-m and 30.5-m seines. The length frequency distribution of spot caught by beach seine was typically unimodal; mostly young-of-the-year (Figure 9). Some smaller yearlings were taken occasionally (Figure 9, 1974, mode II) and individuals >135 mm TL were captured only with the 30.5-m seine (Figure 9, August and September 1972).

In summary, young-of-the-year spot entered the York River in April and used the estuary as a nursery ground. In December, most spot left though some smaller fish stayed in the estuary through the winter, joining the yearlings as they returned to the river in the next spring. The yearlings left the estuary after an extended feeding period from March to October.

**OTHER STUDIES.**—Selected length frequency data for spot along the Atlantic and Gulf of Mexico coasts of the United States are summarized (Table 1) for comparison with the present study. Hildebrand and Schroeder (1928) and Pacheco (1957, 1962a) reported length frequency of spot from the present study area (York River and Chesapeake Bay). Across all areas (Table 1), young-of-the-year spot (Group 0 on Table 1) enter the estuarine nursery grounds during the first half of the year. They may enter estuaries as early as January (Table 1; Hildebrand and Cable 1930; Springer and Woodburn 1960; Sundararaj 1960). Spot first enter the

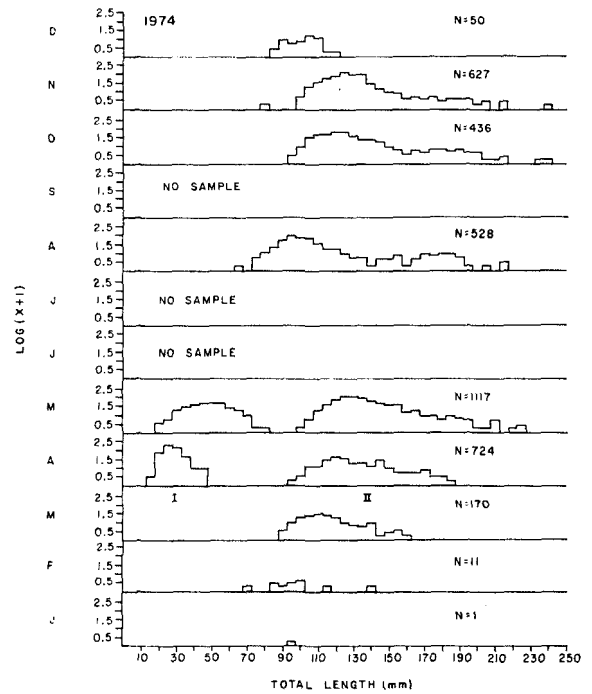
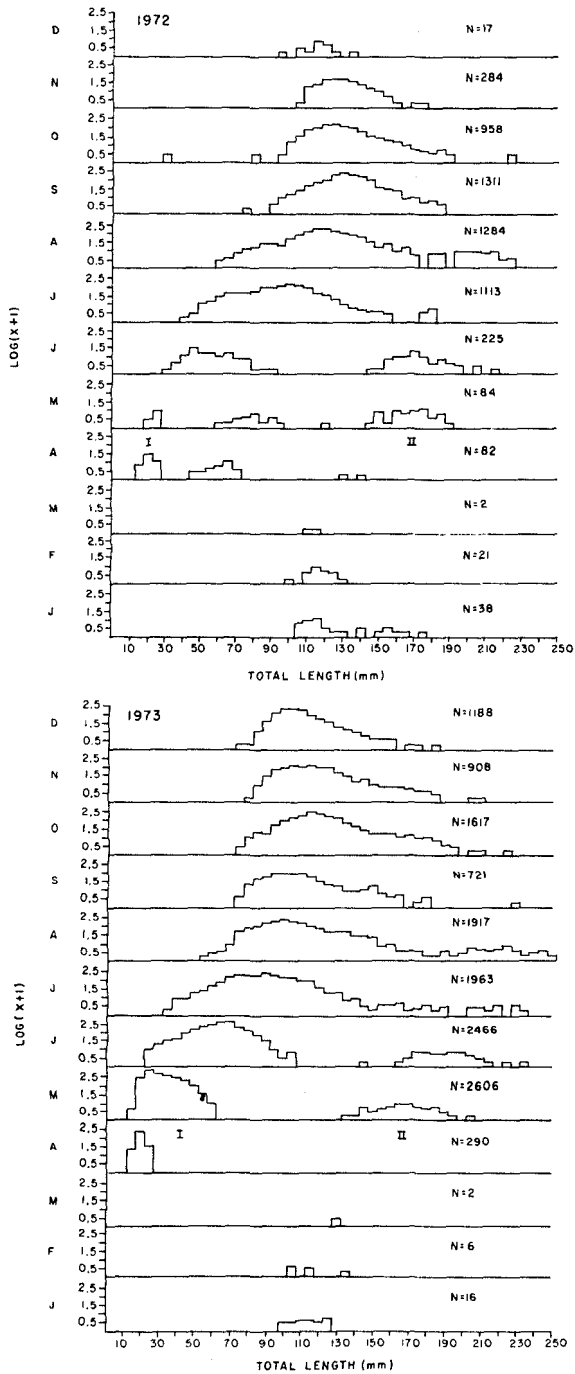


FIGURE 6.—Monthly length-frequency distributions of juvenile spot, *Leiostomus xanthurus*, from York River, 1972-74. Mode I, young-of-the-year; mode II, yearlings. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments. Only the lower portion of river (strata A-D) is represented in 1974.

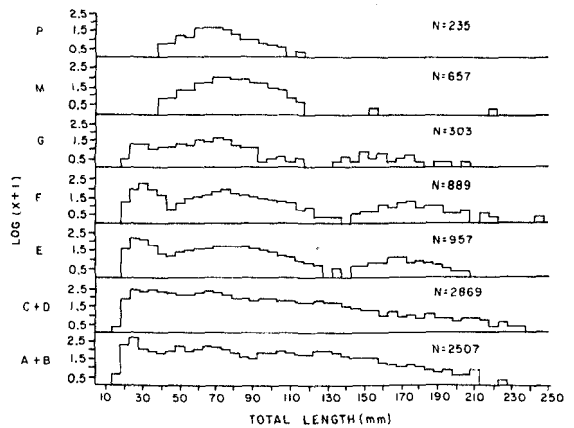


FIGURE 7.—Length-frequency distributions of spot, *Leiostomus xanthurus*, by river distance (strata) upstream in the York River estuary. Pooled total, May to July 1972-74. Strata: A-G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments.

estuary in February along the Atlantic coast of Georgia (Music 1974) and the Gulf of Mexico coast of Florida (Townsend 1956), Louisiana (Dunham 1972), and Texas (Parker 1971). In South Carolina (Dawson 1958; Shealy et al. 1974), North Carolina

(Hildebrand and Cable 1930), and the lower Chesapeake Bay (Hildebrand and Schroeder 1928

TABLE 1.—Growth of spot, *Leiostomus xanthurus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Thomas 1971		Young 1953		Hildebrand and Schroeder 1928		Pacheco 1957		Chao 1976	
Locality	Delaware River, Del.		Chesapeake Bay, Md.		Chesapeake Bay		Lower Chesapeake Bay and York River, Va.		York River, Va.	
Period	June 1968–Sept. 1970		May–Oct. 1951		Prior to 1928		May 1955–Feb. 1956		Jan. 1972–Dec. 1974	
Gear <sup>1</sup>	16-ft T and S		75 x 4 ft Haul S.		?		P and 30-ft T		16-ft T and S	
Source	Table 68		Tables 4 and 5		Table on p. 273		Table 3		Fig. 6 (present study)	
Length (mm)	Total length		Total length		Total length		Total length		Total length	
Age-group <sup>2</sup>	0	I	0	I	0	I	0	I	0	I
January						75-149			155-255	95-175
February									150-275	70-140
March					15-19					90-160
April					20-24					95-185
May					15-74	155-174	80-105	130-225		20-95
June	19.2		26-80		20-99	115-174	115-(140)	(145)-210		25-105
July	30- 80	90-140	(26-130)		40-124	135-209	115-(150)	(155)-230		35-155
August	45-100	110-165	86-90		65-149		125-(180)	(200)-245		55-(175)
September		120-170	86-106		94-170	190-209	135-(185)	(190)-260		70-185
October		125-175	(71-155)		100-184	190-299	135-(235)			80-(195)
November					75-184		165-(205)			(170)-240
December					75-119		155-185	220-240		75-190
Author	Hildebrand and Cable 1930		Shealy et al. 1974		Music 1974		Townsend 1956		Springer and Woodburn 1960	
Locality	Beaufort, N.C.		South Carolina		Georgia		Alligator Harbor, Fla.		Tampa Bay, Fla.	
Period	Prior to 1930		Feb. 1973–Jan. 1974		Oct. 1970–Sept. 1973		Mar. 1955–May 1956		Jan.–Dec. 1958	
Gear <sup>1</sup>	Pl and T		20-ft T		40-ft T, 12-ft S, 300-ft G		150- and 600-ft S		T, 80-ft S, and Pu	
Source	Tables 7 and 8		Table 27		Fig. 10		Table 1		Table 13	
Length (mm)	Total length		Total length		Total length		Total length		Standard length	
Age-group <sup>2</sup>	0	1	0	1	0	1	0	1	0	
January	4-21	82-195		88-207		80-250				13-31
February	3-27	91-200		83-142	10-35	85-225	10-34	95-159		13-49
March	10-39	93-200		113-182	10-40	95-225	15-54	105-175		10-73
April	7.5-54	84-214	18-52	107-162	15-75	95-280	20-74	105-184		19-79
May	11-94	97-215	23-82	88-147	30-100	120-260	20-89	125-189		25-85
June	29-119	122-198	33-(132)		40-130	135-270	60-89	145-164		31-103
July	43-127	130-228	23-(152)		45-(170)	(170)-280	60-99	145-159		48-118
August	67-139	140-219	48-117	153-157	45-(175)	(175)-280	75-99	165-169		49-103
September	81-153	155-234	73-132	148-152	65-150	150-265	100-109			52-82
October	92-170	175-269	78-127		80-150	150-250	70-124	145-169		52-97
November	90-188	190-264	78-127		75-115	120-250	85-129			67-91
December	1.5-9.2	84-188	83-147	168-192	65-95	100-260				76-109
Author	Nelson 1969		Parker 1971		Pearson 1929		Sundararaj 1960		Dunham 1972	
Locality	Mobile Bay, Ala.		Galveston Bay, Tex.		Sabine River to Rio Grande, Tex.		Lake Pontchartrain, La.		Louisiana coast	
Period	May 1963–Apr. 1964		Jan. 1963–Dec. 1965		Mar. 1926–May 1927		July 1953–May 1955		July 1969–June 1972	
Gear <sup>1</sup>	16-ft T		4.0-m T		Tr, T, S, and G		T, Tr, S, and R		16-ft T	
Source	Table 9		Table 2		Table 31		Fig. 17		Table 1	
Length (mm)	Total length		Total length		Total length		Total length		Total length	
Age-group <sup>2</sup>	0	I	0	I	0	I	0	I	0	I
January		75-160		60-170			15-25	90-165		100-170
February		90-125	30	70-180			15-40	115-165	10-80	110-170
March		90-180	10-30	60-190			10-75	140-230	20-100	110-170
April	45-70	90-165	10-70	90-160	10-90	120-250	30-100	140-255	40-110	
May	45-(125)	(130)-171	30-100	110-190	40-120	130-250	45-120	(120)-240	50-125	
June	50-140	170-180	30-110	140-190	70-(150)	(150)-230	55-145	150-255	50-155	
July	55-145	200	30-140	170	80-140	150-230	40-160	165-250	20-155	
August	80-135		30-150	170-180	110-(220)	230-270	85-(180)	(180)-215	70-160	
September			30-160		110-(240)	250-260	95-(150)	(150)-210	90-170	110-210
October	95-(190)		50-160		110-(170)	(170)-260	90-150	170-190	120-160	
November	95-165		60-150		130-190	200-250	110-(170)	(170)-205	100-180	
December	90-175	200	70-180		130-190	200-250	135-165		70-180	

<sup>1</sup>Gear: G, gill net; P, pound net; Pl, plankton net; Pu, push net; R, rotenone; S, seine; T, trawl; Tr, trammel net.

<sup>2</sup>Age-group: 0 represents smallest group of young-of-the-year first taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group I. Parentheses indicate that the boundary of age-group 0 and I is indistinguishable.

and the present study), young-of-the-year spot first entered the estuary in April (Table 1). In upper Chesapeake Bay (Young 1953) and Delaware River (Thomas 1971), young-of-the-year spot probably do not appear until May (Table 1). The smallest young-of-the-year spot from trawl catches are about 15 to 20 mm TL in all areas which indicates that the young-of-the-year spot in

northern areas enter the estuary later than in southern areas. When spot first enter estuaries, gear selectivity (Table 1) affects the size ranges of spot captured; beach seines usually catch only the small specimens (Young 1953; Figure 9), but pound nets (Pacheco 1957) and large otter trawls (Music 1974) usually catch larger fishes. Offshore movements of spot during the winter season are

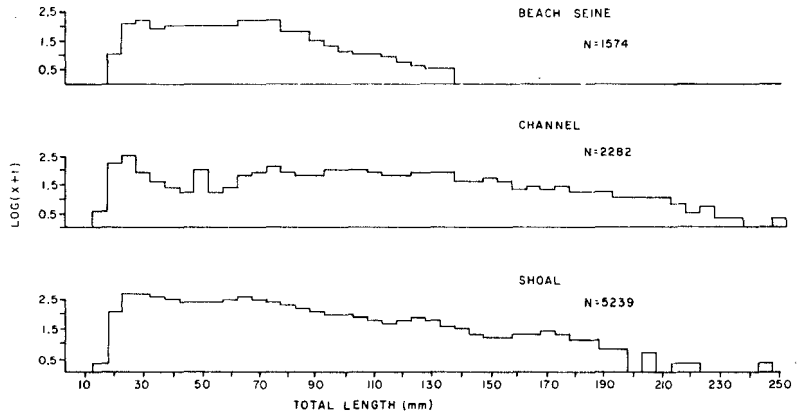


FIGURE 8.—Length-frequency distributions of spot, *Leiostomus xanthurus*, by depth of York River. Pooled total, May to July 1972-74. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments.

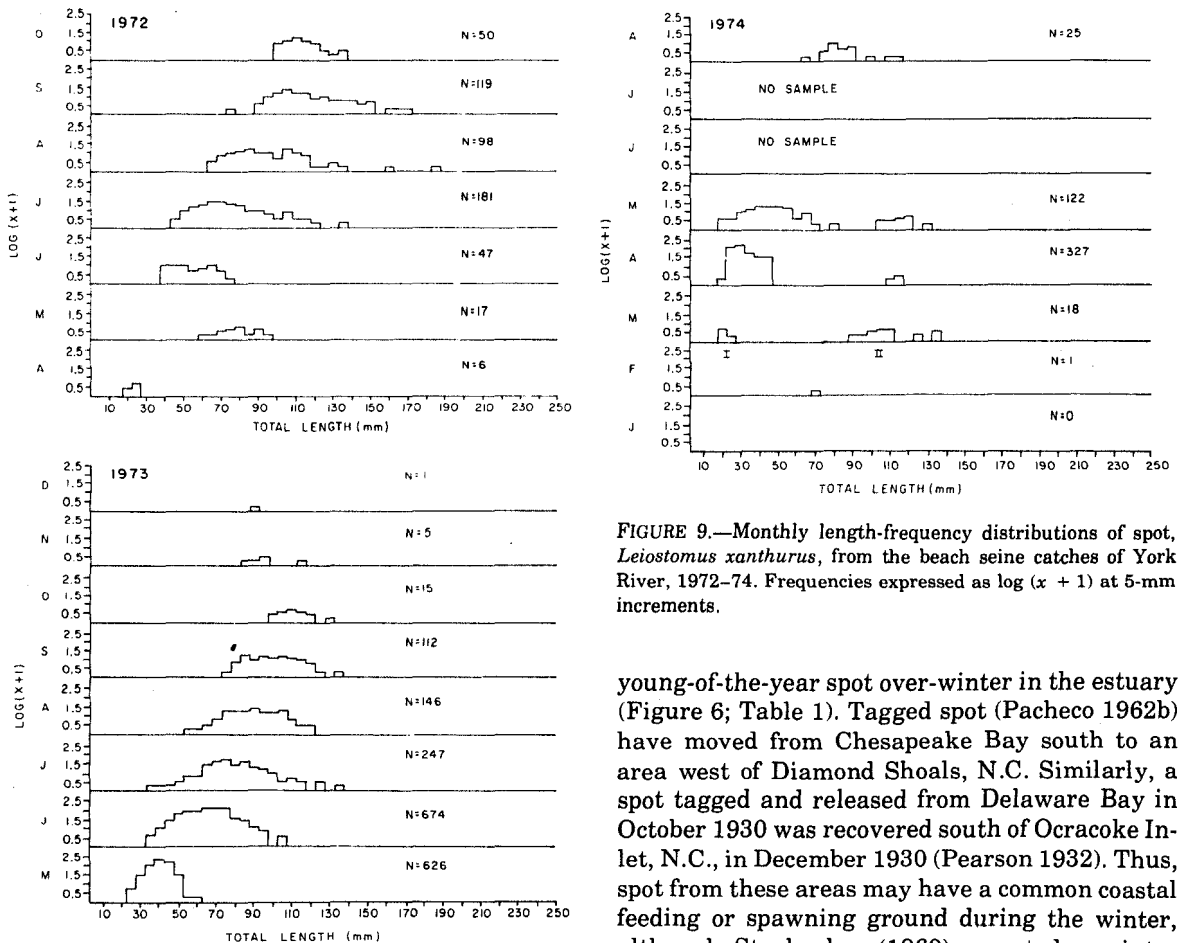


FIGURE 9.—Monthly length-frequency distributions of spot, *Leiostomus xanthurus*, from the beach seine catches of York River, 1972-74. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments.

evident in all areas studied because spot are completely absent or in low abundance in inshore catches. Yearling or older spot (Table 1, group I) usually leave the estuary after September and do not return until spring of the next year. Some

young-of-the-year spot over-winter in the estuary (Figure 6; Table 1). Tagged spot (Pacheco 1962b) have moved from Chesapeake Bay south to an area west of Diamond Shoals, N.C. Similarly, a spot tagged and released from Delaware Bay in October 1930 was recovered south of Ocracoke Inlet, N.C., in December 1930 (Pearson 1932). Thus, spot from these areas may have a common coastal feeding or spawning ground during the winter, although Struhsaker (1969) reported a winter offshore movement of spot into deeper water (lower-shelf habitat off South Carolina). These offshore spot may be a mixture of northern and southern populations or just southern residents. The late fall or early winter spawning time of spot may be the same in both Atlantic and Gulf of

Mexico waters (Welsh and Breder 1923). Later spawning by a northern component of the population is evidenced from the length ranges of post-larvae and juvenile spot (Table 1).

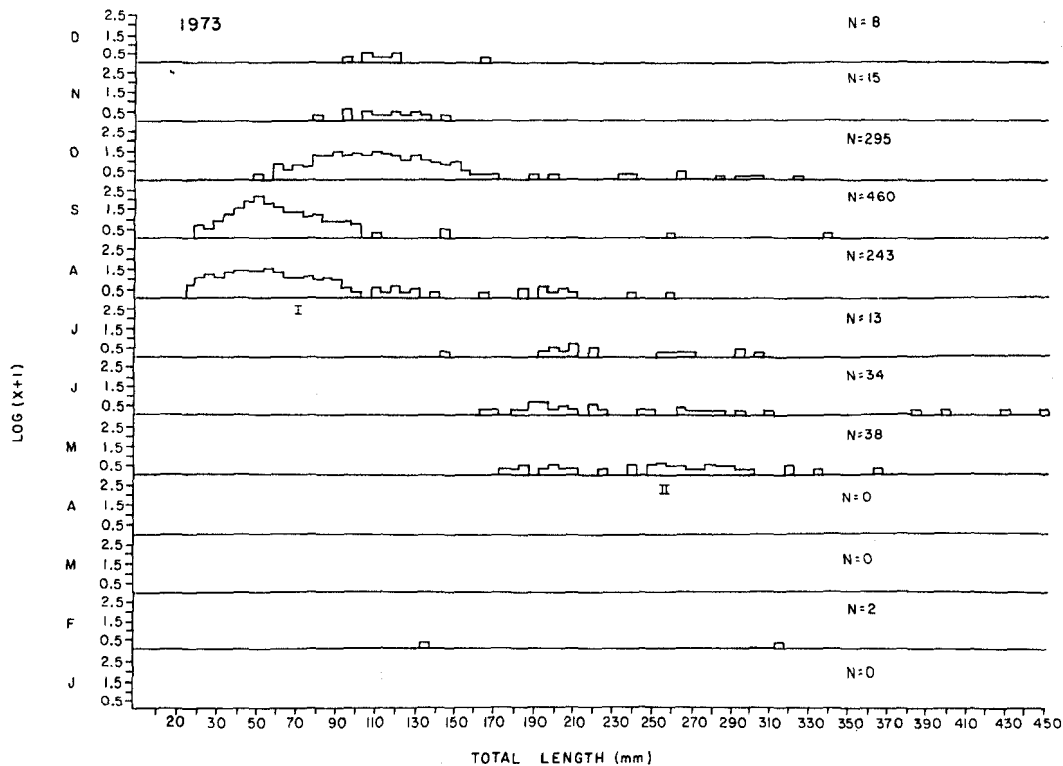
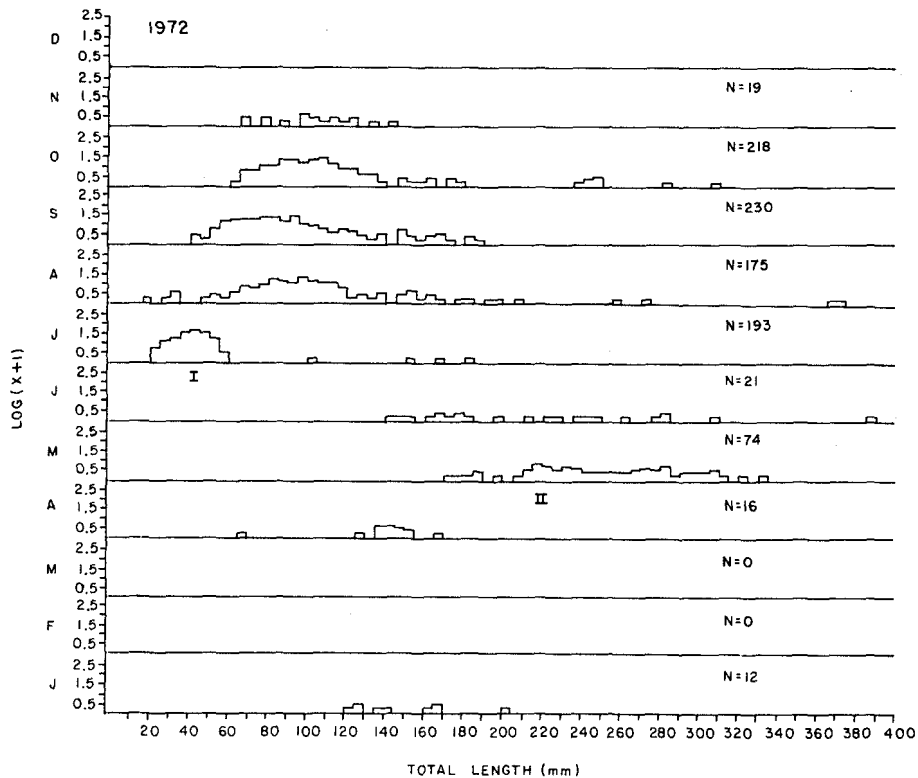
*Cynoscion regalis* (Bloch and Schneider)—  
Weakfish

**EARLY LIFE HISTORY IN YORK RIVER.**—Young-of-the-year weakfish first entered trawl catches in July or August and virtually left the estuary in the winter (Figure 10, mode I). Yearling weakfish returned to the river in April or May and left in September or October (Figure 10, mode II). Larger weakfish (2 yr or older) were caught only sporadically during this study because of gear avoidance. The length mode of small weakfish in August showed a rapid increase (Figure 10). This increase may be due to the recruitment of yearlings or an earlier spawned group of young-of-the-year. Length frequencies for weakfish (<250 mm TL) caught from August to October 1972–74, were pooled to compare distribution by size in the York River and its tributaries (Figure 11). Smaller fishes were more abundant in the Pamunkey and Mattaponi rivers than in the York River proper. Yearling weakfish also showed a movement upriver (Figure 11). This suggests that young weakfish entered the low salinity nursery ground (upper portion of the York River) and then moved downriver as they grew. Pooled length frequency distributions revealed an apparent difference between shoal and channel areas of the York River (Figure 12). Yearling weakfish (or larger ones) were proportionally more abundant in the channel. The 15.25-m beach seine catches contained no weakfish, but occasionally the 30.5-m seine caught some young-of-the-year weakfish in the summer.

**OTHER STUDIES.**—Major populations of weakfish are confined to the Atlantic coast of the United States from New York to Georgia. Existing data indicate young-of-the-year weakfish enter estuarine or coastal catches from May to July (Table 2). The smallest sizes of the weakfish in the catches differ with area and may be due to gear and/or time of sampling. Small fishes with less size variation (about 5 mm) were taken over a longer period of time in southern areas than northern areas (Table 2). Young-of-the-year weakfish do not occur in catches during winter months in northern coastal areas or estuaries (Perlmutter 1956;

Massmann et al. 1958; Thomas 1971; Markle 1976). Year-round catches of weakfishes from North Carolina (Hildebrand and Cable 1934) and Georgia (Mahood 1974) were from sounds and short coastal rivers. Most of the studies suggest the age-group 0 on Table 2 was a combination of young-of-the-year and yearlings. No distinct mode could be identified for young-of-the-year from these studies. This may be due to the multiple spawning (Merriner 1973, 1976) and/or the recruitment of the young-of-the-year from different spawning populations.

The reproductive biology of weakfish is better known than other sciaenid fishes studied here. Welsh and Breder (1923) described the eggs and development of weakfish and noted that Delaware Bay was a spawning ground for weakfish. Merriner (1973) indicated that weakfish have an extended spawning season in North Carolina (March–August) and are characterized by high fecundity and possible multiple spawning by some females. Pearson (1941) took plankton tows in lower Chesapeake Bay from May to August in 1929 and 1930 and reported greater densities of weakfish larvae (1.5–17 mm TL) in subsurface tows (average 67/tow) than in surface tows (average 13/tow). The density of planktonic weakfish decreased at those stations within Chesapeake Bay, compared with sites near the bay mouth. Harmic (1958) reported that newly hatched larval weakfishes averaged 1.8 mm TL. Soon after hatching, the larvae became demersal and were dispersed into the nursery areas of Delaware Bay by means of the "salt wedge." The smallest weakfishes taken in the bottom trawl were 6 to 10 mm TL (Hildebrand and Cable 1934). The young-of-the-year weakfish in York River are probably progeny from adults spawning near the mouth of Chesapeake Bay. Weakfish tagged and released in lower Chesapeake Bay (Nesbit 1954) were later recovered to the north in New York and New Jersey, and southward in North Carolina. Nesbit (1954), Perlmutter et al. (1956), and Harmic (1958) cited the presence of a northern spawning population in New York and northern New Jersey waters and a southern spawning population from New Jersey to North Carolina. Seguin (1960) found that morphometric and meristic variation of weakfish exists along the middle Atlantic coast and suggested that three possible population segments may exist: a New York group, a Delaware and lower Chesapeake group, and a North Carolina group. Joseph (1972) questioned the



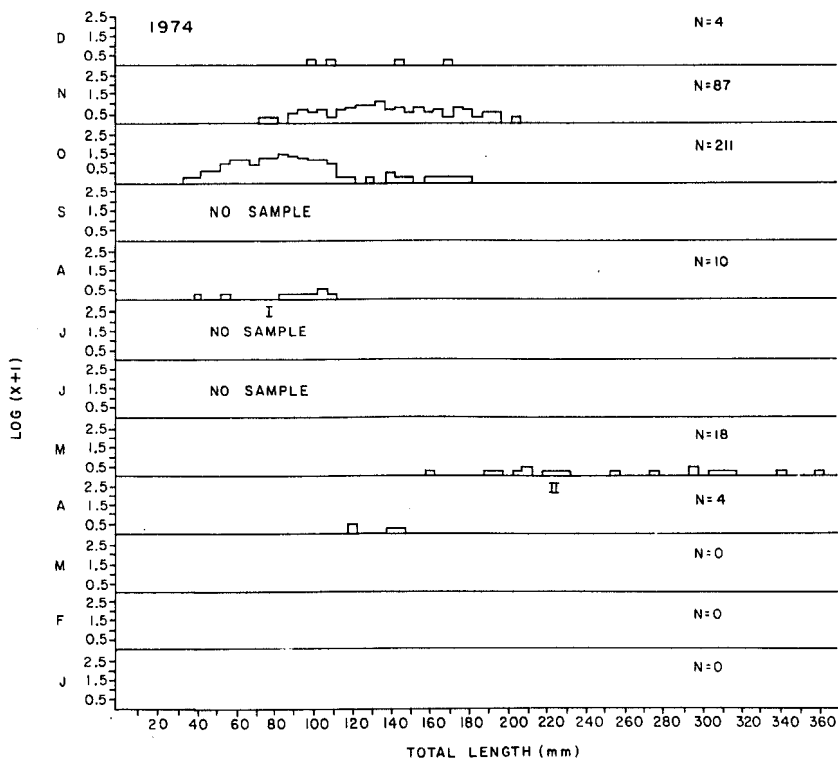


FIGURE 10.—Monthly length-frequency distributions of weakfish, *Cynoscion regalis*, from York River, 1972-74. Mode I, young-of-the-year; mode II, yearlings. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments. Only the lower portion of river (strata A-D) is represented in 1974.

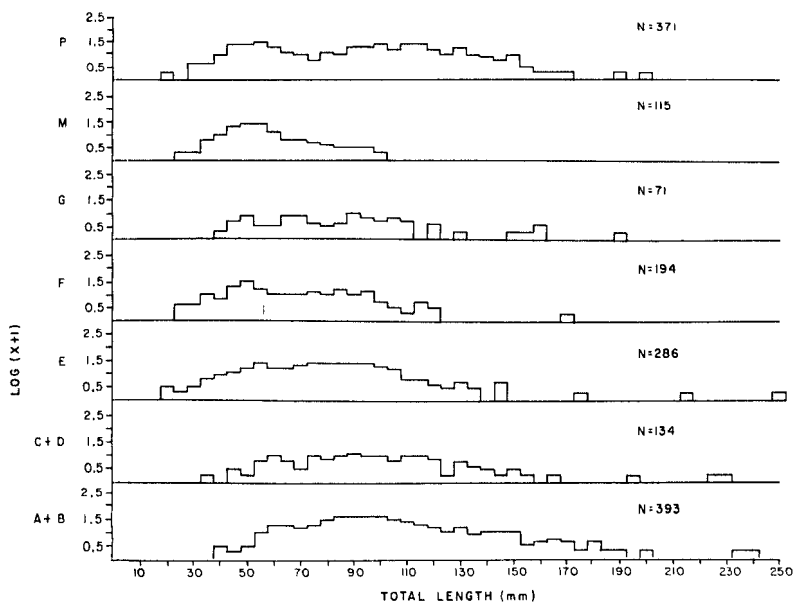


FIGURE 11.—Length-frequency distributions of weakfish, *Cynoscion regalis*, by river distance (strata) upstream of the York River estuary. Pooled total, August to October 1972-74. Strata: A-G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments.

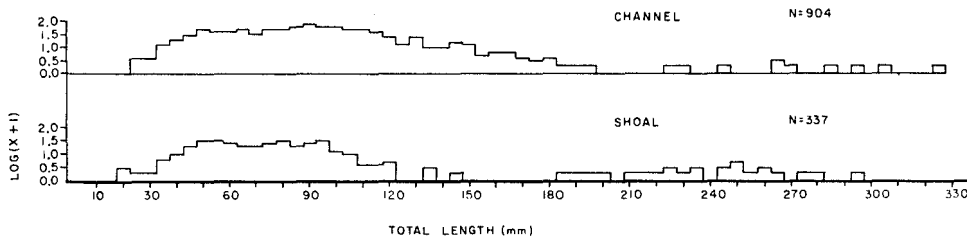


FIGURE 12.—Length-frequency distributions of weakfish, *Cynoscion regalis*, by depth of York River. Pooled total, August to October, 1972-74. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments.

TABLE 2.—Growth of weakfish, *Cynoscion regalis*, from different estuarine areas along U.S. Atlantic coast.

Author	Thomas 1971	Pearson 1941	Chao 1976
Locality	Delaware River, Del.	Lower Chesapeake Bay	York River, Va.
Period	1969	1929-30	Jan. 1972-Dec. 1974
Gear <sup>1</sup>	T and S	PI and P	16-ft T
Source	Table 4	Fig. 23	Fig. 10 (present study)
Length (mm)	Total length	Total length	Total length
Age group <sup>2</sup>	0	0	0
January			120-205
February			130-315
March			
April		130-250	65-175
May			155-330
June	5-70		140-385
July	15-125	20-(150)	20-55
August	15-(185)	30-(160)	10-(95)
September	70-(185)		70-(110)
October	40-(175)	(130)-180	115-300
November			35-(135)
December			65-(140)
			140-205
			95-(170)
Author	Hildebrand and Cable 1934	Shealy et al. 1974	Mahood 1974
Locality	Beaufort, N.C.	South Carolina coast	Georgia Coast
Period	?	Feb. 1973-Jan. 1974	Oct. 1970-Sept. 1973
Gear <sup>1</sup>	PI, P, and T	20-ft T	40-ft T
Source	Table 4	Table 32	Table 7
Length (mm)	Total length	Total length	Total length
Age group <sup>2</sup>	0	0	0
January	75-204		68-438
February	105-274		68-388
March	90-230		83-358
April	80-284	118-188	78-408
May	4-9	125-224	48-358
June	4-44	95-279	23-47
July	4-(39)	40-379	23-(52)
August	4-(64)	65-369	23-(72)
September	10-(79)	80-314	23-(67)
October	45-(94)	100-329	28-(72)
November	45-(99)	(100)-329	68-72
December	85-(94)	(95)-299	88-92
			108-197
			53-(233)
			(238)-348

<sup>1</sup>Gear: P, pound net; PI, plankton net; S, seine; T, trawl.

<sup>2</sup>Age-group: 0 represents smallest groups of young-of-the-year taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group 1. Parentheses indicate that the boundary of age-groups 0 and 1 is indistinguishable.

division of weakfish into northern and southern stocks and did not consider the decline of weakfish in Chesapeake Bay to be a result of the trawl fisheries in the shallow coastal waters and bays of North Carolina. He indicated Chesapeake Bay as a major spawning area and nursery ground, but also cited failure to obtain one weakfish larva/tow in extensive VIMS ichthyoplankton studies dur-

ing 1959-63. However, weakfish eggs and larvae were reported from Chesapeake Bay by Hildebrand and Schroeder (1928) and Pearson (1941). Massmann (1963) implied that Chesapeake Bay weakfish are from southern spawning populations or stocks. Therefore, the question remains whether lower Chesapeake Bay and nearshore waters are a major spawning ground for weakfish



(Merriner 1976). Pearson (1932) described the winter trawl fishery off North Carolina and cited higher total catches of weakfish from area B (southwest of Cape Hatteras) than from area A (northeast of Cape Hatteras) in deeper waters. It is possible that most young-of-the-year and larger weakfish that leave the York River move southward to their wintering ground off Cape Hatteras. In spring, weakfish disperse from the wintering ground. Some fish move north and spawning may occur from late spring to summer along the coast from North Carolina to New York.

*Bairdiella chrysoura* (Lacepède)—Silver Perch

**EARLY LIFE HISTORY IN THE YORK RIVER.**—Silver perch were present from April to December and were most abundant from August to October (Figure 13). Total catches were reduced in 1973 and 1974. Young-of-the-year silver perch first entered the catches in July and most silver perch left the river in November. Yearlings may enter the river as early as April and most left the river in November. There were no silver perch

taken from January to March during the present study (1972-74). Pooled length frequencies from August to October, 1972 to 1974, indicated that silver perch were most concentrated in the lower part of the York River (Figure 14) and larger specimens tended to stay in the channel (Figure 15). The 30.5-m beach seine caught young-of-the-year occasionally but the 15.25-m seine rarely caught any silver perch.

**OTHER STUDIES.**—Silver perch occur along the U.S. coast from New York to Texas. The seasonal distribution pattern is similar in all Atlantic coastal states (Table 3). Young-of-the-year silver perch were first caught in bottom trawls during June or July. Size of the smallest young-of-the-year silver perch during a given month decreases as latitude of the nursery ground increases on the Atlantic coast and west coast of Florida (Table 3). Silver perch are present almost all year round south of Chesapeake Bay (Table 3), which may be due to the higher salinity or temperature of those study areas. The embryonic development of silver perch from Beaufort, N.C., was described by Kuntz

TABLE 3.—Growth of silver perch, *Bairdiella chrysoura*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Thomas 1971	Chao 1976	Hildebrand and Cable 1930
Locality	Delaware River, Del.	York River, Va.	Beaufort, N.C.
Period	1969	Jan. 1972-Dec. 1974	Spring 1926-Summer 1927
Gear <sup>1</sup>	16 ft T	16 ft T	PI and T
Source	Table 28	Fig. 13 (present study)	Tables 5 and 6
Length (mm)	Total length	Total length	Total length
Age-group <sup>2</sup>	0	0	0
January			74-204
February			90-209
March			98-204
April			93-195
May			85-204
June	5-20	85-200	1-6
July	5-65	145-185	1-38
August	45-100	20-60	9-76
September	70-120	120-190	110-210
October	65-130	15-85	105-224
November		100-205	20-92
December		65-135	130-204
		160-210	45-122
		60-135	135-189
		70-155	73-115
		73-110	145-224
			68-143
			150-229
			78-124
Author	Shealy et al. 1974	Springer and Woodburn 1960	Reid 1954
Locality	South Carolina coast	Tampa Bay, Fla.	Cedar Key, Fla.
Period	Feb. 1973-Jan. 1974	Oct. 1957-Dec. 1958	June 1950-May 1951
Gear <sup>1</sup>	20 ft T	T, S, and Pu	15 ft T, S, and Pu
Source	Table 42	Fig. 12	Fig. 10
Length (mm)	Total length	Standard length	Standard length
Age-group <sup>2</sup>	0	0	0
January	18-(72)	67	55-60
February	93-182	52-76	
March	88-137	67-73	65-95
April	98-172		
May	73-182		
June	113-152	13-25	5-40
July	123-132	16-52	15-50
August	33-87	16-70	20-70
September	58-107	16-82	5-80
October	73-132	25-85	10-82
November	78-(187)	28-91	40-95
December	98-(172)	19-97	50-70
	98-(182)	46-106	

<sup>1</sup>Gear: PI, plankton net; Pu, puchnet; S, seine; T, trawl.

<sup>2</sup>Age-group: 0 represents smallest group of young-of-the-year first taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group 1. Parentheses indicate that the boundary of age-groups 0 and 1 is indistinguishable.

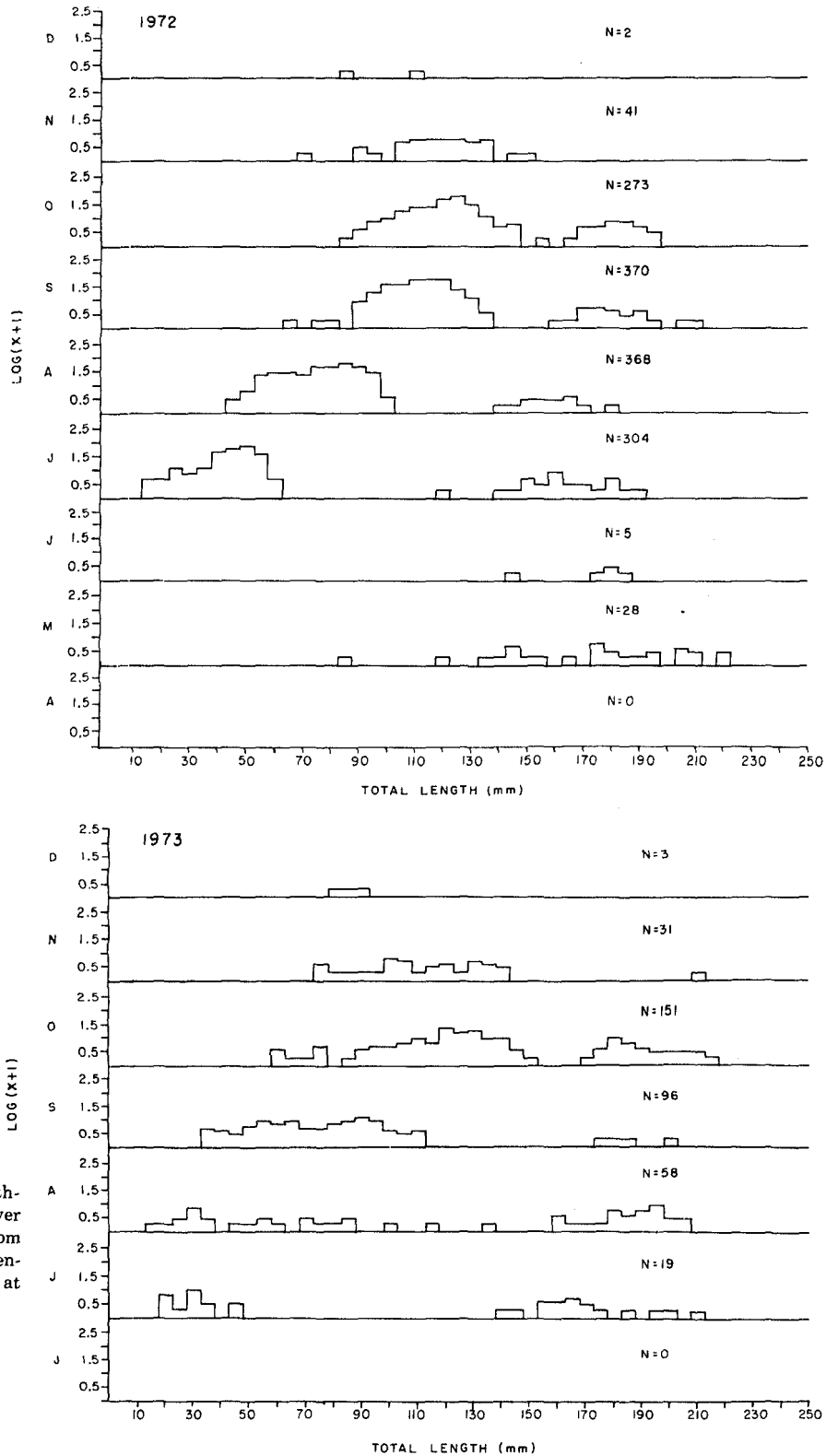


FIGURE 13.—Monthly length-frequency distributions of silver perch, *Bairdiella chrysoura*, from York River, 1972-73. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments.

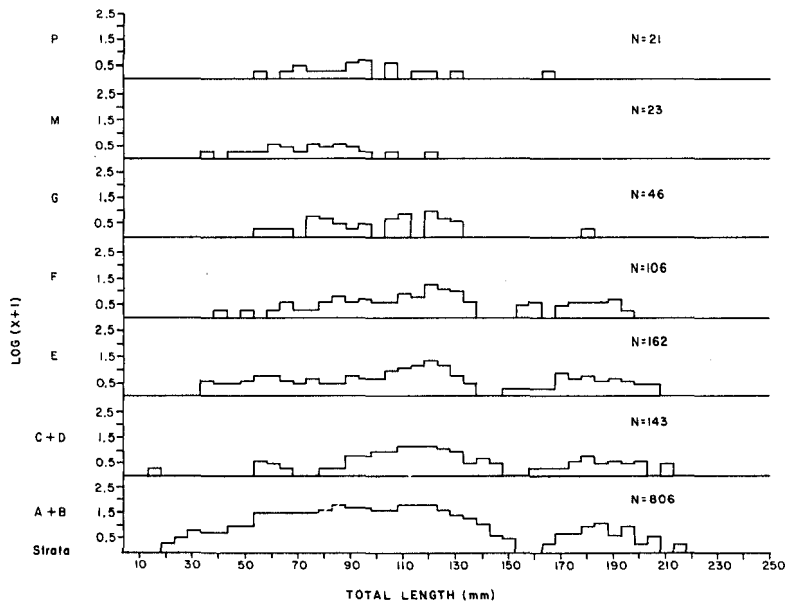


FIGURE 14.—Length-frequency distributions of silver perch, *Bairdiella chrysoura*, by river distance (strata) upstream of the York River estuary. Pooled total, August to October 1972–74. Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments.

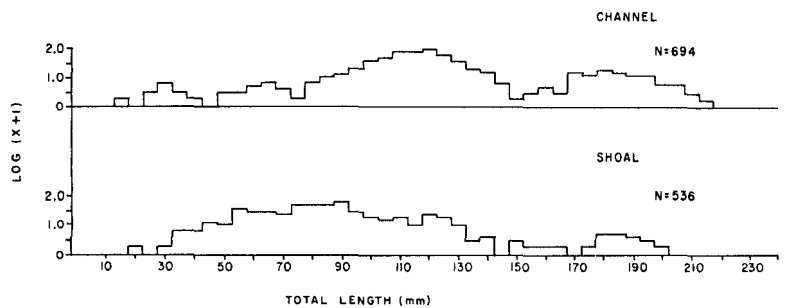


FIGURE 15.—Length-frequency distributions of silver perch, *Bairdiella chrysoura*, by depth of York River. Pooled total, August to October 1972–74. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments.

(1914). Welsh and Breder (1923) made further observations from material obtained at Atlantic City, N.J. Jannke (1971) described larval silver perch from the Everglades National Park, Fla., and showed that larvae of 2 to 3 mm “notochord” length were present all year round. Hildebrand and Schroeder (1928) reported ripe fish of both sexes in Chesapeake Bay (24 m deep, off Chrisfield, Md.) as early as 16 May. This suggests that silver perch may spawn in the deeper waters of lower Chesapeake Bay and nearshore waters in late spring and early summer. Because of its relatively small size, commercial landings of silver perch are relatively small. Silver perch move oceanward and probably to the south of Chesapeake Bay in winter. Large numbers captured by commercial haul seines between Virginia Beach, Va., and Kitty Hawk, N.C., have been observed in fall (J. A. Musick, pers. obs.).

*Micropogonias undulatus* (Linnaeus)—Atlantic Croaker

**EARLY LIFE HISTORY IN YORK RIVER.**—Young-of-the-year croaker first entered the trawl and beach seine catches in August and stayed in the York River throughout the winter (Figure 16, mode I). They left the estuary between August and September of the following year as yearlings (Figure 16, mode III). Large croaker (more than 1.5 yr old) were caught only sporadically in this study due to gear avoidance, but they were present from February to September. There were apparently two to three length groups (modes) of young-of-the-year croaker in September 1972–74. Mode II was different from mode I and mode III of 1972 and 1974 (Figure 16). The former group did not stay in the York River over winter, but entered the estuary as early as May (Figure 16, mode II). Most of this group left in November 1972–74.

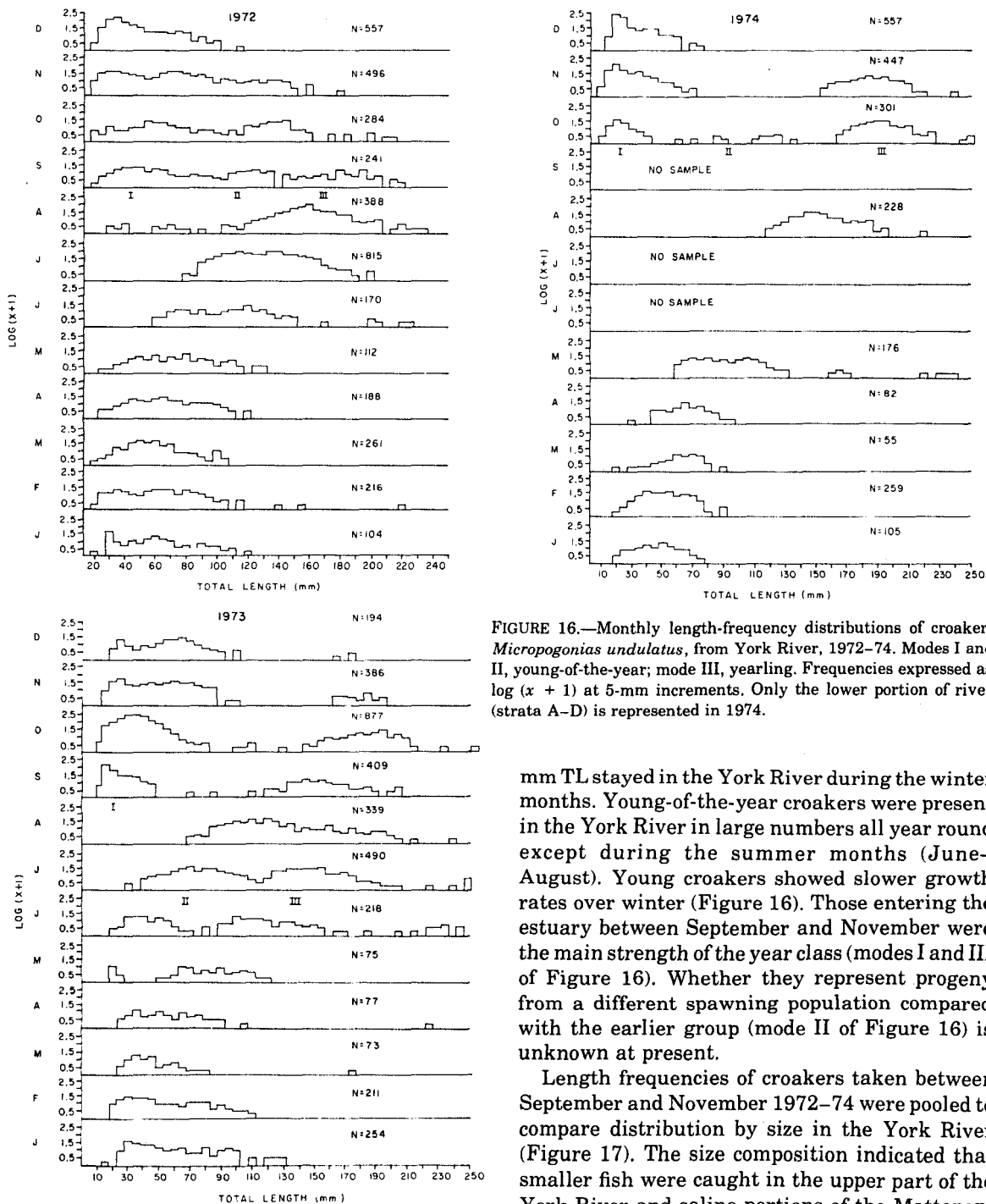


FIGURE 16.—Monthly length-frequency distributions of croaker, *Micropogonias undulatus*, from York River, 1972–74. Modes I and II, young-of-the-year; mode III, yearling. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments. Only the lower portion of river (strata A–D) is represented in 1974.

mm TL stayed in the York River during the winter months. Young-of-the-year croakers were present in the York River in large numbers all year round except during the summer months (June–August). Young croakers showed slower growth rates over winter (Figure 16). Those entering the estuary between September and November were the main strength of the year class (modes I and III of Figure 16). Whether they represent progeny from a different spawning population compared with the earlier group (mode II of Figure 16) is unknown at present.

Length frequencies of croakers taken between September and November 1972–74 were pooled to compare distribution by size in the York River (Figure 17). The size composition indicated that smaller fish were caught in the upper part of the York River and saline portions of the Mattaponi and Pamunkey rivers. Larger fish were proportionally more abundant in the lower part of the river. Larger fish also constituted a larger portion of the croaker catch in the channel than in the shoal area (Figure 18). The 30.5-m beach seine

Size may be a determining factor for migration of young croakers from the York River. From 1972 to 1974, length frequencies (Figure 16) indicated that very few young-of-the-year croakers >130

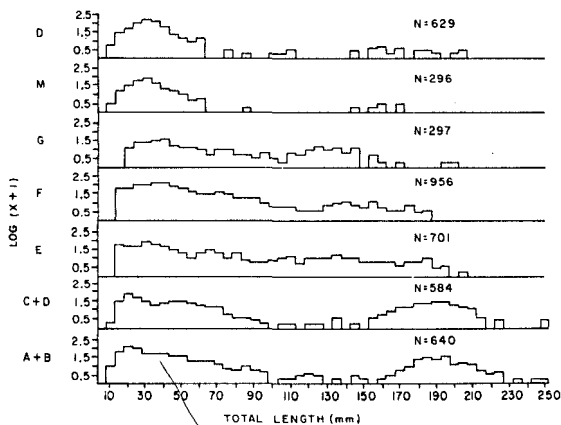


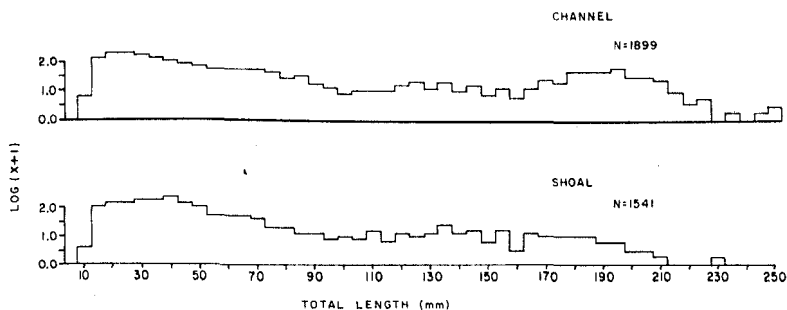
FIGURE 17.—Length-frequency distributions of croaker, *Micropogonias undulatus*, by river distance (strata) upstream of the York River estuary. Pooled total, September to November 1972–74. Strata: A–G in York River, M = Mattaponi River, P = Pamunkey River. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments.

(Figure 19) caught yearlings exclusively. The 15.25-m seine caught almost no croakers.

In summary, young-of-the-year croaker entered the estuary in May and from August on. The earlier group entered in May and left the estuary in November, as did older year classes. The later group (August–November) stayed in the estuary until the summer months of the following year. Young croaker moved to the upper part of the York River and the saline portions of major tributaries after first entry, then moved down the York River into more saline waters as they grew. Smaller fishes (<130 mm TL) stayed in the river throughout the winter.

**OTHER STUDIES.**—Croakers occur from the Gulf of Maine to Argentina, along the coasts of the Atlantic and Gulf of Mexico. Length-frequency distributions exist for different areas of the United States [see Wallace (1940) and Haven (1957) for

FIGURE 18.—Length-frequency distributions of croaker, *Micropogonias undulatus*, by depth of York River. Pooled total, September to November 1972–74. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments.



the lower Chesapeake Bay and York River (Table 4)]. Studies usually show that small croakers (10–20 mm TL) are present in the estuary during all except the summer months (June–August). Croakers seemingly have a long spawning season since small individuals (<20 mm TL) are present from September to May in different estuarine areas (Table 4). Some croakers may be very small (<15 mm TL) in spring because of slow growth of fish spawned late in winter, or because they were spawned in spring. Such a group was also found in the present study (Figure 16, mode II) but not in previous Chesapeake Bay studies. Croakers from Maryland and Virginia tagged by Haven (1959) showed springtime movement of croakers up the estuaries and up Chesapeake Bay, and oceanward and southerly in fall (some recoveries were from off the North Carolina coast). Pearson (1932) reported a high percentage of croakers in the catches of the commercial trawl fishery during November (88%) and December (76%) from the fishing grounds off the North Carolina coast. Hildebrand and Cable (1930) implied that croaker spawning probably began in August in Chesapeake Bay and northward, in September at Beaufort (North

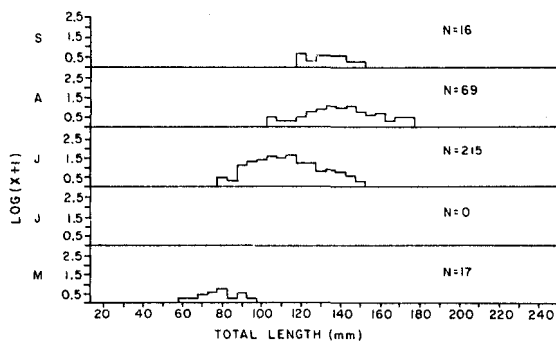


FIGURE 19.—Length-frequency distributions of croaker, *Micropogonias undulatus*, from beach seine catches of York River, May to September 1972. Frequencies expressed as  $\log(x + 1)$  at 5-mm increments.

TABLE 4.—Growth of croaker, *Micropogonias undulatus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author	Thomas 1971	Haven 1957	Chao 1976	Hildebrand and Cable 1930	Shealy et al. 1974					
Locality	Delaware River, Del.	York River, Va.	York River, Va.	Beaufort, N.C.	South Carolina coast					
Period	June 1968-Dec. 1970	Oct. 1952-July 1953	Jan. 1972-Dec. 1974	Spring 1926-Summer 1927	Feb. 1973-Jan. 1974					
Gear <sup>1</sup>	16-ft T	30-ft T	16-ft T and S	T and Pl	20-ft T					
Source	Table 70	Fig. 7	Fig. 16 (present study)	Tables 9 & 10	Table 22					
Length (mm)	Total length	Total length	Total length	Total length	Total length					
Age-group <sup>2</sup>	0      I	0      I	0      I	0      I	0      I					
January		15-(85)	(95)-105	20-120	3-24	25-269	18-97	108-297		
February		10-60	(45)-100	20-155	3-29	40-294	28-82	113-187		
March		10-(70)	(70)-120	20-175	2-24	40-294	13-102	123-173		
April		10-(65)	70-100	25-120	25-19	100-259	18-(132)	138-192		
May		25-(90)	70-140	20-30	(20)-240	195-239	28-112			
June		40-(120)	(120)-155	20-70	(60)-245	8-25	31-284	33-142		
July		75-145	(135)-175	30-(110)	(80)-250		43-234	28-(182)		
August		N.S.	N.S.	30-(90)	(70)-240		66-289	53-177		
September		N.S.	N.S.	10-(100)	(70)-195	2-9	80-279	78-182		
October	20	135-140	10-(40)	(40)-85	10-(110)	(100)-250	2-50	98-294	68-182	
November	25		15-(60)	(60)-115	15-100	(60)-250	1.5-66	85-284	43-153	
December	20-50		10-(60)	(60)-120	20-110	165-175	2.5-69	85-259	48-163	183-197
Author	Hoesle 1973	Hansen 1969	Suttkus 1955	Parker 1971						
Locality	Georgia coast	Pensacola, Fla.	Lake Pontchartrain and Louisiana coast	Galveston Bay, Tex.						
Period	Aug. 1956-Aug. 1966	Aug. 1963-Dec. 1965	July 1953-Oct. 1954	Jan. 1963-Dec. 1965						
Gear <sup>1</sup>	30- and 40-ft T	5-m T	T and S	4.9-m T						
Source	Fig. 12	Fig. 2	Table 1	Fig. 21						
Length (mm)	Total length	Total length	Total length	Total length						
Age-group <sup>2</sup>	0      I	0      I	0      I	0      I						
January	10-80	120-130	15-20	45-95	10-79	120-189	10-(80)	90-200		
February	20-80		20-25	40-95	10-89	130-179	10-(90)	(90)-250		
March	20-80	110-120	15-35	75-85	20-119	120-259	10-(90)	(100)-250		
April	40-100		N.S.	N.S.	20-129	130-339	10-(120)	(130)-250		
May	20-110		20-(75)	(60)-135	30-139	140-319	10-(130)	(130)-240		
June	50-140	200-210	30-(95)	(90)-150	30-139	140-329	40-(140)	(156)-250		
July	60-140		35-(90)	(90)-145	50-159	160-380	30-(150)	(160)-230		
August	90-160	190-200	35-(110)	(100)-150	80-169	170-319	60-160	170-250		
September	60-150		40-(90)	(90)-150	80-169	170-319	60-(170)	(170)-190		
October	100-180		45-(110)	(110)-150	90-189	(170)-349	10-40	60-220		
November			50-105		20-59	130-309	10-(60)	60-210		
December			10-95		10-79	120-299	10-(70)	70-230		

<sup>1</sup>Gear: Pl, plankton net; S, seine; T, trawl.

<sup>2</sup>Age-group: 0 represents smallest group of young-of-the-year first taken from January on, other fishes (including overwintering young-of-the-year) are included in age-group I. Parentheses indicate that the boundary of age-groups 0 and I is indistinguishable. N.S.; no sample.

Carolina), and in October in Texas. Arnoldi et al. (1973) "tagged" young-of-the-year croakers (9-48 mm TL). Their successful recaptures indicated that individual croaker remained in the particular marsh for only 1 to 4 mo, which was much shorter than the total length of time croaker were observed in the marsh (October-June). Thus, they also suggested that several croaker "populations" may utilize coastal marsh as nursery ground during the course of the year. White and Chittenden (1977) indicated that some croakers in the Gulf of Mexico may lack the first (overwinter) ring on the scales. This suggests that some croakers may spawn in the spring in the Gulf of Mexico.

Massmann and Pacheco (1960) reported the disappearance of young croakers from the York River, but their conclusion may have been in error because of selectivity of their fishing gear. Haven's (1957) length frequencies for croakers during 1952 and 1953 differ from those presented by Massmann and Pacheco (1960) for the same years. No fish <100 mm TL were reported by Massmann and Pacheco (1960), but their gear was a net with

¾-in (about 1.9-cm) mesh, whereas Haven (1957) used ¼-in (about 0.6-cm) mesh. Joseph (1972) attributed the decline of croaker in the commercial catches of the middle Atlantic coast to climatic trends. Present data support his hypothesis. The apparent increase in juvenile croakers in 1973 and 1974 was probably due to warmer winter months. Mean bottom temperatures of the York River channel were about 3.6°C and 3.2°C in January and February, respectively, from 1967 to 1971 (Markle 1976). It was 6.7°C for January and 6.3°C for February in 1973 and 1974 (Figure 2). The year class strength of croaker in the York River was dependent on the success of the late young-of-the-year group (Figure 16, mode I), which stayed in the estuary through the winter. Historical York River trawl data show mass mortalities of young-of-the-year croaker during some cold winters (VIMS, Ichthyology Department, unpubl. data).

### Feeding Mechanisms

The Sciaenidae have the widest spectrum of

feeding niches of any fish family in the Chesapeake Bay. The four most abundant species, *Cynoscion regalis*, *Bairdiella chrysoura*, *Micropogonias undulatus*, and *Leiostomus xanthurus*, are most abundant in the estuary from late spring to fall, especially young-of-the-year and yearlings (see previous sections). Under these conditions, food resources may be limiting and division of feeding niches may have evolved in order to reduce competitive exclusion among the dominant species. Fishes that are closely related and show feeding niche segregation also often show morphological differentiation in the feeding apparatus (Keast and Webb 1966; Davis 1967; Keast 1970; Davis and Birdsong 1973; Emery 1973). This section of the paper examines the morphology of the feeding apparatus in *Larimus fasciatus*, *C.*

*regalis*, *B. chrysoura*, *M. undulatus*, *Menticirrhus saxatilis*, and *Leiostomus xanthurus* to test the hypothesis that adaptations to feeding niche division have evolved among those six species.

Characters important in feeding were examined including mouth position and size, dentition, number of gill rakers, and intestine length. These directly affect the size and kind of food ingested and digested. Other accessory characters examined were the pore and barbel system on the snout and/or lower jaw, the nares, and body shape.

Mouth Position

Mouth position and size of the opening limit the size of prey and habitats in which a predator can effectively capture prey. These characters were

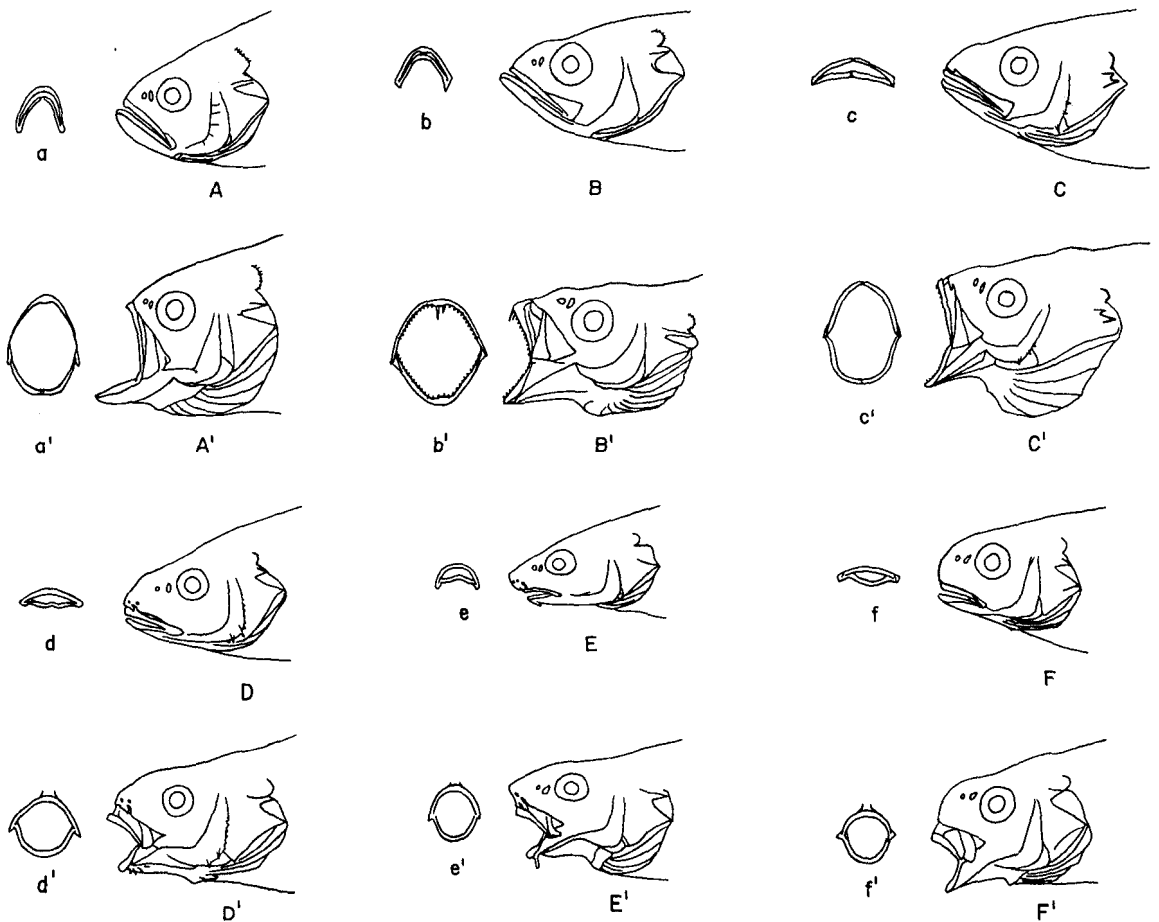


FIGURE 20.—Mouth position and opening in juveniles of six species of sciaenids: A, A', a, a', *Larimus fasciatus*; B, B', b, b', *Cynoscion regalis*; C, C', c, c', *Bairdiella chrysoura*; D, D', d, d', *Micropogonias undulatus*; E, E', e, e', *Menticirrhus saxatilis*; F, F', f, f', *Leiostomus xanthurus*. A-F, mouth closed. A'-F' mouth wide open. Front view of mouth openings (lower case letters) in corresponding positions.

studied from freshly caught and preserved specimens. *Larimus fasciatus* has the most oblique mouth (Figure 20A) with the lower jaw projecting strongly in front of the nonprotrusible upper jaw. The maxilla (Figure 21A) is under the lateral margin of the rostral fold and its anterior end is firmly attached to the premaxilla and skull (dermethmoid). As the mouth opens, the distal ends of the premaxilla and maxillae push forward as the lower jaw is lowered (Figure 20A'). The mouth opens widely. *Cynoscion regalis* has a large oblique mouth with the tip of the lower jaw projecting in front of the nonprotrusible upper jaw (Figure 20B). The anterior end of the maxilla is firmly attached to the premaxilla and articulates with the dermethmoid (Figure 21B). As the mouth is opened, the posterior end of the premaxilla and the lower jaw move forward (Figure 20B'). The mouth opens widely. *Bairdiella chrysoura* has a similar mechanism of jaw movement (Figure 20C'), but

the mouth is only slightly oblique with the lower jaw about equal in length to the upper jaw (Figures 20C, 21C). *Micropogonias undulatus* has an inferior mouth with the tip of the lower jaw enclosed by the protrusible upper jaw (Figure 20D). The anterior end of the maxilla is loosely attached to the premaxilla (Figure 21D). As the mouth is opened, the entire premaxilla and the lower jaw move anteroventrally (Figure 20D'). The mouth opens widely. *Menticirrhus saxatilis* and *Leiostomus xanthurus* have a similar mechanism of jaw movement but their upper jaws seem more protrusible (Figures 20E', F'; 21E, F). Their gape is small. In *M. saxatilis*, the mouth is inferior and the lower jaw is enclosed by the upper jaw (Figure 20E). *Leiostomus xanthurus* also has a small inferior mouth (Figure 20F) with a small gape.

The mouth position indicates that *Larimus fasciatus*, *C. regalis*, and *B. chrysoura* are pelagic feeders (Figure 20A-C) and that *Micropogonias*

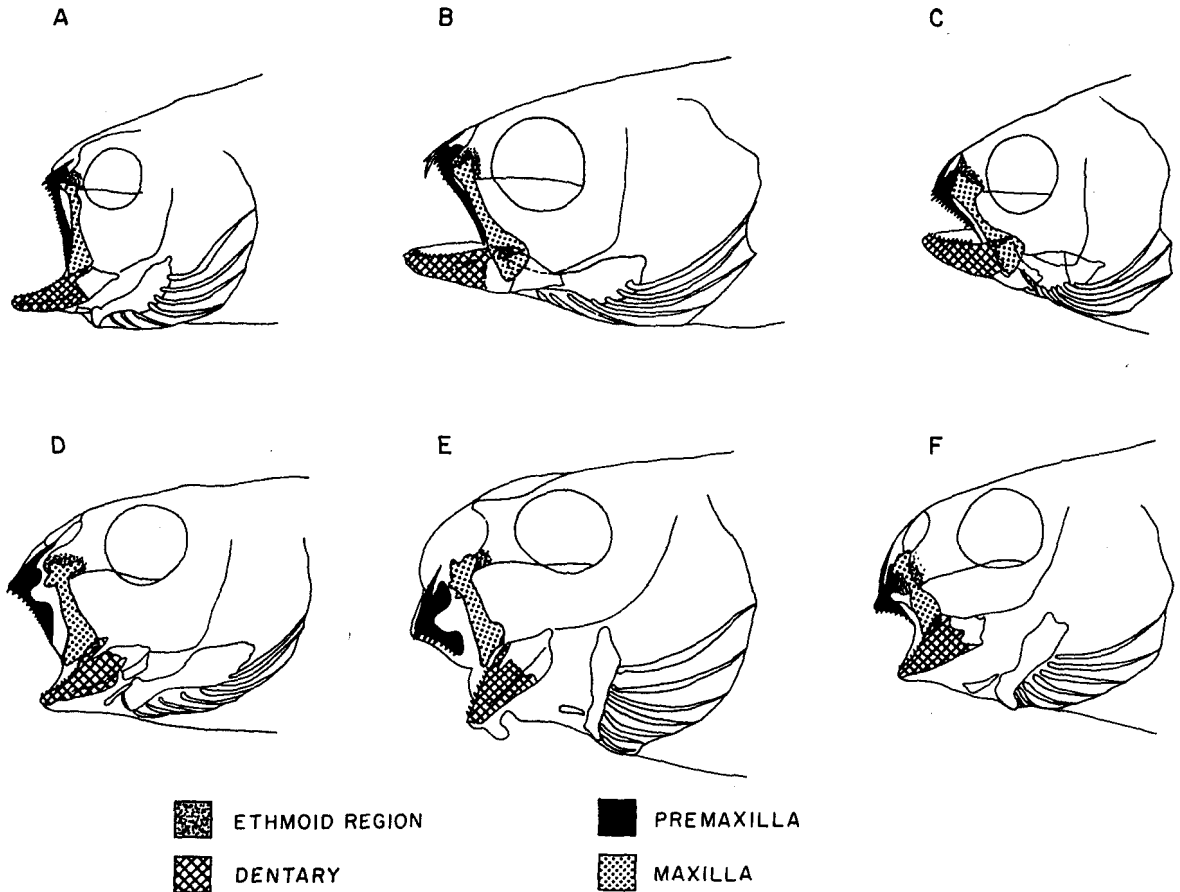


FIGURE 21.—Jaw bones involved in mouth opening in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*.



*undulatus*, *Menticirrhus saxatilis*, and *Leiostomus xanthurus* feed on the bottom (Figure 20D-F). The relative length of the premaxilla and dentary bones decreases and the height of the anterior dorsal process of the premaxilla increases from fishes adapted to feed in "midwater" to those adapted to feed on the bottom (Figure 21). This trend is also evident in the relative mouth size and angle (Figure 21A-F). An index number (Table 5), the length of the upper jaw multiplied by the length of the lower jaw then divided by head length, decreases through the series of species towards a bottom feeding habit.

Bottom feeders, *M. undulatus*, *L. xanthurus*, and *Menticirrhus saxatilis*, have protrusible premaxillae (Figures 20D'-F', 21D-F). This can be advantageous in getting the mouth opening close to food that is to be sucked in from the bottom (Alexander 1967). Midwater feeders, *Larimus fasciatus*, *C. regalis*, and *B. chrysoura*, lack the protrusibility of the premaxillae (Figures 20A'-C'; 21A-C); *C. regalis* and *B. chrysoura* may compensate for this with faster swimming speed. Gero (1952) and Nyberg (1971) have discussed this aspect in detail. *Larimus fasciatus* differs from other sciaenids studied here. It may swim around with its mouth open using its gill rakers as a filter similar to that of *Engraulis* (Günther 1962).

Dentition

Teeth on the premaxilla and dentary are important in capturing prey whereas the pharyngeal teeth are used for grinding and/or transporting food to the esophagus. Members of the genus *Cynoscion* usually have a pair of enlarged canine teeth at the tip of the upper jaw (Figures 21B, 22B). Other teeth are conical and present on narrow bands of the premaxilla and dentary. The tips of the upper and lower jaws are broad and have several rows of teeth which decrease in number to a single prominent row on the narrower posterior

portion of the jaws. Small teeth also develop inside the larger row of upper jaw teeth and outside the lower jaw teeth. *Bairdiella chrysoura* has a narrow band of teeth similar to *C. regalis* but lacks large canine teeth at the tip of the upper jaw (Figure 22C). *Micropogonias undulatus*, *Leiostomus xanthurus*, and *Menticirrhus saxatilis* have villiform teeth set in broad bands on the premaxillae and dentaries, and also lack canine teeth (Figure 22D-F). The teeth on the outer row of the premaxillae and inner row of the dentaries are slightly enlarged. *Larimus fasciatus* is unique in having only one or two rows of small teeth on both jaws (Figure 22A).

Pharyngeal teeth are generally conical in sciaenids (Figure 23). The lower pharyngeal teeth form a pair of separate narrow tooth patches and are situated on the most medial pairs of ceratobranchial bones. The upper pharyngeal teeth occur mainly as two pairs of patches on the two most medial pairs of epibranchial bones. The pharyngeal plates are relatively small and narrow in *L. fasciatus* and *C. regalis* compared with the other sciaenids examined (Figure 23A, B). The pharyngeal teeth of *L. fasciatus* and *C. regalis* are sharp, conical, and directed backward, but in *B. chrysoura* the pharyngeal teeth are blunt and the median ones are enlarged (Figure 23C). *Micropogonias undulatus* has much stronger and more enlarged pharyngeal teeth along the median rows (Figure 23D). *Menticirrhus saxatilis* has fine and sharp pharyngeal teeth (Figure 23E). *Leiostomus xanthurus* develops molariform teeth medially on the pharyngeal plates (Figure 23F). These sequential morphological differences in pharyngeal teeth reflect the feeding niche differentiation from midwater to benthic.

Gill Rakers

Gill rakers on the branchial arches of fishes are important in protecting the delicate gill filaments

TABLE 5.—Relative size of mouth and eye diameter in juveniles of six species of sciaenids from the York River.

Species	SL (mm)	Head length (mm)	Index of mouth size <sup>1</sup>				Eye diameter in % of SL			
			Range	x	SD	N	Range	x	SD	N
<i>Larimus fasciatus</i>	55.3-107	18.7-36.3	3.17-5.90	4.634	0.957	20	7.38- 9.84	8.602	0.672	21
<i>Cynoscion regalis</i>	35.2- 75.3	12.7-29.6	1.93-3.54	2.827	0.518	22	8.20-11.45	9.55	0.782	26
<i>Bairdiella chrysoura</i>	38.4- 77.5	14.3-27.4	1.76-3.08	2.494	0.431	17	8.27-10.82	9.407	0.677	20
<i>Micropogonias undulatus</i>	35.5-116	12.1-39.3	1.20-2.41	1.686	0.325	30	6.45- 9.46	7.850	0.837	30
<i>Menticirrhus saxatilis</i>	29.2- 99.6	9.3-29.0	0.50-1.37	0.957	0.264	30	6.03- 8.56	7.043	0.644	30
<i>Leiostomus xanthurus</i>	47.4-146	18.0-41.3	0.77-2.64	1.472	0.477	30	7.05-11.11	9.139	0.889	46

<sup>1</sup>Index of mouth size = (upper jaw length × lower jaw length)/head length.

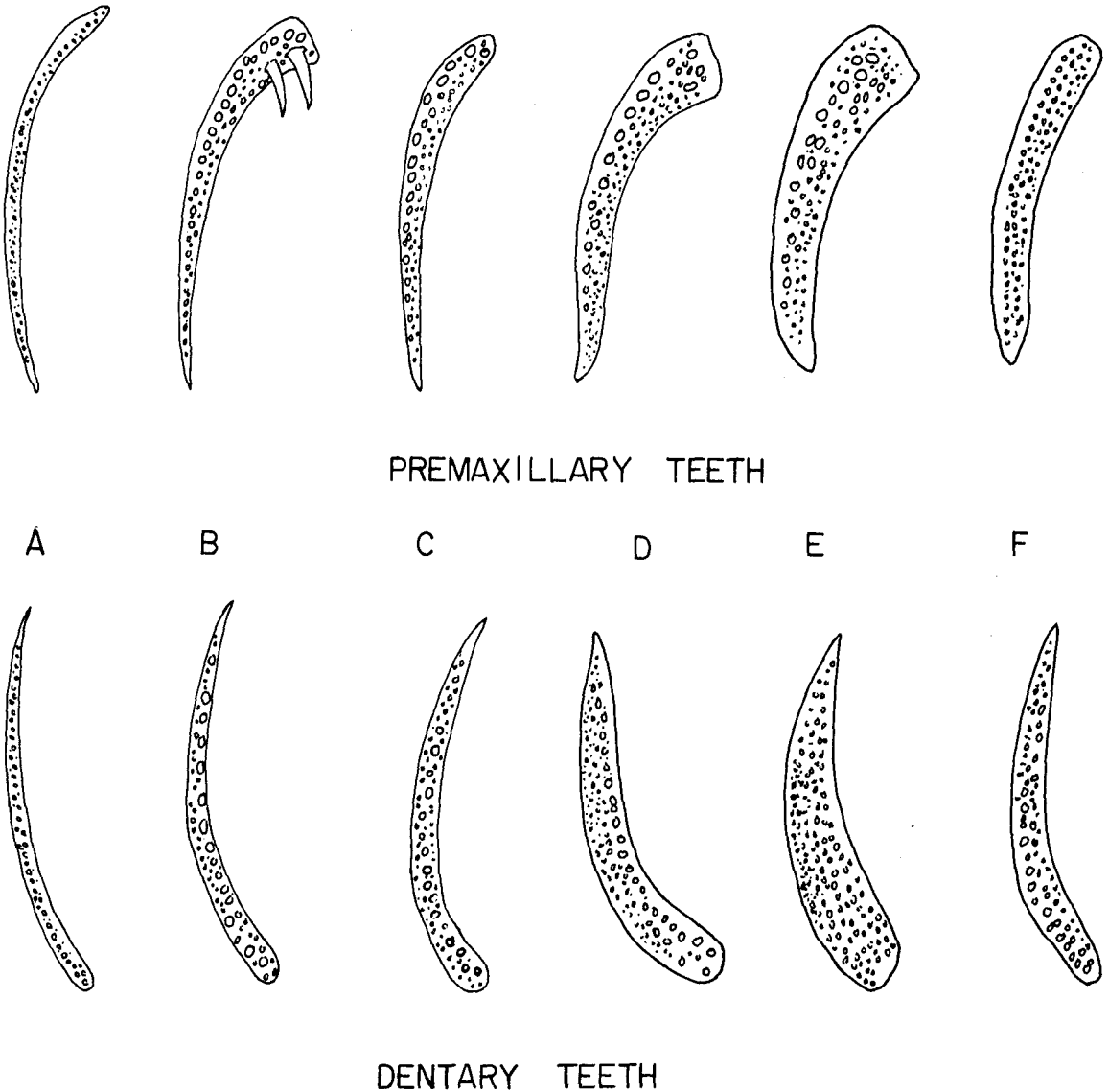


FIGURE 22.—Dentition of right premaxilla and dentary in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*. Posterior end toward the middle of the figure.

from abrasion by ingested materials and may also be adapted to particular food and feeding habits. In sciaenids, the gill rakers reflect feeding niche by their numbers, size, and shape. They are found on the dorsolateral surface of the branchial arch (Figure 24) and along its inner surface. The lateral gill rakers are well developed only on the first gill arch and the inner (or medial) gill rakers occur only as tubercles on all five gill arches. Only the

rakers on the first gill arch are discussed here.

*Menticirrhus saxatilis* and *C. regalis* have the fewest gill rakers (Table 6). *Bairdiella chrysoura* and *Micropogonias undulatus* have an intermediate number and *L. xanthurus* and *Larimus fasciatus* have the most gill rakers. Numbers of inner gill rakers (Table 6) follow a similar sequence. The relative size of the gill rakers and their morphology differ among species (Figure 24).

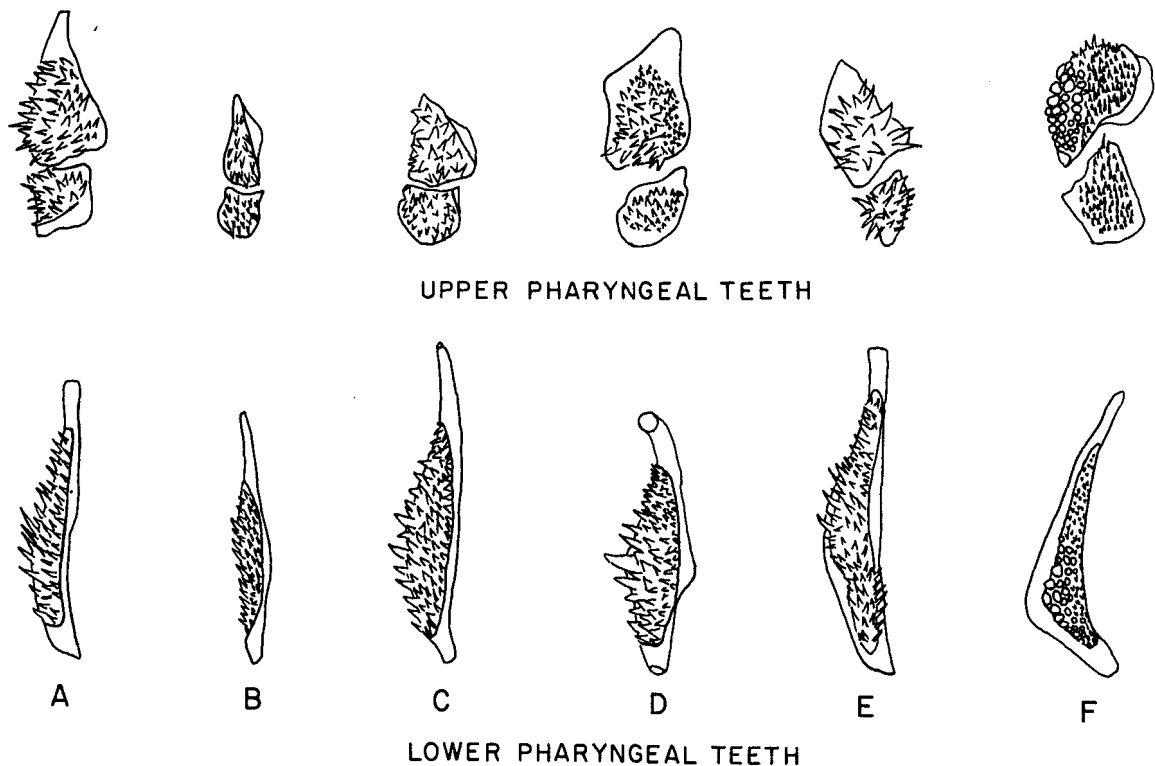


FIGURE 23.—Portions of left pharyngeal teeth in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*. Posterior end toward the middle of the figure.

TABLE 6.—Total number of lateral and inner gill rakers in juveniles of six species of sciaenids from the York River.

Species (size in mm SL)	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	N	$\bar{x}$		
<i>Menticirrhus saxatilis</i> (29.2-99.6)						6	11	9	3	1											30	12.04		
<i>Cynoscion regalis</i> (35.2-75.3)											1	8	13	13	2							37	17.19	
<i>Micropogonias undulatus</i> (35.5-116)															1	—	3	16	15	7		42	22.55	
<i>Bairdiella chrysoura</i> (38.4-75.3)																	2	3	13	14	1	33	24.27	
																						[20]	[15.70]	
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	N	$\bar{x}$
<i>Leiostomus xanthurus</i> (47.4-148)													4	7	6	12	9	13	3	1			55	32.29
<i>Larimus fasciatus</i> (55.3-107)																							[44]	[27.18]
																							22	38.00
																							[21]	[21.04]

[ ] medial gill rakers.

*Larimus fasciatus* has the longest and the most closely spaced gill rakers (Figure 24A). Each raker has many minute spicules scattered on it (Figure 24a). *Cynoscion regalis* and *B. chrysoura* have moderately long gill rakers compared with the length of the gill filaments (Figure 24B, C). Numerous minute spicules are also present on each raker, especially the basal portion (Figure 24b, c). *Micropogonias undulatus* has relatively

shorter gill rakers (Figure 24D) with seemingly strong serrations limited to the basal half of the raker (Figure 24d). The relative lengths of the lateral gill rakers in *Menticirrhus saxatilis* and *Leiostomus xanthurus* are the shortest (Figure 24E, F) and lack strong spicules (Figure 24e, f). *Leiostomus xanthurus* has only slightly denticulate gill rakers and *M. saxatilis* has smooth gill rakers.

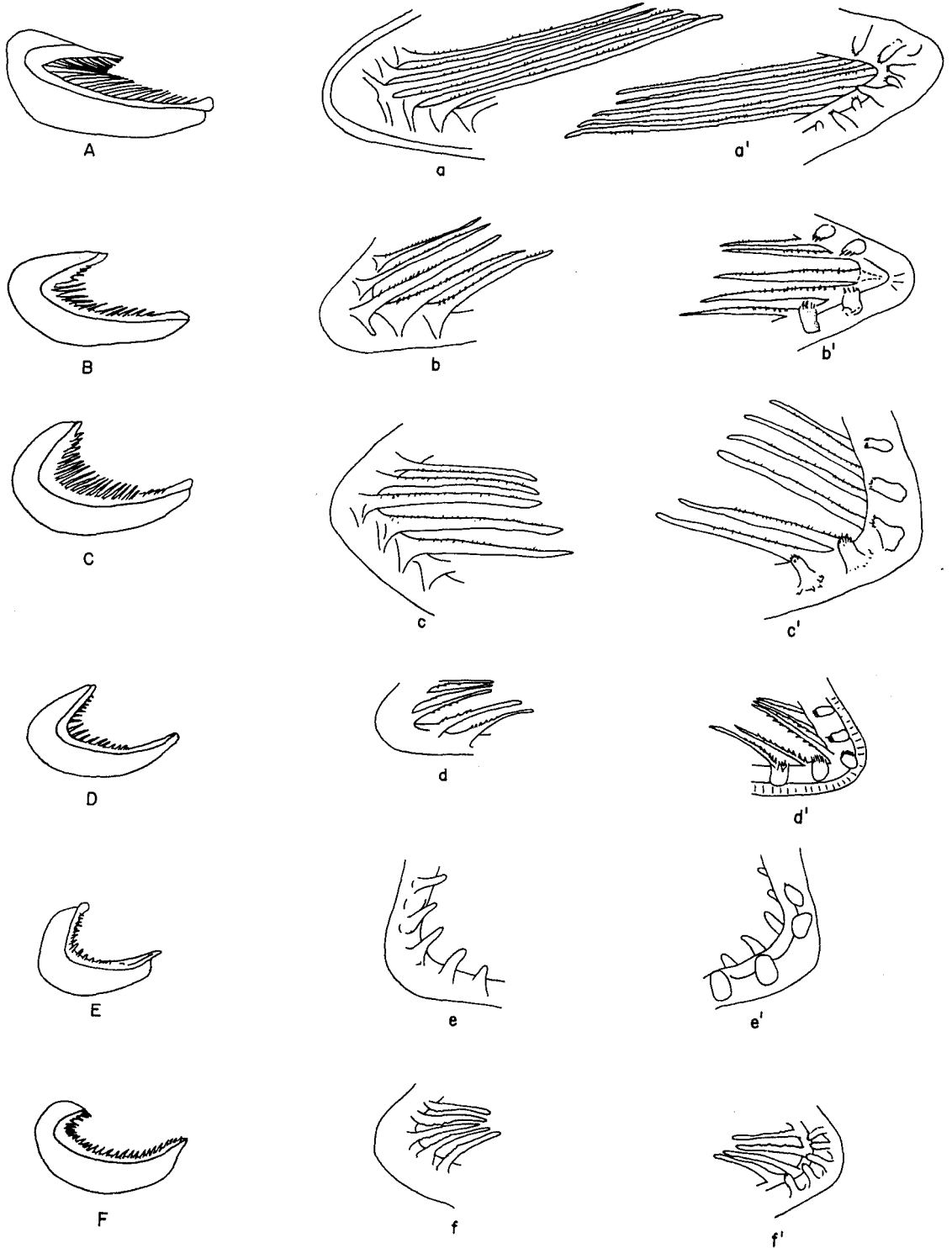


FIGURE 24.—First right gill arch in juveniles of six species of sciaenids: A, a, a', *Larimus fasciatus*; B, b, b', *Cynoscion regalis*; C, c, c', *Bairdiella chrysoura*; D, d, d', *Micropogonias undulatus*; E, e, e', *Menticirrhus saxatilis*; F, f, f', *Leiostomus xanthurus*. a-f, lateral view at the corner, a'-f', medial view at the corner.

The inner gill rakers are knoblike, sometimes with spicules or teeth on their distal ends (Figure 24a'-f'). *Cynoscion regalis*, *Micropogonias undulatus*, and *Menticirrhus saxatilis* have broad, short inner gill rakers, with the height not longer than the width of the base. *Cynoscion regalis* and *Micropogonias undulatus* have prominent spicules at the distal ends of their inner gill rakers (Figure 24b', d'). *Menticirrhus saxatilis* lacks spicules on its inner gill rakers (Figure 24e'). *Larimus fasciatus*, *B. chrysoura*, and *Leiostomus xanthurus* have long inner gill rakers, with the height longer than the width of the base. *Larimus fasciatus* and *B. chrysoura* have prominent spicules at the distal ends of their inner gill rakers (Figure 24b', c'). *Leiostomus xanthurus* has minute spicules on its inner gill rakers (Figure 24f'). Furthermore, in *Larimus fasciatus* a small inner gill raker is often present in between the larger inner gill rakers (Figure 24a'). This is rather common among western Atlantic sciaenids (Chao in press).

The lateral and inner gill rakers on the second to fifth gill arches are similar in size and structure to the inner gill rakers on the first gill arch. The gill arches of these six species also differ in the relative lengths of the epibranchial (upper) arm and ceratobranchial (lower) arm (Figure 24). *Leiostomus xanthurus* has the shortest upper arm and *M. saxatilis* has the shortest lower arm. The numbers and size of the gill rakers indicate that midwater feeders have lateral rakers longer than those of bottom feeders. The relative lengths of inner rakers are longer in fishes with higher numbers of lateral rakers, e.g., *Larimus fasciatus* and *Leiostomus xanthurus* (Figure 24a', f'; Table 6). Although *Micropogonias undulatus* has the strongest spicules on the lateral gill rakers (Figure 24d), the midwater feeders usually have better developed spicules on the lateral rakers than the bottom feeders (Figure 24). Higher numbers of rakers (both inner and lateral) are associated with filter feeding.

Digestive Tract

The digestive tract of sciaenids includes four parts: esophagus, stomach, pyloric caeca, and intestine. The intestine usually has two loops (Figure 25), except that of *C. regalis* which is a straight tube from stomach to anus (Figure 25B). The relative position and size of the stomach and intestine vary with the amount of food present. The num-

bers of pyloric caeca and the relative length of the intestine may be correlated with feeding habits (Suyehiro 1942). The relative length of the intestine of these six species of sciaenid fishes (Table 7) may be grouped into three general categories. *Cynoscion regalis* has the shortest intestine, less than half the standard length. *Bairdiella chrysoura* has an intermediate intestine length. *Micropogonias undulatus*, *Menticirrhus saxatilis*, *Larimus fasciatus*, and *Leiostomus xanthurus* have long intestines. The numbers of pyloric caeca (Table 8) in these six sciaenid fishes show a similar trend. *Cynoscion regalis* has the fewest pyloric caeca, four or five. *Bairdiella chrysoura* and *M. saxatilis* usually have 6 or 7, and *Micropogonias undulatus* and *L. xanthurus* have 7 to 10 pyloric caeca. *Larimus fasciatus* has the most, 10 or 11. *Larimus fasciatus* and *Leiostomus xanthurus* have both a longer intestine and more pyloric caeca, but *Larimus fasciatus* is a midwater feeder and *Leiostomus xanthurus* is a bottom feeder. They both consume large numbers of small crustaceans (see "Food Specialization" section). *Cynoscion regalis* has the shortest intestine and the fewest pyloric caeca. Its diet is mainly composed of large crustaceans and fishes. Thus, the relative lengths of the intestine and the numbers of pyloric caeca in these sciaenids may be correlated with the size of the food rather than the feeding position in the water column.

TABLE 7.—Relative length of intestine in juveniles of six species of sciaenids from the York River.

Species	SL (mm)	Intestine length in % of SL			
		Range	$\bar{x}$	SD	N
<i>Cynoscion regalis</i>	35.2-152	35.5-49.6	40.24	3.07	36
<i>Bairdiella chrysoura</i>	30.0-151	46.1-64.1	55.34	5.92	30
<i>Micropogonias undulatus</i>	35.5-145	52.3-88.6	65.57	6.56	39
<i>Menticirrhus saxatilis</i>	29.2-91.2	56.6-88.2	76.06	6.67	26
<i>Larimus fasciatus</i>	35.3-99.8	73.1-97.7	83.87	9.08	14
<i>Leiostomus xanthurus</i>	47.4-166	73.6-97.8	84.69	6.95	30

TABLE 8.—Number of pyloric caeca in juveniles of six species of sciaenids from the York River.

Species (size in mm SL)	4	5	6	7	8	9	10	11	N	$\bar{x}$	
<i>Cynoscion regalis</i> (35.2-82.4)	20	14							34	4.41	
<i>Bairdiella chrysoura</i> (30.0-75.3)			8	20	1				29	6.76	
<i>Menticirrhus saxatilis</i> (29.2-99.6)			11	19					30	6.63	
<i>Micropogonias undulatus</i> (35.5-116)					1	25	11		37	8.27	
<i>Leiostomus xanthurus</i> (47.4-148)					6	13	8	1	28	8.14	
<i>Larimus fasciatus</i> (55.3-107)								9	6	15	10.4

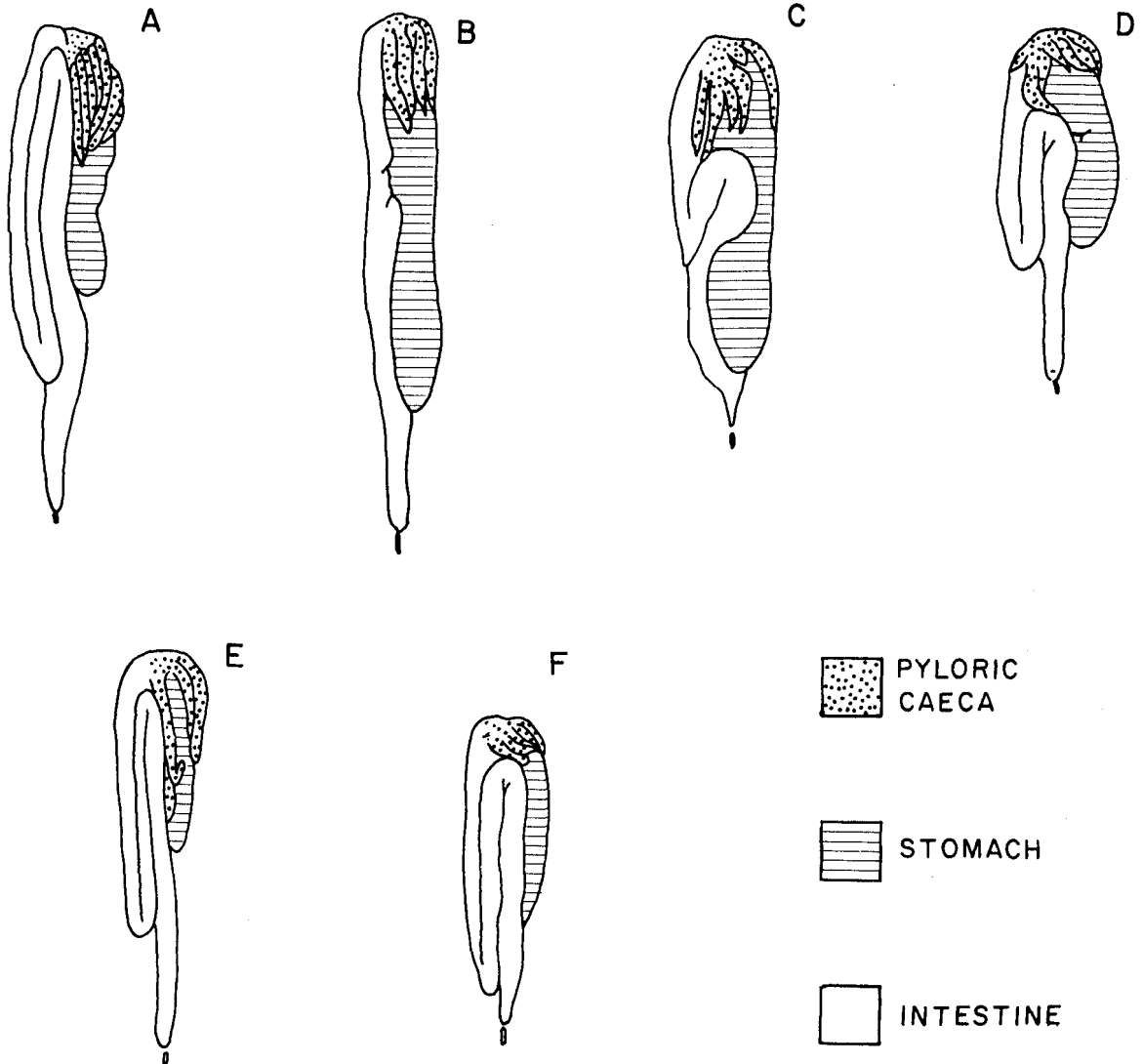


FIGURE 25.—Ventral view of the digestive tract in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*.

#### Pores and Barbels

The pores on the snout and the tip of the lower jaw, and mental barbels in fishes are sense organs probably involved in touch, taste, or both. The number and arrangement of the pores and barbels in sciaenid fishes are closely related to their feeding habitats (Chao 1976). These six species of sciaenid fishes show a gradual increase in the number and size of pores from upper water column feeders to lower water column and bottom feeders (Figure 26). *Larimus fasciatus* has five marginal

pores on the snout and four minute pores at the tip of the underside of the lower jaw (Figure 26A, a). *Cynoscion regalis* has only two marginal pores on the snout and no pores or barbels on the lower jaw (Figure 26B, b). *Bairdiella chrysoura* has five marginal and five upper pores on the snout, and six mental pores at the tip of the lower jaw (Figure 26C, c). *Leiostomus xanthurus* has five marginal and five upper pores on the snout, and five mental pores at the tip of the lower jaw (Figure 26F, f).

*Micropogonias undulatus* also has five marginal and five upper pores on the snout, and five mental

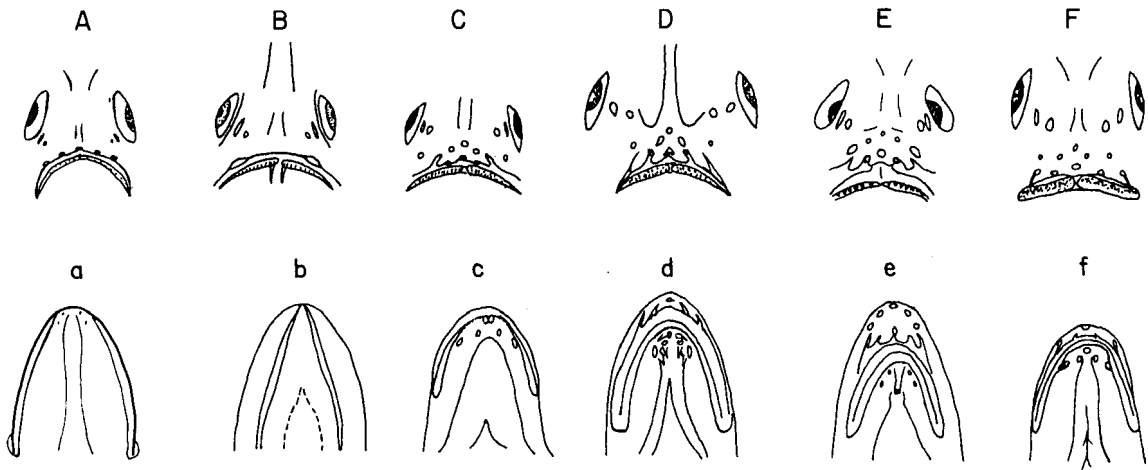


FIGURE 26.—Anterior view of snout (capital letters) and ventral view of lower jaw (lower case letters) in juveniles of six species of sciaenids: A, a, *Larimus fasciatus*; B, b, *Cynoscion regalis*; C, c, *Bairdiella chrysoura*; D, d, *Micropogonias undulatus*; E, e, *Menticirrhus saxatilis*; F, f, *Leiostomus xanthurus*.

pores plus six minute barbels at the tip of the lower jaw (Figure 26D, d). *Menticirrhus saxatilis* has five marginal pores and three upper pores on the snout, and four mental pores and a short, rigid barbel at the tip of the lower jaw (Figure 26E, e). An apical pore is also present on the barbel of *M. saxatilis*. The anterior margin of the snout (rostral fold) in *Larimus fasciatus* and *C. regalis* is complete without notches (Figure 26A, B). *Bairdiella chrysoura* and *Leiostomus xanthurus* have a slightly indented rostral fold (Figure 26C, F), although the former has a terminal mouth and the latter has an inferior mouth (Figure 26c, f). Both *M. saxatilis* and *Micropogonias undulatus* have deeply notched rostral folds (Figure 26D, E), correlated with their inferior mouth positions. The mental pores of *Larimus fasciatus* (Figure 26a) are the smallest of these sciaenids. The barbels of *M. undulatus* and *Menticirrhus saxatilis* may differ in function as well as in number, because the single barbel of *M. saxatilis* has a pore at the tip, whereas barbels of *Micropogonias undulatus* do not (Figure 26d, e). The numbers and size of pores increase from species to species as the feeding niche tends toward the bottom; barbels are present only in the bottom feeders.

of skin is sometimes also present along the posterior margin of the anterior nostril in bottom feeding species. The nasal cavity is generally oval shaped with a cluster of olfactory laminae forming a nasal rosette anteriorly. *Larimus fasciatus* has the shortest nasal cavity from anterior to posterior nostril (Figure 27A), and *Leiostomus xanthurus* has the longest (Figure 27F). The shape of the nasal rosettes and olfactory laminae are similar in these six species of sciaenid fishes. The mean number of laminae (averaging both sides per specimen and rounding upwards) differs among these species (Table 9) and is variable within a species. The numbers of laminae are 11 to 14 in *Larimus fasciatus*; 12 to 22 in *C. regalis*; 12 to 25 in *B. chrysoura*; 10 to 31 in *M. undulatus*; 11 to 22 in *Menticirrhus saxatilis*; and 16 to 30 in *Leiostomus xanthurus*. *Larimus fasciatus*, *C. regalis*, and *B. chrysoura* average fewer laminae than *Micropogonias undulatus*, *L. xanthurus*, and *Menticirrhus saxatilis* (Table 9). Within a species, the number of nasal laminae seems higher in larger specimens. The maximum number of nasal laminae tends to be greater in bottom feeding fishes.

#### Other Morphological Characters

Differences in body shape, mouth structure, food specialization, and habitat preferences of fishes may act to restrict interspecific competition within a fauna (Keast and Webb 1966). The six species of sciaenid fishes discussed here show a

#### Nares

Sciaenid fishes have two pairs of closely set nostrils. The anterior one is usually round; the posterior one is oval and elongate (Figure 27). A flap

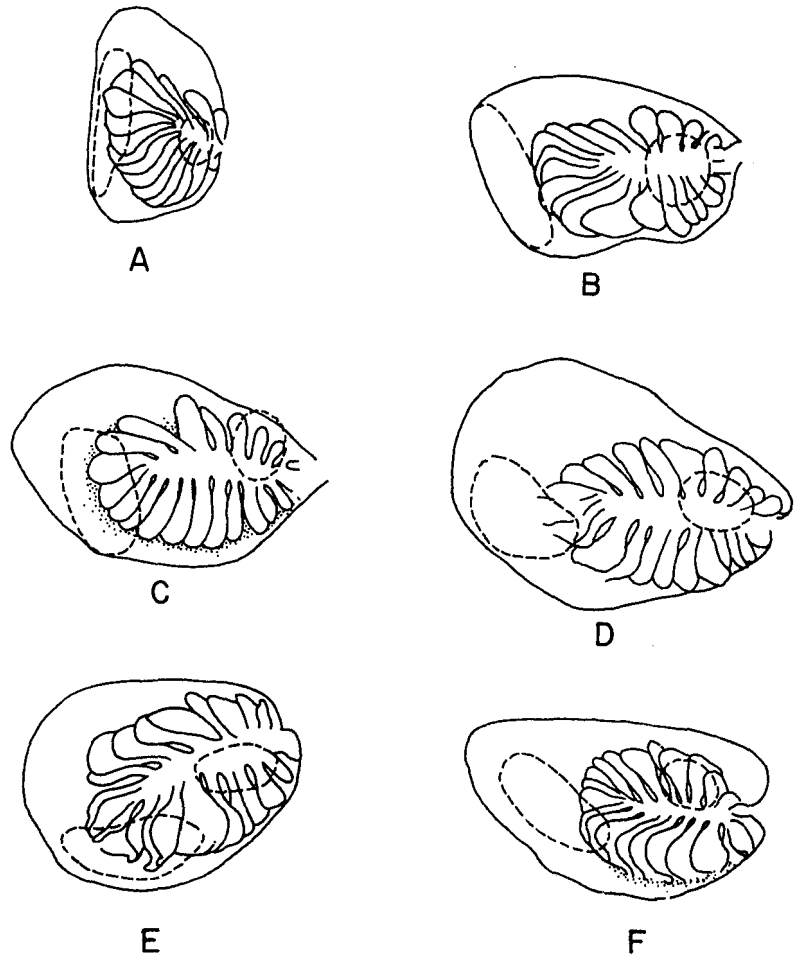


FIGURE 27.—Right olfactory rosette and nasal cavity in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*. Dotted circles represent nostrils, the anterior nostril to the right.

TABLE 9.—Number of laminae in olfactory rosettes in juveniles of six species of sciaenids from the York River.

Species (size in mm SL)	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	N	$\bar{x}$	
<i>Larimus fasciatus</i> (55.3-107)		3	5	2	5																		15	12.6	
<i>Cynoscion regalis</i> (35.2-86.4)			1	6	6	4	7	5	1	2	1	1	2											36	15.9
<i>Bairdiella chrysoura</i> (30.0-75.3)			2	2	2	8	4	6	2	6	3	—	—	1	—	1								37	16.8
<i>Micropogonias undulatus</i> (35.5-116)	1	1	—	—	3	3	4	3	3	—	2	1	2	3	2	—	2	1	1	1		1	34	19.5	
<i>Menticirrhus saxatilis</i> (29.2-99.6)		1	—	—	1	6	6	3	3	6	3	2	1											32	17.3
<i>Leiostomus xanthurus</i> (47.4-148)								1	2	4	4	3	2	7	6	—	1	5	1	—	—	1		37	21.7

correlation between body shape and feeding habitat (Figure 28). Young *Larimus fasciatus* are oblong, relatively deep, and have a compressed body and a double truncate tail (Figure 28A). These features, in combination with a strong oblique mouth and large eyes (Figure 20A, A'; Table 5), indicate that *L. fasciatus* is a moderate swimmer that feeds in the upper water column by sight.

Young *C. regalis* have a more fusiform and compressed body, and a long pointed tail (Figure 28B). These features, in combination with a large lique mouth and relatively large eyes (Figure 20B, 20B, B'; Table 5), indicate that *C. regalis* is a fast swimmer that feeds in the upper to middle water column by sight. Young *B. chrysoura* have an oblong and compressed body, and a broad and



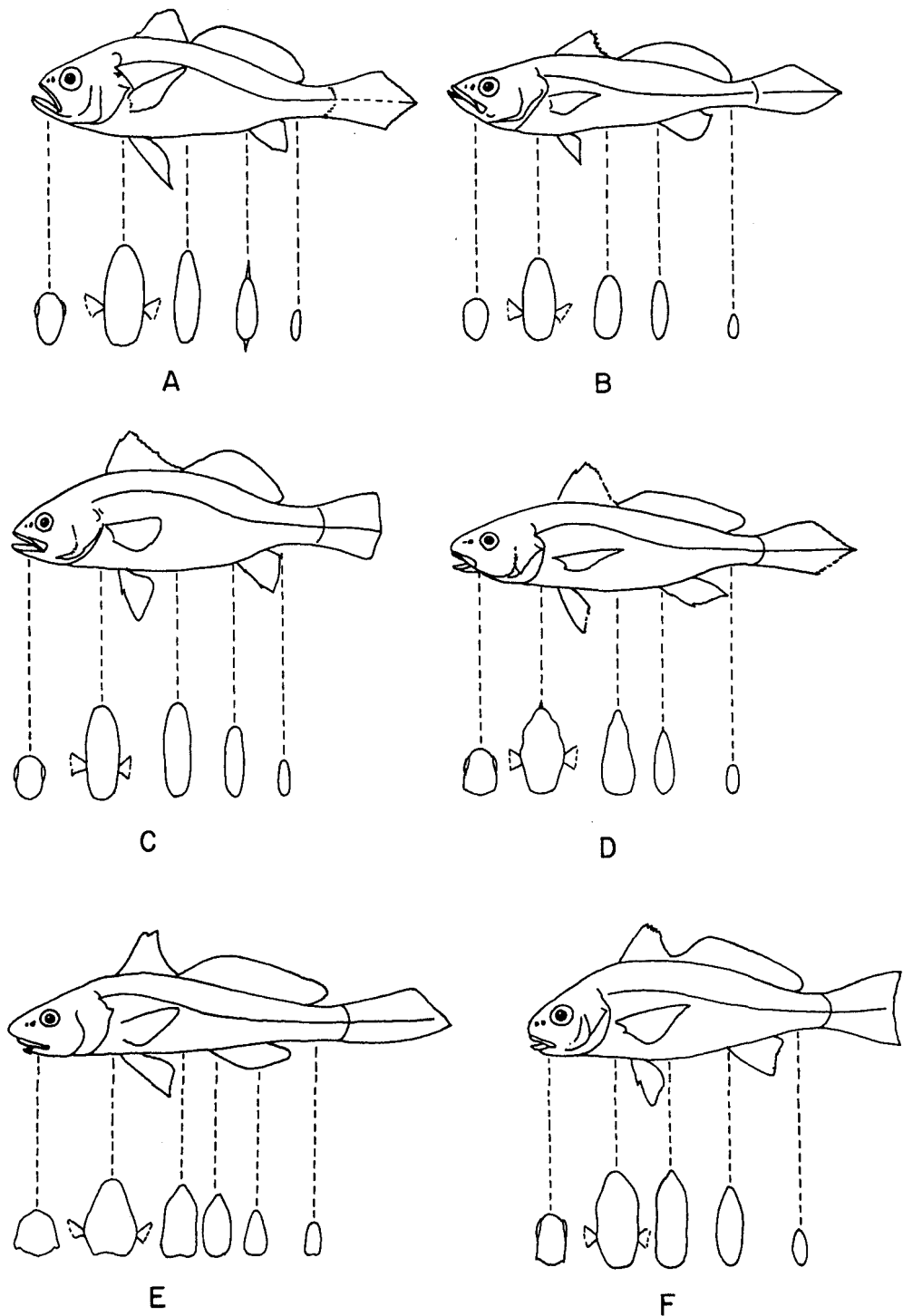


FIGURE 28.—Body shape and cross sections in juveniles of six species of sciaenids: A. *Larimus fasciatus*; B. *Cynoscion regalis*; C. *Bairdiella chrysoura*; D. *Micropogonias undulatus*; E. *Menticirrhus saxatilis*; F. *Leiostomus xanthurus*.

slightly rounded to truncate tail (Figure 28C). These features, together with its terminal mouth and relatively large eyes (Figure 20C, C'; Table 5), indicate that *B. chrysoura* is a moderately fast swimmer that feeds in the middle water column by sight. Young *Micropogonias undulatus* have an elongate and less compressed body and a long pointed tail (Figure 28D). These features, combined with an inferior mouth with barbels and relatively smaller eyes (Figure 20D, D'; Table 5), indicate that *M. undulatus* is a moderately fast swimmer that feeds in the lower water column by sight, olfaction, and touch. Young *Leiostomus xanthurus* have a rather short and deep body, and a broad and truncate tail (Figure 28F). These features, combined with an inferior mouth and large eyes (Figure 20F, F'; Table 5), indicate that *L. xanthurus* is a slow swimmer that feeds in the lower water column by sight and olfaction. Young *Menticirrhus saxatilis* have an elongate, round, and narrow body, and a relatively pointed tail (Figure 28E). These features, combined with an inferior mouth with a pored-barbel (Figure 26e) and relatively smaller eyes (Figure 20E, E'; Table 5), indicate that *M. saxatilis* is a slow swimmer that feeds in the lower water column by olfaction and touch.

The cross sections of these young sciaenid fishes (Figure 28) also reflect their habitat. *Larimus fasciatus*, *C. regalis*, and *B. chrysoura* are compressed and have relatively narrow ventral surfaces (Figure 28A–C) in comparison to *Micropogonias undulatus*, *Leiostomus xanthurus*, and *Menticirrhus saxatilis* (Figure 27D–F). Some of these morphological characters, such as the shape of the tails and the size of the eyes, vary ontogenetically. Generally, most juvenile sciaenids have pointed tails and relatively larger eyes than adults.

### Food Specialization

The food habits of young sciaenids have been studied by numerous authors and the information reported by them is scattered and presented in different ways. Some of this work has been summarized for comparison with the present study (Tables 10–14). Only those studies having some sort of quantitative analysis were chosen for the comparison. Different authors have used different taxonomic categories to analyze their information. The classification of the food items in the present study has been modified from Darnell (1961) and Qasim (1972). Six major food groups

were employed more or less according to their vertical occurrence in the water column, from the upper water column to the bottom. They were fishes, macrozooplankton, microzooplankton, epibenthos, infauna, and other organic matter. Within each food group, several items were listed and the generic and specific names of the primary prey species in the study area were indicated. Boundaries for these six food groups are not definite because some prey taxa move vertically in the water column and some taxa may also include both pelagic and benthic species. Generalized terms used by many authors such as shrimps, annelids, mollusks, crabs, etc., were placed under respective food groups for the convenience of comparison. Food habits of each species were compared with previous studies from different geographic areas and seasons. Food items were listed in different categories for each species. Under each listed item, there were cases where more than a single food taxon was listed by the original authors. Then, the one that had the highest frequency (by occurrence, volume, or weight) was chosen to represent that item.

All fish specimens used for stomach analyses in this study were randomly selected from specimens collected in June to November (1972 to 1974). During this period, these sciaenids reach their maximum abundance and degree of sympatry. All specimens were young-of-the-year or yearlings.

#### *Larimus fasciatus*

Stomachs of 12 *L. fasciatus* (14–125 mm TL) were examined. All stomachs contained crustaceans, exclusively: *Neomysis americana* in seven stomachs, Cumacea in five, Amphipoda (mostly *Gammarus* spp.) in four, and calanoid copepoda (mostly *Acartia tonsa*) in two. Most of these prey species were of small size.

Published information on the food habits of *L. fasciatus* was scarce. Welsh and Breder (1923) reported on food of four *L. fasciatus* (50–110 mm SL) from Mississippi and Texas. Only two stomachs had food, one with a post-larval clupeoid and the other with "schizopodous forms" (crustacean remains).

#### *Cynoscion regalis*

Stomachs of 36 *C. regalis* (67–183 mm TL) were examined (Table 10). They fed mostly on *Anchoa mitchilli* and *N. americana*. *Anchoa mitchilli* was very abundant in the same area as *C. regalis* in the

TABLE 10.—Stomach contents of weakfish, *Cynoscion regalis*, from different estuarine areas along U.S. Atlantic coast.

Author Locality	Welsh and Breder 1923						Merriner 1975 Panlico Sound and Morehead City, N.C. June 1967-Jan. 1970 Table 1
	Chao 1976 York River, Va. June -Aug. 1973 Original	Acushnet River, Mass. Sept. 1882 p. 159	Cape Charles, Va. Sept. 1916 p. 160	Winyah Bay, S.C. July 1915 p. 161	Fernandina, Fla. Mar. 1920 p. 161		
Number of specimens	36	28	45	34	105	2,159	
Empty stomachs	2	5	0	5	74	1,342	
Length of specimens	70-183 mm TL	7-11 cm SL	43-11.5 cm SL	2.8-6.2 cm SL	5-17 cm SL	135-481 mm SL	
Quantitative method	% of occurrence	% of volume	% of volume	% of volume	% of volume	% of occurrence % of volume	
<b>Fishes:</b>							
<i>Anchoa mitchilli</i>	72.2					58.1	15.6
Others and remains	8.3	48.0	2.0	9	18	15.7	74.0
<b>Macrozooplankton:</b>							
Mysidace	2.8						
<i>Neomysis americana</i>	63.9					31.0	0.9
Isopoda		0.5		6			
Decapoda (shrimps)		47.0	0.5		46	0.1	
Others and remains			91.0	83	18	1.5	1.2
<b>Microzooplankton:</b>							
Copepoda			3.5	2			
<b>Epibenthos:</b>							
Polychaeta		0.5				0.5	
Amphipoda			3.0				0.1
Others and remains						1.5	
Unidentified remains	5.6	4.0			18	96.8	8.2
<b>Author</b>							
Thomas 1971							Stickney et al. 1975
Locality	Delaware River, Del.					Savannah River and	
Period	Aug. 1969					Ossabaw Sound, Ga.	
Source	June 1969 Table 20	July 1969 Table 20	Table 20	Sept. 1969 Table 20	Oct. 1969 Table 20	May 1972-July 1973 Table 1	
Number of specimens	71	94	94	120	66	120	
Empty stomachs	10	11	10	18	12	35	
Length of specimens	11-76 mm TL	5-123 mm TL	15-180 mm TL	20-180 mm TL	61-180 mm TL	30-169 mm SL	
Quantitative method	% of occurrence	% of occurrence	% of occurrence	% of occurrence	% of occurrence	% of occurrence	
<b>Fishes:</b>							
<i>Anchoa mitchilli</i>	17.0	114.9	116.0	133.3	134.8		
Others and remains	1.4	2.1	1.1	3.3	4.5		2.5
Others and remains	2.8	7.4	13.8	12.5	30.3		31.7
<b>Macrozooplankton:</b>							
Mysidace	74.6	59.6	65.8	66.7			0.8
<i>Neomysis americana</i>							55.0
Isopoda		4.3	2.1	1.7			2.5
Decapoda (shrimps)		2.1	3.2	6.7	10.6		2.5
Others and remains							
<b>Microzooplankton:</b>							
Copepoda	19.7	4.3	2.1	3.3			5.0
Calanoid							2.5
Others and remains	9.9	4.3	1.1	0.8	1.5		
<b>Epibenthos:</b>							
<i>Neris succinea</i>							15.0
Amphipoda							2.5
<i>Gammarus</i> sp.	9.9	58.5	58.5	28.3	28.8		1.7
Others and remains							9.2
Unidentified remains							2.5

<sup>1</sup>All fishes combined.

same months (Colvocoresses 1975; Markle 1976). Fishes and planktonic crustaceans were the major food items of *C. regalis* (Table 10). A shift of food habits with growth was noted by Thomas (1971), Merriner (1975), and Stickney et al. (1975). The smaller weakfish fed more on mysid shrimp and the larger weakfish fed more on fishes.

*Bairdiella chrysoura*

Stomachs of 68 *B. chrysoura* (57-190 mm TL) were examined (Table 11). They fed mainly on *N. americanus* and *A. mitchilli*. In other areas, juvenile *B. chrysoura* fed mainly on crustaceans

and fishes (Table 11). Smaller specimens (<40 mm SL) fed mostly on copepods but as they grew they fed more on *N. americanus*, amphipods, and other larger crustaceans. Fishes became more important food items for specimens over 70 mm SL (Thomas 1971; Carr and Adams 1973; Stickney et al. 1975).

*Micropogonias undulatus*

Stomachs of 69 *M. undulatus* (65-199 mm TL) were examined (Table 12). They showed as wide a variety of prey items as have previous studies from other geographic areas (Table 12). Polychaetes

TABLE 11.—Stomach contents of silver perch, *Bairdiella chrysoura*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author Locality Period Source	Chao 1976 York River, Va. June-Aug. 1973 Original	Thomas 1971 Delaware River, Del. Aug.-Oct. 1969 Table 46	Welsh and Breder 1923 Cape Charles, Va. Sept. 1916 p. 174-175
Number of specimens	68	99	21
Empty stomachs	10	9	0
Length of specimens	57-153 mm TL	5-130 mm TL	6-8.2 cm TL
Quantitative method	% of occurrence	% of occurrence	% of occurrence
Fishes		112.1	
<i>Anchoa mitchilli</i>	5.1	3.0	
Others and remains	20.7	8.1	1
Macrozooplankton:			
Mysidace	1.7	89.9	
<i>Neomysis americana</i>	74.1		
Isopoda	1.7	1.0	
Decapoda (shrimp)	10.3	17.2	5
Others and remains	1.7		87
Epibenthos:			
Annelida (polychaete)	3.5		2
<i>Neris succinea</i>	3.5		
Cumacea	1.7		
Amphipoda	1.7	15.2	5
<i>Gammarus</i> sp.	3.5	62.6	
Crabs		3.0	
Others and remains	1.7		
Infaua (bivalve and Nematoda)	3.5		
Unidentified remains	6.9	2.0	
Author Locality Period Source	Stickney et al. 1975 Savannah River and Ossabaw Sound, Ga. May 1972-July 1973 Table 1	Reid, 1954 Cedar Key, Fla. June 1950-May 1951 Table 5	Carr and Adams 1973 Crystal River, Fla. Oct. 1970-Aug. 1971 Estimate from Fig. 9
Number of specimens	161	45	6
Empty stomachs	48	0	0
Length of specimens	30-149 mm TL	25-99 mm SL	100-130 mm SL
Quantitative method	% of occurrence	% of occurrence	% of occurrence
Fishes:			
<i>Anchoa mitchilli</i>	2.7		
Others and remains	6.6	4.4	16.6
Macrozooplankton:			31.2
Mysidace	0.6		
<i>Neomysis americana</i>	25.1		
Isopoda	1.1		
Decapoda (shrimp)	5.5	73.3	33.3
Others and remains	8.2	4.4	66.6
Microzooplankton			51.6
Copepoda	3.9	4.0	
Others and remains	2.2		
Epibenthos:			
Annelida (polychaete)	0.6	2.2	7.3
<i>Neris succinea</i>	8.2		
Amphipoda	2.2	33.3	16.6
<i>Gammarus</i> sp.	6.0		
Crabs	8.2		16.6
Others and remains	0.6	6.6	
Unidentified remains			8

<sup>1</sup>All fishes combined.

and crustaceans were the main food items of the juvenile *M. undulatus* in the study area. Juvenile *M. undulatus* fed on a large variety of invertebrates and sometimes fishes (Table 12). Stickney et al. (1975) indicated that smaller specimens (<100 mm SL) depend extensively on harpacticoid copepods, which are mainly bottom dwellers. As the fish grow, they become more generalized feeders (Parker 1971). Geographic variation in food habits of juvenile *M. undulatus* (Table 12) probably is attributable to availability of prey species in the area.

#### *Menticirrhus saxatilis*

Stomachs of 20 *M. saxatilis* (36.5–118 mm TL) were examined. All contained crustaceans and

polychaetes were also important in their diet. The occurrence of organic detritus was also frequent suggesting that *M. saxatilis* is a bottom feeder. The literature also indicates that juvenile *M. saxatilis* feed mainly on crustaceans and polychaetes (Table 13). Welsh and Breder (1923) indicated that *M. saxatilis* fed mainly on relatively large crustaceans.

#### *Leiostomus xanthurus*

Stomachs of 77 *L. xanthurus* (73–205 mm TL) were examined. Although they showed a wide variety of food species, the major part of the food was benthic. *Pectinaria gouldii*, a burrowing polychaete, was a major food item in the diet of *L. xanthurus* in the study area. Stickney et al. (1975)

TABLE 12.—Stomach contents of croaker, *Micropogonias undulatus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author Locality	Chao 1976 York River, Va.	Thomas 1971 Delaware River, Del. Nov.-Dec. 1970 Table 71	Roelofs 1954 North Carolina coast All seasons 1950 Table 1	Welsh and Breder 1923		Stickney et al. 1975 Savannah River and Ossabaw Sound, Ga. May 1972-July 1973 Table 1	Hansen 1969 Pensacola, Fla. Aug. 1963-Dec. 1965 Table 5	Parker 1971					
				Winyah Bay, Cape Cana- veral, Fla. S.C. July 1915 p. 184	24 6			Lake Pontchartrain, La. Jan. 1963-Dec. 1965 Table 28	Clear Lake, Tex.				
Period Source	June-Aug. 1973 Original												
Number of specimens	69	25	159	37	24	196	2,520	63	44	1,866	475		
Empty stomachs	5	3	?	0	6	15	?	2	6	194	15		
Length of specimens	56-199 mm TL	23-50 mm TL	60-140 mm TL	4.2-6.2 cm SL		39-180 mm SL	76-173 mm TL	10-74 mm TL	75-124 mm TL	10-96 mm TL	70-110 mm TL		
Quantitative method	% of occurrence	% of occurrence	% of occurrence	% of volume		% of occurrence	% of volume		% of occurrence				
Fish and remains	20.3		3.1	0.7		7.5	15.9	11	9	4	5		
Macrozooplankton							114.3						
Mysidace	3.1	64.0	5.7			1.0		5	4.5	2	2		
<i>Neomysis americana</i>	35.9					16.9							
Isopoda	1.6	4.0				1.0		6.5	8.0	10.5	18.0		
Decapoda (shrimp)	9.4		3.1	7.0	24.0	3.0		17.0	18.5	19.5	14.5		
Insecta	1.6					0.5		3	18.5	13.0	20.0		
Others and remains	3.1			7.0									
Microzooplankton:													
Copepoda	3.1	76.0	25.2			7.0		2.0	6.5	1.0	3.0		
Calanoid	10.9					1.0							
Harpacticoid						10.0							
Ostracoda						0.5		8.0	12.0	9.0	8.0		
Others and remains	6.3		4.4	2.0									
Epibenthos:													
Annelids													
(polychaetes)	67.2		89.9	29.0	3.0	12.4	61.5	17.0	6.5	6.0	7.0		
<i>Neris succinea</i>	18.8					3.0							
<i>Glycinde solitaria</i>	9.4												
Phyllodocid	1.6												
Spionid	6.3												
Cumacea	4.7			2.0		6.0		4.0	4.5	5.0	16.0		
Amphipoda	21.9		5.7			8.0							
<i>Gammarus</i> sp.	7.9					9.5		17.0	10.0	16.0	10.5		
Crabs	3.1			1.8		4.5		17.0	18.5	22.0	18.0		
Others and remains	6.3			1.0	2.5	7.0							
Infauna:													
<i>Pectinaria gouldii</i>	15.6												
Ampharetid	1.6												
Gastropoda	1.6												
Pelecypoda			11.3			2.5	23.5	29.0	23.0	218.0	218.0		
Nematoda			0.6				0.3						
Unidentified remains and organic matters	23.5		4.4	22.0	48.0	35.6	2.5	17.0	14.0	12.0	9.0		

<sup>1</sup>Arthropods.<sup>2</sup>Mollusks.

TABLE 13.—Stomach contents of northern kingfish, *Menticirrhus saxatilis*, from different estuarine areas along U.S. Atlantic coast.

Author	Chao 1976	Welsh and Breder 1923 <sup>1</sup>	
Locality	York River, Va.	Cape May, N.J.	Falmouth, Mass.
Period	Mar. 1972- Dec. 1974	Aug. 1916	Aug. 1892
Source	Original	p. 194	p. 194
Number of specimens	20	21	17
Empty stomachs	0	0	4
Length of specimens	37-118 mm TL	1.9-7.2 cm SL	2.4-7.4 cm SL
Quantitative methods	% of occurrence	% of vol.	% of vol.
<b>Macrozooplankton:</b>			
<i>Neomysis americana</i>	35.0		
Isopoda		5.0	
Decapoda (shrimp)		9.0	42.0
<i>Crangon septemspinosa</i>	5.0		
<i>Palaemonetes</i>	10.0		
Insecta	5.0		
Others and remains	70.0	9.0	42.0
<b>Microzooplankton:</b>			
Copepoda	5.0		
Calanoid	5.0		
<b>Epibenthos:</b>			
Polychaetes	70.0	19.0	
<i>Glycinidae solitaria</i>	10.0		
Spionids	15.0		
Amphipoda	35.0	30.0	
<i>Gammarus</i> sp.	15.0		
Others and remains	40.0		
Unidentified remains and organic matters	50.0	26.0	16.0

found that harpacticoid copepods were the main food for juvenile *L. xanthurus* and that seasonal variations in diet were slight. Organic detritus and unidentified remains were also common in stomachs (Table 14).

#### Food Partition

To compare the feeding habits of the juveniles of the six sciaenid species, a chart (Figure 29) has been prepared for the six food groups defined previously. The main food group of *Larimus fasciatus* was mostly planktonic and the primary food species was *Neomysis americana*. *Cynoscion regalis* and *B. chrysoura* fed mainly on fishes and macrozooplankton; the primary food species were *Anchoa mitchilli* and *N. americana*, respectively. *Micropogonias undulatus* fed on a wide variety of food including all six food groups, with the dominant food organisms being *N. americana* and *Nereis succinea*. *Menticirrhus saxatilis* fed mainly on macrozooplankton and epibenthos, with the primary food organisms being *N. americana* and polychaetes. *Leiostomus xanthurus* fed on a wide variety of food including five food groups. The dominant food organisms were *Pectinaria gouldii* and other polychaetes.

*Neomysis americana* was very abundant and available to all species of sciaenids in the study

area. This shrimp migrates vertically in response to change in ambient light (Herman 1962). *Neomysis americana* is negatively phototactic. In shallow turbid water (as in the study area) during daylight it might concentrate near the bottom in the darkest sector of the vertical light gradient (Stickney et al. 1975). Because of the abundance and availability of *N. americana*, the other prey items should provide a better indication of feeding specialization. As has been repeatedly shown (Tables 10-14), most fishes were sufficiently opportunistic in their food habits to take advantage of extremely abundant prey species. All the fishes in the present study were sampled by bottom trawl during the daytime. Therefore, both prey and predators probably were dwelling close to the bottom.

Polychaetes were a major food resource for the bottom feeders (Tables 12-14), *Micropogonias undulatus*, *L. xanthurus*, and *Menticirrhus saxatilis*. But *Micropogonias undulatus* fed more on the "crawling" species of worms (Table 12) such as *Nereis* and *Nephtys* (Barnes 1968) and *L. xanthurus* fed more on "tubicolous" or "burrowing" species of worms (Table 14), such as *Pectinaria* and *Amphitrite*. This is contradictory to the findings of Roelofs (1954) and Stickney et al. (1975). Observations of the feeding behavior of these two species in aquarium generally agreed with Roelofs (1954). But *L. xanthurus* seemed to "dive" into the bottom sand much more often than *M. undulatus*, and the depth of the dives by *L. xanthurus* was not shallower than *M. undulatus* as stated by Roelofs (1954).

#### Correlation of Feeding Structures and Food Habits

*Larimus fasciatus* and *C. regalis* have oblique mouths (Figure 20A, B) and their upper jaws are slightly or not protrusible (Figure 21A, B). These features allow them to feed anteriorly and dorsally to the longitudinal axis of their bodies along their swimming course. Their mouths open as the lower jaws drop anteroventrally and the distal ends of the premaxillae move forward (Figure 20A', B'). The mouth openings of *L. fasciatus* and *C. regalis* are relatively larger than in the other species studied (Table 5). The anterior views of their mouths (Figure 20a, a', b, b') show that the upper jaws (premaxillae) are longer or equal to the lower jaws (dentaries). Although both of them feed "anterodorsally" and pelagically, they did show differences in diet (Figure 29). The following mor-

TABLE 14.—Stomach contents of spot, *Leiostomus xanthurus*, from different estuarine areas along U.S. Atlantic and Gulf of Mexico coasts.

Author Locality	Chao 1976	Roelofs 1954	Stickney et al. 1975	Welsh and Breder 1923	Townsend 1956	Parker 1971	
	York River, Va.	North Carolina	Savannah River and Ossabaw Sound, Ga. May 1972-July 1973 Table 1	St. Vincent Sound, Fla.	Aligator Harbor, Fla. June 1955-May 1956 Table 3	Lake Pontchartrain, La. July 1959-Mar. 1961 Table 13	Clear Lake, Tex.
Period Source	June-Aug. 1973 Original	All seasons 1950? Table 1		Apr. 1915 p. 179			
Number of specimens	77	73	126	50	45	22	457
Empty stomachs	4	0	7	0	9	4	60
Length of specimens	73-202 mm TL	60-140 mm TL	50-149 mm SL	2.1-3.5 cm SL	16-163 mm SL	40-99 mm TL	18-99 mm TL
Quantitative method	% of occurrence	% of occurrence	% of occurrence	% of volume	% of occurrence	% of occurrence	
Fish & remains	8.2	6.8	5.0		11.1	19	14
Macrozooplankton:							
Mysidace	8.2	4.1				14.5	8.5
<i>Neomysis americana</i>	27.4	7.4					
Isopoda	2.7					7.0	16.0
Decapoda (shrimp)	1.4	5.5	0.8		5.5	19.0	15.0
Insecta	2.7	1.4	1.7			14.0	19.0
Others and remains	1.4		0.8				
Microzooplankton:							
Copepoda	21.9	100		8.0	66.7	3.0	1.0
Cyclopoid	19.2						
Calanoid	13.7		33.1				
Harpacticoid	20.5		88.4				
Ostracoda		2.7	5.8	72.0	2.8	5.0	3.0
Others and remains	1.4	6.8	7.4	1.0		14.5	13.0
Epibenthos:							
Annelids (polychaete)	56.6	32.9	11.6	1.0		14.5	13.0
<i>Neris succinea</i>	27.4		9.1				
<i>Glycine solitaria</i>	37.0						
<i>Nephtys</i> sp.	11.0						
Phyllodocid	6.8						
Spionid	6.8						
Oligochaete	4.1		1.7				
Cumacea	21.9		13.2				
Amphipoda	24.7			2.0		7.0	8.5
<i>Gammarus</i> sp.	12.3		11.6		16.7		
Crabs	1.4						
Cnidaria	9.6						
Others and remains	5.5	13.7	2.5	0.5	16.6	19.0	12.0
Infauna:							
<i>Pectinaria gouldii</i>	53.4						
Ampharetid	19.2						
Gastropoda	20.5		0.8			4.0	17.0
Pelecypoda	27.4	11.0				1.5	10.0
Nematoda	34.2	71.2			30.6		
Others and remains	5.5		5.0				
Unidentified remains and organic matters	42.5	23.3	35.6	14.0	36.1	14.5	7.0

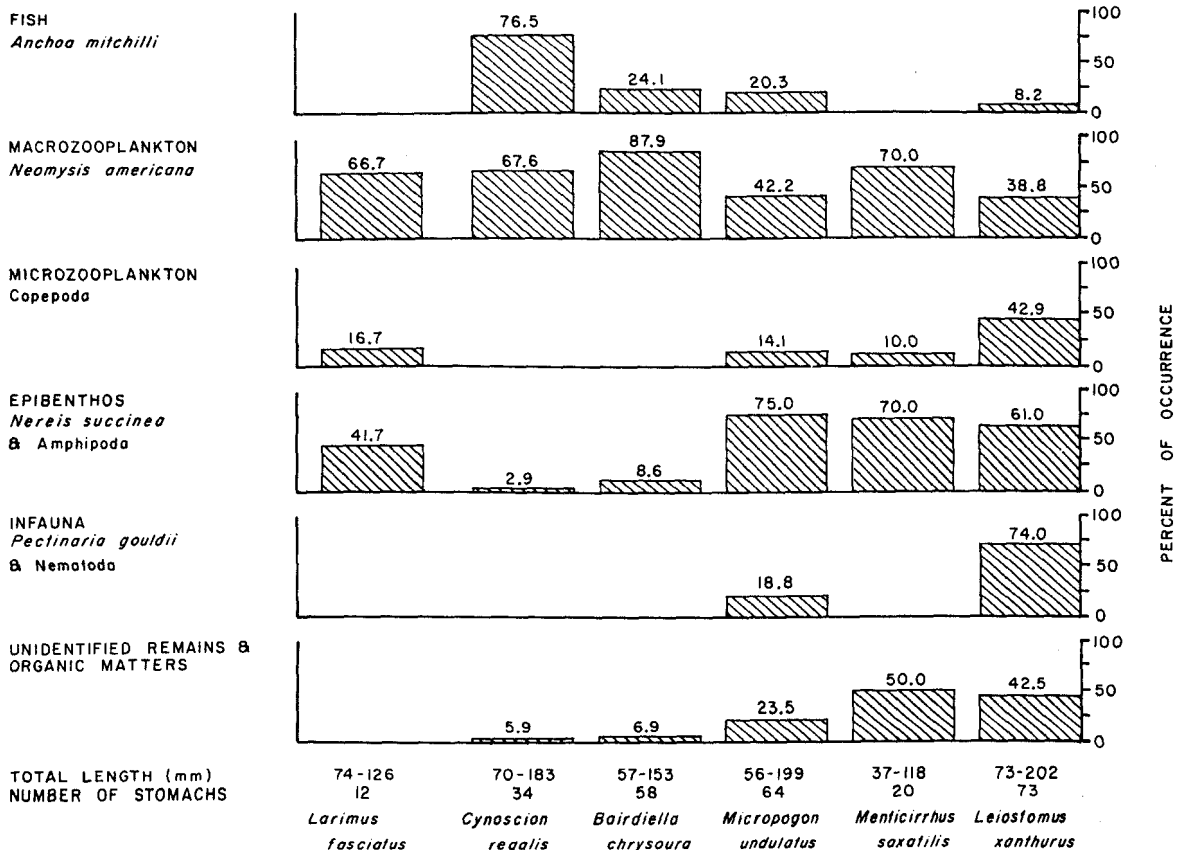


FIGURE 29.—Frequencies of occurrence of various categories of food groups in stomachs of juveniles of six species of sciaenids from the York River and lower Chesapeake Bay estuary.

phological characters are correlated with the dietary differences. The premaxillary and dentary teeth of both species are sharp and set in narrow ridges or bands (Figure 22A, B). *Cynoscion regalis* has much larger teeth than *L. fasciatus*, especially a pair of large canines at the tip of upper jaw in *C. regalis*. These large sharp teeth are adaptations for grasping larger swimming prey. Both species have small sharp pharyngeal teeth (Figure 23A, B). The arrangement and size of the gill rakers (Figure 24A, B) in *L. fasciatus* are much denser and longer than those of *C. regalis*. These differences reflect the food contents in the stomachs of *L. fasciatus*, which consisted of small crustaceans collected by filtering. The stomach contents of *C. regalis* consisted of large crustaceans and fishes (Table 10). *Larimus fasciatus* has a much longer two-looped intestine than the straight intestine of *C. regalis* (Figure 25A, B; Table 7). The number of pyloric caeca in *L. fasciatus* (10 or 11) is also

higher than in *C. regalis* (4 or 5). These morphological differences are probably correlated with the size of food ingested. The cephalic pore systems of *C. regalis* and *L. fasciatus* are not well developed. *Cynoscion regalis* has only two marginal pores on the snout (Figure 26B) whereas *L. fasciatus* has five minute marginal pores on the snout and four pores on the underside of the lower jaw (Figure 26A). In addition, the more fusiform *C. regalis* (Figure 28B) is adapted for fast swimming and active predation. The robust, and presumably slower moving, *L. fasciatus* (Figure 28A) shows adaptations characteristic of a plankton grazing type of feeding.

*Bairdiella chryssoura* has a slightly oblique terminal mouth (Figure 20C) and a slightly protrusible upper jaw (Figure 20C'). These features allow the fish to feed directly in front of its body axis along its swimming course. Its mouth opens as the lower jaw drops anteroventrally and the premaxil-



lae move forward (Figure 20C'). The relative size of the mouth opening in *B. chrysoura* (Table 5) is similar to *C. regalis*. The anterior view of its mouth opening shows equal upper and lower jaws (Figure 20c, c'). Although *B. chrysoura* feeds anteriorly, a pelagic feeder, its stomach contents are similar to those of *C. regalis* (Figure 29), except for a smaller proportion of fishes. The jaw teeth of *B. chrysoura* are strong, conical, and arranged in narrow bands, but canines are absent at the tip of the premaxilla (Figure 22C). Its pharyngeal teeth are relatively stronger and blunter than in *C. regalis* (Figure 23B, C), especially along the median rows. Gill rakers of *B. chrysoura* are intermediate between *L. fasciatus* and *C. regalis* in number (Table 6) and length (Figure 24A–C). The intestine of *B. chrysoura* has two loops and its relative length and number of pyloric caeca (6–8) are also intermediate between *L. fasciatus* and *C. regalis* (Figure 25C; Tables 7, 8). These intermediate features reflect the intermediate feeding habits of *B. chrysoura* (Figure 29). In addition, the body shape of *B. chrysoura* is oblong (Figure 28C) and not fusiform as in *C. regalis*, thus resulting in slower swimming and less efficiency in capturing fishes, as reflected in the diet. The relatively well-developed cephalic pore systems of *B. chrysoura* (Figure 26C), three upper and five marginal pores on the snout and six mental pores on the tip of the lower jaw, also may indicate that *B. chrysoura* depends more on "taste" feeding lower in the water column than *L. fasciatus* and *C. regalis*.

*Micropogonias undulatus*, *Leiostomus xanthurus*, and *Menticirrhus saxatilis* have inferior mouths (Figure 20D–F) and rather protrusible premaxillae (Figure 21D–F). These features enable them to feed anteriorly and ventrally to their body axis along their swimming courses. Their mouths open as the lower jaws drop ventrally backward and the premaxillae protrude anteroventrally (Figure 20D'–F'). Their mouths are relatively smaller than those of the pelagic feeders described previously (Table 5). The anterior views of their mouths (Figure 20d, d', e, e', f, f') show that the upper jaws (premaxillae) are shorter or equal to the lower jaws (dentaries). Although they all feed anteroventrally and benthically, there are differences in their feeding habits (Figure 29). These differences are reflected in the structural differences in the feeding apparatus and feeding behavior among them. The jaw teeth of *M. saxatilis*, *Micropogonias undulatus*, and *L. xanthurus* are all set in bands and the outer row of teeth on

the upper jaws and an inner row of teeth on the lower jaws are slightly enlarged (Figure 22D–F). The pharyngeal teeth of *M. undulatus* and *Menticirrhus saxatilis* are conical (Figure 23D, E) and the median rows are larger and blunt. *Leiostomus xanthurus* has smaller pharyngeal teeth and the median ones are molariform (Figure 23F). The gill rakers of these three bottom feeding sciaenids differ in number (Table 6) and size (Figure 24D–F). *Menticirrhus saxatilis* has the fewest and shortest gill rakers among them. *Micropogonias undulatus* has fewer but longer gill rakers than *L. xanthurus*. The inner gill rakers of *L. xanthurus* are longest (Figure 24f') and most numerous (Table 6). This is reflected in the larger numbers of small crustaceans (e.g., copepods) ingested by *L. xanthurus* (Table 14). The relative length of intestines (Table 7) and their in situ position (Figure 25D–F) are similar among these benthic feeders. The average relative intestinal length of *M. undulatus* and *Menticirrhus saxatilis* is slightly shorter than in *L. xanthurus* (Table 7). The numbers of pyloric caeca of these bottom feeders are similar (Table 8). The cephalic pore and barbel system differ among *Micropogonias undulatus*, *L. xanthurus*, and *Menticirrhus saxatilis*. They all have five upper and five marginal pores on the tip of snout (Figure 26D–F). *Micropogonias undulatus* and *Menticirrhus saxatilis* also have a deeply notched rostral fold. Ventrally, *Micropogonias undulatus* has five pores and six miniature barbels (Figure 26d); *Menticirrhus saxatilis* has four pores and a short rigid barbel with an apical pore (Figure 26e); *L. xanthurus* has five pores and no barbel (Figure 26f). *Menticirrhus saxatilis* also has the most pronounced snout and most elongate and rounded body form (Figure 28E). *Leiostomus xanthurus* has the least pronounced snout and shortest and deepest body form (Figure 28F). *Micropogonias undulatus* is intermediate in snout and body form between *Menticirrhus saxatilis* and *L. xanthurus*.

The length of snout and body form reflect the feeding habits of these three species. Food habits (Figure 29) indicate that *M. saxatilis* and *Micropogonias undulatus* feed on the substrate, on the epifauna, more than they feed "into" the substrate on the infauna. *Leiostomus xanthurus* feeds more on the infauna. The long projecting snout seems to be an obstacle for fishes with an inferior mouth to forage into the bottom for food. Roelofs' (1954) observations on feeding behavior of *M. undulatus* and *L. xanthurus* in aquaria with sandy bottoms were repeated during the present study. Juveniles

of both species foraged into the bottom sand often, especially when the substrate was freshly dug from the beach. Foraging tapered off gradually, especially in *M. undulatus*, apparently as the food in the substrate decreased. Brine shrimp, *Artemia*, were fed to these two species in the aquarium. Both *M. undulatus* and *L. xanthurus* were able to feed on brine shrimp just below the water surface. *Micropogonias undulatus* fed on the surface shrimp in an oblique to vertical position. To feed on brine shrimp close to the surface, *L. xanthurus* occasionally maneuvered in an oblique upside-down position, with the dorsal fin pointing toward the bottom to overcome the inferior position of its mouth.

Other accessory organs of feeding, such as the nares and eyes, also reflect the feeding habits of young sciaenid fishes. The numbers of nasal laminae of the six species (Table 9) overlap, partly due to ontogenetic changes; the absolute numbers of nasal laminae increase as the fishes grow larger. Generally, the bottom feeders, *M. undulatus* and *L. xanthurus*, have more nasal laminae than *Larimus fasciatus*, *C. regalis*, and *B. chrysoura* (Table 9). *Menticirrhus saxatilis* has relatively fewer nasal laminae than other benthic feeders, but it has a pored mental barbel on the lower jaw. This suggests that *M. saxatilis* depends more on touch for foraging than other benthic feeders. The relative eye size of *M. saxatilis* is smaller than in other sciaenid fishes studied here (Table 5). Larger eyes were found among the pelagic feeders, *L. fasciatus*, *C. regalis*, and *B. chrysoura* (Table 5). Allometrically, the relative eye size of all these sciaenid fishes is larger in young specimens and smaller in adults. For benthic feeders, decrease in relative eye size with growth is faster than for the pelagic feeders. The relative roles of olfaction, touch, and vision in feeding in young sciaenids studied may be hypothesized as follows. The benthic feeders, *Micropogonias undulatus*, *L. xanthurus*, and *Menticirrhus saxatilis*, depend more on their senses of smell or touch or both to locate their prey. The pelagic feeders, *Larimus fasciatus*, *C. regalis*, and *B. chrysoura*, depend more on sight to catch their prey, especially *C. regalis* and *B. chrysoura* which prey on *Anchoa mitchilli*, an active small anchovy.

Morphological differences in the feeding apparatus, especially the mouth position, size, and protrusibility, the form of teeth, and the gill raker structure are limiting factors for the level of water column and the size of the prey species which can

be eaten by the fish. The pelagic feeders, *L. fasciatus*, *C. regalis*, and *B. chrysoura*, almost completely lack any sedentary benthos in their diets (Figure 29). Even among the bottom feeders, *Micropogonias undulatus* feeds more on epibenthic polychaete species (Table 12) and *Leiostomus xanthurus* feeds more on burrowing polychaete species (Table 14).

Morphological differences in the digestive tract, the number of pyloric caeca, and the length of intestine may be adaptations to more efficient use of food. As is evident in *Larimus fasciatus* and *Leiostomus xanthurus*, size of the food items is important; *Larimus fasciatus* fed exclusively on small crustaceans (small Mysidacea and Amphipoda), *Leiostomus xanthurus* fed mainly on copepods (Table 14). *Larimus fasciatus* is mainly a pelagic feeder and *Leiostomus xanthurus* is mainly a benthic feeder. Both species have longer intestines (Table 7) and more pyloric caeca (Table 8) than other species in their respective groups (pelagic and benthic).

Svetovidov reported a similar relationship between the number of gill rakers and size of food items in Caspian shads (Nikolsky 1963). However, he also found more pyloric caeca in shad that fed on fishes than in species that ate small crustaceans, a relationship opposite to that found here. In feeding, the role of gill rakers is in ingestion and the role of the pyloric caeca is in digestion. Although there are morphological and numerical correlations among the ingestive apparatuses and digestive organs, they are highly adaptive and may be variable among fishes.

The so-called "selective feeding habits" of these young sciaenids reported by many previous authors (see citations of Tables 10-14) are not evident in the present study. Partitioning of food among these young sciaenids depends more on the habits of the prey species than on "selective preferences" of the fishes. Juvenile sciaenids feed opportunistically in a limited depth range in the water column, probably within or close to 2 m above the bottom. Within this layer of the water column, *Larimus fasciatus*, *C. regalis*, and *B. chrysoura* feed in the upper portion of the water column and *M. undulatus*, *Leiostomus xanthurus*, and *Menticirrhus saxatilis* feed in the lower portion of the water column to the bottom. Feeding niche division and resulting dietary differences among these species of sciaenids in the Chesapeake estuary area are probably attributable to differences in feeding behavior imposed

upon these species by adaptive morphological limitations rather than to selective feeding per se.

## CONCLUSION

In the Sciaenidae, a family of primarily coastal marine fishes, many species utilize the same coastal area as common nursery and seasonal feeding grounds. In the York River estuarine system, the coexistence of sciaenid fishes may be attributed to: 1) Differences in their temporal and spatial distributions. Juveniles of the four most abundant sciaenid fishes entered the estuary at different times of the year. Within a given period, the highest catches of each species were usually in different areas (upper and lower reaches) and depths (beach zone, shoals, and channel) of the York River system. Also, the size distributions of each species were often separated temporally and spatially. 2) Differences in their habitat adaptations and food habits. The diverse morphological features of these sciaenid fishes enable them to utilize food resources from different levels (microhabitats) of the water column. Correlations of feeding apparatus, digestive system, and food habits are evident and result in niche division. 3) The abundant food resources of the study area. At times some prey organism (e.g., *Neomysis americanus*) may be ubiquitous and very abundant, providing food for several species of juvenile sciaenids. Then food would not be a limiting resource and intrafamilial competition may not occur.

## ACKNOWLEDGMENTS

We thank D. F. Boesch, B. B. Collette, G. C. Grant, P. A. Haefner, Jr., and J. V. Merriner for their helpful suggestions and critical review of this manuscript. We also express our appreciation to the following persons from VIMS: R. Bradley, J. Gilley, and M. Williams for preparation of graphs; Susan Barrick and her staff at the VIMS library; William H. Kriete, Jr., James Colvocoresses, Douglas F. Markle, Jerome E. Illowsky, and James Green who helped in field work, including trawling, collecting, and measuring fishes during the study; Deborah A. Sprinkle and Julia F. Milten who typed many drafts of this manuscript; Joyce S. Davis who answered many questions about different surveys; Genie Shaw who retrieved all the hydrographic data from the VIMS computer data storage; and to our colleagues, K.

W. Able, J. Colvocoresses, D. F. Markle, J. D. McEachran, L. P. Mercer, G. Sedberry, and C. A. Wenner for allowing us to talk to them about sciaenids and for helpful suggestions.

Our special appreciation goes to Bruce B. Collette, Systematics Laboratory, National Marine Fisheries Service, NOAA, Washington, D.C., who instigated this joint adventure a few years ago.

D. E. McAllister, National Museums of Canada, reviewed the final draft of the manuscript and offered helpful suggestions. J. McConnell and her staff at the Word Processing Centre, National Museums of Canada, typed the final draft.

## LITERATURE CITED

- ALEXANDER, R. McN.  
1967. The functions and mechanisms of the protrusible upper jaws of some acanthopterygian fish. *J. Zool. (Lond.)* 151:43-64.
- ANDERSON, M., W. J. DAVIS, M. P. LYNCH, AND J. R. SCHUBEL (compilers).  
1973. Effect of hurricane Agnes on the environment and organisms of Chesapeake Bay. *Va. Inst. Mar. Sci., Spec. Rep. Mar. Sci. Ocean Eng.* 29, 172 p.
- ARNOLDI, D. C., W. H. HERKE, AND E. J. CLAIRAIN, JR.  
1973. Estimate of growth rate and length of stay in a marsh nursery of juvenile Atlantic croaker, *Micropogon undulatus* (Linnaeus), "sandblasted" with fluorescent pigments. *Gulf Caribb. Fish. Inst., Proc. 26th Annu. Sess.*, p. 158-172.
- BARNES, R. D.  
1968. *Invertebrate zoology*. 2d ed. W. B. Saunders Co., Phila., 743 p.
- BOESCH, D. F.  
1971. Distribution and structure of benthic communities in a gradient estuary. Ph.D. Thesis, College of William and Mary, Williamsburg, Va., 120 p.
- BOIE, B. F.  
1826. *Oder encyclopaedische Zeitung*. Isis (Jena) 19:970-982.
- CARR, W. E. S., AND C. A. ADAMS.  
1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. *Trans. Am. Fish. Soc.* 102:511-540.
- CHAO, L. N.  
1976. Aspects of systematics, morphology, life history and feeding of western Atlantic Sciaenidae (Pisces: Perciformes). Ph.D. Thesis, Coll. William and Mary, Williamsburg, Va., 342 p.  
In press. A basis for classifying western Atlantic Sciaenidae (Teleostei: Perciformes). U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ.
- COLVOCORESSES, J.  
1975. Fish and major decapods: trawl analysis. Part II. In R. A. Jordan, R. W. Virnstein, J. E. Illowsky, and J. Colvocoresses. *Yorktown power station ecological study*. Phase II. Final technical report, p. 415-462. *Va. Inst. Mar. Sci., Spec. Sci. Rep.* 76, 462 p.

- DARNELL, R. M.  
1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. *Ecology* 42:533-568.
- DAVIS, W. P.  
1967. Ecological interactions, comparative biology and evolutionary trends of thirteen pomadasyid fishes at Alligator Reef, Florida Keys. Ph.D. Thesis, Univ. Miami, Coral Gables, 127 p.
- DAVIS, W. P., AND R. S. BIRDSONG.  
1973. Coral reef fishes which forage in the water column. A review of their morphology, behavior, ecology and evolutionary implications. *Helgol. wiss. Meeresunters.* 24:292-306.
- DAWSON, C. E.  
1958. A study of the biology and life history of the spot, *Leiostomus xanthurus* Lacépède, with special reference to South Carolina. *Contrib. Bears Bluff Lab.* 28, 48 p.
- DUNHAM, F.  
1972. A study of commercially important estuarine-dependent industrial fishes. *La. Wildl. Fish. Comm., Tech. Bull.* 4, 63 p.
- EMERY, A. R.  
1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. *Bull. Mar. Sci.* 23:649-770.
- GERO, D. R.  
1952. The hydrodynamic aspects of fish propulsion. *Am. Mus. Novit.* 1601, 32 p.
- GÜNTHER, K.  
1962. Über Kieferfunktionen bei Knochenfischen, mit Hinweisen auf die Sardelle (*Engraulis encrasicolus*) und ihre Regulation-seinrichtung für die Strömung arteriellen Blutes. *Sitzungsb. Ges. Naturforsch. Freunde Berl. (N.F.)* 2:135-149.
- GUTHERZ, E. J., G. M. RUSSELL, A. R. SERRA, AND B. A. ROHR.  
1975. Synopsis of the northern Gulf of Mexico industrial and food fish industries. *Mar. Fish. Rev.* 37(7):1-11.
- HANSEN, D. J.  
1969. Food, growth, migration, reproduction, and abundance of pinfish, *Lagodon rhomboides*, and Atlantic croaker, *Micropogon undulatus*, near Pensacola, Florida, 1963-65. *U.S. Fish Wildl. Serv., Fish. Bull.* 68:135-146.
- HARMIC, J. L.  
1958. Some aspects of the development and the ecology of the pelagic phase of the gray squeteague, *Cynoscion regalis* (Bloch and Schneider) in the Delaware estuary. Ph.D. Thesis, Univ. Delaware, Newark, 84 p. + 80 p. append.
- HAVEN, D. S.  
1957. Distribution, growth and availability of juvenile croaker, *Micropogon undulatus*, in Virginia. *Ecology* 38:88-97.  
1959. Migration of the croaker, *Micropogon undulatus*. *Copeia* 1959:25-30.
- HERMAN, S. S.  
1962. Spectral sensitivity and phototaxis in the opossum shrimp, *Neomysis americana* Smith. *Biol. Bull. (Woods Hole)* 123:562-570.
- HILDEBRAND, S. F., AND L. A. CABLE.  
1930. Development and life history of fourteen teleostean fishes at Beaufort, N.C. *Bull. U.S. Bur. Fish.* 46:383-488.  
1934. Reproduction and development of whittings or kingfishes drums, spot, croaker, and weakfishes or sea trouts family Sciaenidae, of the Atlantic coast of the United States. *U.S. Bur. Fish., Bull.* 48:41-117.
- HILDEBRAND, S. F., AND W. C. SCHROEDER.  
1928. Fishes of Chesapeake Bay. *Bull. U.S. Bur. Fish.* 43(1), 366 p.
- HOESE, H. D.  
1973. A trawl study of nearshore fishes and invertebrates of the Georgia coast. *Contrib. Mar. Sci., Univ. Tex.* 17:63-98.
- HUBBS, C. L., AND K. F. LAGLER.  
1964. Fishes of the Great Lakes region. Revised ed. Univ. Mich. Press, Ann Arbor, 213 p.
- JANNKE, T. E.  
1971. Abundance of young sciaenid fishes in Everglades National Park, Florida, in relation to season and other variables. Univ. Miami Sea Grant Program, Sea Grant Tech. Bull. 11, 128 p.
- JOSEPH, E. B.  
1972. The status of the sciaenid stocks of the middle Atlantic coast. *Chesapeake Sci.* 13:87-100.
- KEAST, A.  
1970. Food specialization and bioenergetic interrelations in the fish faunas of some small Ontario waterways. In J. H. Steele (editor), *Marine food chains*, p. 277-411. Oliver and Boyd, Edinb.
- KEAST, A., AND D. WEBB.  
1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. *J. Fish. Res. Board Can.* 23:1845-1874.
- KUNTZ, A.  
1914. The embryology and larval development of *Bairdiella chrysura* and *Anchovia mitchilli*. *Bull. U.S. Bur. Fish.* 33:1-19
- LACEPÈDE, B. G. E. V.  
1803. *Histoire naturelle des poissons.* Vol. 4, 728 p.
- MAHOOD, R. K.  
1974. Seatrout of the genus *Cynoscion* in coastal waters of Georgia. *Ga. Dep. Nat. Res., Contrib. Ser.* 26, 36 p.
- MARKLE, D. F.  
1976. The seasonality of availability and movements of fishes in the channel of the York River, Virginia. *Chesapeake Sci.* 17:50-55.
- MASSMANN, W. H.  
1962. Water temperatures, salinities, and fishes collected during trawl surveys of Chesapeake Bay and York and Pamunkey rivers, 1956-59. *Va. Inst. Mar. Sci., Spec. Sci. Rep.* 27, 51 p.  
1963. Age and size composition of weakfish, *Cynoscion regalis*, from pound nets in Chesapeake Bay, Virginia 1954-58. *Chesapeake Sci.* 4:43-51.
- MASSMANN, W. H., AND A. L. PACHECO.  
1960. Disappearance of young Atlantic croakers from the York River, Virginia. *Trans. Am. Fish. Soc.* 89:154-159.
- MASSMANN, W. H., J. P. WHITCOMB, AND A. L. PACHECO.  
1958. Distribution and abundance of gray weakfish in the York River System, Virginia. *Trans. 23d. North Am. Wildl. Conf.*, p. 361-369.
- MCHUGH, J. L.  
1967. Estuarine nekton. In G. Lauff (editor), *Estuaries*, p. 581-620. *Am. Assoc. Adv. Sci., Wash., D.C.*
- MERRINER, J. V.  
1973. Assessment of the weakfish resource, a suggested management plan, and aspects of life history in North

- Carolina. Ph.D. Thesis, North Carolina State Univ., Raleigh, 201 p.
1975. Food habits of the weakfish, *Cynoscion regalis*, in North Carolina waters. Chesapeake Sci. 16:74-76.
1976. Aspects of the reproductive biology of the weakfish, *Cynoscion regalis* (Sciaenidae), in North Carolina. Fish. Bull., U.S. 74:18-26.
- MUSIC, J. L., JR.  
1974. Observations on the spot (*Leiostomus xanthurus*) in Georgia's estuarine and close inshore ocean waters. Dep. Nat. Res., Game Fish Div., Coastal Fish Off., Contrib. Ser. 28, 29 p.
- MUSICK, J. A.  
1972. Fishes of Chesapeake Bay and the adjacent coastal plain. In M. L. Wass et al. (compilers), A check list of the biota of lower Chesapeake Bay, p. 175-212. Va. Inst. Mar. Sci., Spec. Sci. Rep. 65, 290 p.
- NELSON, W. R.  
1969. Studies on the croaker, *Micropogon undulatus* Linnaeus, and the spot, *Leiostomus xanthurus* Lacépède, in Mobile Bay, Alabama. J. Mar. Sci. Ala. 1:4-92.
- NESBIT, R. A.  
1954. Weakfish migration in relation to its conservation. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 115, 81 p.
- NIKOLSKY, G. V.  
1963. The ecology of fishes. (Translated from Russ. by L. Birkett), Academic Press, N.Y., 352 p.
- NYBERG, D. W.  
1971. Prey capture in the largemouth bass. Am. Midl. Nat. 86:128-144.
- PACHECO, A. L.  
1957. The length and age composition of spot, *Leiostomus xanthurus*, in the pound net fishery of lower Chesapeake Bay. M.S. Thesis, Coll. William and Mary, Williamsburg, Va., 34 p.  
1962a. Age and growth of spot in lower Chesapeake Bay, with notes on distribution and abundance of juveniles in the York River system. Chesapeake Sci. 3:18-28.  
1962b. Movements of spot, *Leiostomus xanthurus*, in the lower Chesapeake Bay. Chesapeake Sci. 3:256-257.
- PARKER, J. C.  
1971. The biology of the spot, *Leiostomus xanthurus* Lacépède, and Atlantic croaker, *Micropogon undulatus* (Linnaeus), in two Gulf of Mexico nursery areas. Texas A&M Univ., Sea Grant Publ. TAMU-SG-71-210, 182 p.
- PEARSON, J. C.  
1929. Natural history and conservation of redfish and other commercial sciaenids on the Texas coast. Bull. U.S. Bur. Fish. 44:129-214.  
1932. Winter trawl fishery off the Virginia and North Carolina coasts. U.S. Bur. Fish., Invest. Rep. 10, 31 p.  
1941. The young of some marine fishes taken in lower Chesapeake Bay, Virginia, with special reference to the gray sea trout *Cynoscion regalis* (Bloch). U.S. Fish Wildl. Serv., Fish. Bull. 50:79-102.
- PERLMUTTER, A., W. S. MILLER, AND J. C. POOLE.  
1956. The weakfish (*Cynoscion regalis*) in New York waters. N.Y. Fish Game J. 3:1-43.
- QASIM, S. Z.  
1972. The dynamics of food and feeding habits of some marine fishes. Indian J. Fish. 19:11-28.
- REID, G. K., JR.  
1954. An ecological study of the Gulf of Mexico fishes, in the vicinity of Cedar Key, Florida. Bull. Mar. Sci. Gulf. Caribb. 4:1-94.
- ROELOFS, E. W.  
1954. Food studies of young sciaenid fishes *Micropogon* and *Leiostomus*, from North Carolina. Copeia 1954:151-153.
- ROITHMAYR, C. M.  
1965. Industrial bottomfish fishery of the northern Gulf of Mexico, 1959-63. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 518, 23 p.
- SEGUIN, R. T.  
1960. Variation in the middle Atlantic coast population of the gray squeteague, *Cynoscion regalis* (Bloch & Schneider) 1801. Ph.D. Thesis, Univ. Delaware, Newark, 70 p. + 9 p. append.
- SHEALY, M. H., J. V. MIGLARESE, AND E. B. JOSEPH.  
1974. Bottom fishes of South Carolina estuaries, relative abundance, seasonal distribution and length-frequency relationships. S.C. Mar. Resour. Cent., Tech. Rep. 6, 189 p.
- SPRINGER, V. G., AND K. D. WOODBURN.  
1960. An ecological study of the fishes of the Tampa Bay area. Fla. State Board Conserv., Mar. Lab., Prof. Pap. Ser. 1, 104 p.
- STICKNEY, R. R., G. L. TAYLOR, AND D. B. WHITE.  
1975. Food habits of five species of young southeastern United States estuarine Sciaenidae. Chesapeake Sci. 16:104-114.
- STRUHSAKER, P.  
1969. Demersal fish resources: Composition, distribution, and commercial potential of the continental shelf stocks off Southeastern United States. U.S. Fish Wildl. Serv., Fish. Ind. Res. 4:261-300.
- SUNDARARAJ, B. I.  
1960. Age and growth of the spot, *Leiostomus xanthurus* Lacépède. Tulane Stud. Zool. 8:40-62.
- SUTTKUS, R. D.  
1955. Seasonal movements and growth of the Atlantic croaker (*Micropogon undulatus*) along the east Louisiana coast. Gulf Caribb. Fish. Inst., Proc. 7th Annu. Sess., p. 151-158.
- SUYEHIRO, Y.  
1942. A study of the digestive system and feeding habits of fish. Jap. J. Zool. 10:1-303.
- TAYLOR, W. R.  
1967. An enzyme method of clearing and staining small vertebrates. Proc. U.S. Natl. Mus. 122(3596), 17 p.
- THOMAS, D. L.  
1971. The early life history and ecology of six species of drum (Sciaenidae) in the lower Delaware river, a brackish tidal estuary. Ichthyol. Assoc. Bull. 3, 247 p.
- TOWSEND, B. C.  
1956. A study of the spot, *Leiostomus xanthurus* Lacépède, in Alligator Harbor, Florida. M.S. Thesis, Florida State Univ., Tallahassee, 43 p.
- WALLACE, D. H.  
1940. Sexual development of the croaker, *Micropogon undulatus*, and distribution of the early stages in Chesapeake Bay. Trans. Am. Fish. Soc. 70:475-482.
- WELSH, W. W. AND C. M. BREDER, JR.  
1923. Contributions to life histories of Sciaenidae of the

Eastern United States Coast. Bull. U.S. Bur. Fish.  
39:141-201.

WHITE, M.L., AND M. E. CHITTENDEN, JR.

1977. Age determination, reproduction, and population  
dynamics of the Atlantic croaker, *Micropogonias un-*  
*dulatus*. Fish. Bull., U.S. 75:109-123.

YOUNG, R. H.

1953. An investigation of the inshore population of the  
spot (*Leiostomus xanthurus*, Lacépède) with particular  
reference to seasonal growth and size distribution in  
Chesapeake Bay. M.S. Thesis, Univ. Maryland, College  
Park, 34 p.