

FEEDING HABITATS OF SPOT, *LEIOSTOMUS XANTHURUS*, IN POLYHALINE VERSUS MESO-OLIGOHALINE TIDAL CREEKS AND SHOALS¹

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ABSTRACT

Young-of-year spot, *Leiostomus xanthurus*, were collected by otter trawl within tidal creeks and on adjacent shoals in polyhaline and meso-oligohaline zones of the York River, Virginia. Total densities of spot at Blevins Creek, a polyhaline system, were twice that of the meso-oligohaline Goaders Creek.

Stomach content analysis confirmed previous studies of the generally opportunistic feeding strategy of juvenile spot. However, distinct differences in food utilization were observed between creeks and among creek and shoal stations. In addition, prey utilization differences due to habitat generally paralleled seasonal distribution patterns of dominant macrobenthos reported for the area.

Two major ontogenetic groups were distinguished. Small spot (<30 mm SL) consumed more planktonic food items (calanoid copepods) than the larger size classes, which fed on more benthic prey and displayed greater overlap in diet. Small spot tended to be selective; larger spot were more opportunistic.

Tidal salt marshes and their associated drainages are recognized primary nurseries for spot, *Leiostomus xanthurus*, (Herke 1971; Parker 1971; Weinstein 1979; Currin et al. 1984). Shortly after recruitment, young spot tend to concentrate in tidal creeks, and by late spring densities in these creeks are often several times higher than in nearby seagrass habitats or shoal areas (Weinstein and Brooks 1983; Smith et al. 1984). Once recruited to tidal creeks, spot seem to take up residence, with limited movement out of (or between) marshes until the fall mass exodus (Weinstein 1983; Weinstein and Brooks 1983; Currin et al. 1984; Weinstein et al. 1984; Weinstein and O'Neil 1986).

The role of marsh nurseries as predation refuges versus feeding areas is currently under debate (Boesch and Turner 1984). As suggested by the studies of Vince et al. (1976), it is likely that the marsh serves in both capacities. Qualitative and quantitative data on food availability and quality and on differences among habitats will be necessary to resolve the food versus refuge question. Ultimately, these data should be supported by experimental studies on growth rates

versus the quality of food resources in different habitats (Weisberg and Lotrich 1982). We report here on one of the steps in the process, a descriptive comparison of gut contents of spot collected in tidal creeks and shoal areas in marshes of two salinity regimes, meso-oligohaline and polyhaline.

Although the food habits of spot have been previously studied, most investigators captured spot in openwater habitats, not in the primary nurseries (Parker 1971; Stickney et al. 1975; Chao and Musick 1977; Sheridan 1979). Only Hodson et al. (1981) studied food utilization of spot in tidal creeks. Their population, however, was restricted mainly to small fish (<40 mm) capable of exploiting the small creek rivulets and susceptible to capture by block net. This study expands the effort of Hodson et al. (1981), and includes the entire seasonal residency period for spot in tidal creeks of the York River estuary, VA. A survey of food utilization was conducted in 1983 for all young-of-year size classes occupying two tidal creeks and nearby river shoals at widely separated salinities. Specific objectives of this effort were to 1) describe food utilization of juvenile spot in each habitat, 2) document any sequential ontogenetic changes in food utilization, and 3) compare the overall food utilization of spot residing in tidal creeks or adjacent shoals dissimilar in salinity. It was anticipated that feeding differences would reflect the availability and types of food in

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the two salinity regimes and microhabitats constituting the creek and shoal sites.

STUDY AREA AND METHODS

The York River estuary, a subestuary of the Virginia portion of the Chesapeake Bay (Fig. 1), covers about 208 km² and extends 46 km from Tue Marsh Light to West Point, where it is formed by the confluence of the Pamunkey and Mattaponi Rivers. At two localities within the estuary, tidal creeks similar in physical dimensions (O'Neil 1983), but differing in salinity regimes, were selected as study sites: Goaders Creek, a meso-oligohaline site (*sensu* Remane 1934 and the Venice System of classification), and Blevins Creek, a polyhaline creek in the Guinea Marshes near the mouth of the river (Fig. 1).

Field Methods

Within each locality three stations were established: 1) in each creek approximately 1,500-2,000 m upstream (where trawling was still possible), 2) immediately inside the creek mouth, and 3) at shoal stations positioned approximately 200

m offshore in the York River proper in approximately 3 m of water.

Monthly collections (March-October 1982) with a 4.9 m semiballoon otter trawl with wings and body of 19 mm mesh and a 6.3 mm mesh cod end liner were made during daylight hours as close to high tide as possible. Four 2-min tows at about 1 m s⁻¹ were made at each station.

To reduce the chances of regurgitation, specimens were initially anesthetized in a mixture of seawater and 0.02 mL quinaldine (mixed in 10 mL acetone). Buffered formalin (10%) was then added for preservation. The abdominal cavities of large fish (>80 mm) were pierced to allow sufficient preservation of food items in the stomach. Water temperature and salinity were recorded prior to trawling at each station.

Laboratory Methods

In the laboratory, spot from each collection were sorted and counted. Individual standard lengths (SL) were measured; when more than 50 spot were captured in a single collection, a random subsample of 30 fish was used for length measurements.

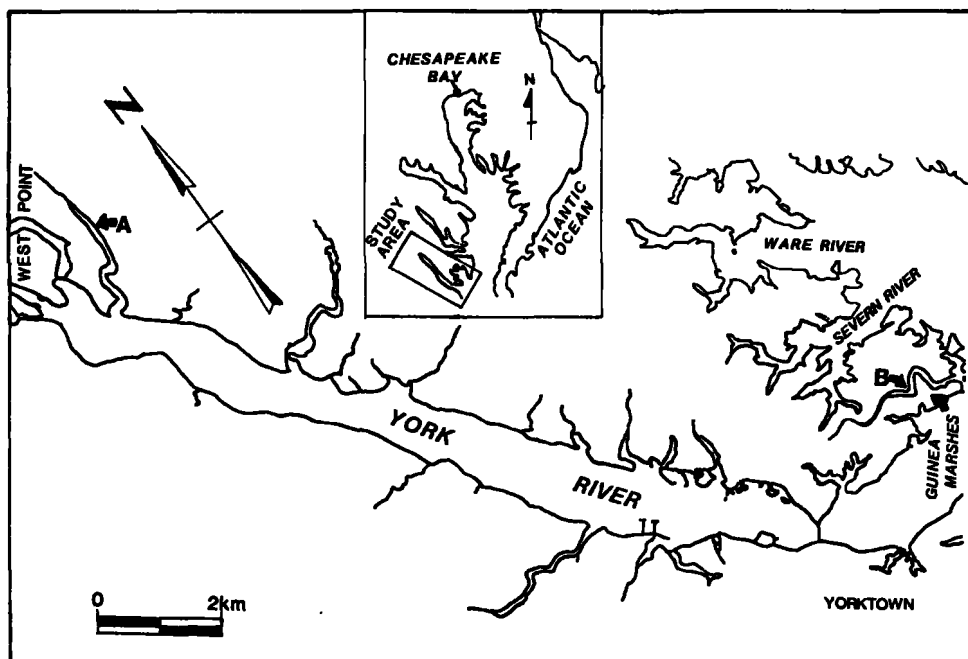


FIGURE 1.—York River, VA, and relative locations of tidal creeks examined. A = Goaders Creek, B = Blevins Creek.

For gut content analysis, fish from each of the four trawl samples representing a given station were pooled and then divided into several size classes. Initially, 5 mm size increments were used in order to corroborate the findings of others concerning an ontogenetic shift in feeding habits of spot. When mean standard lengths exceeded 20 mm, 10 mm size classes were adopted.

Initially, up to 20 stomachs were removed from randomly selected individuals in each size class. Later, based on prey item diversity (Hurtubia 1973) comparisons for the June samples, 12 stomachs per size class was set as the upper limit (O'Neil 1983).

Stomach contents were pooled within size classes and analyzed using the Carr and Adams (1972) sieve fraction technique. After washing stomach contents from each sieve (2, 0.85, 0.425, 0.25, 0.15, and 0.075 mm meshes) into a small fingerbowl, a random subsample of approximately 5 mL was removed. The subsample was placed in a labeled vial and the remainder was filtered onto a preweighed 55 mm filter pad and dried for 24 hours at 60°C. On the assumption that food particles of roughly the same size have approximately the same weight (Carr and Adams 1972), the total dry weight for each sieve fraction was proportioned among the prey types identified from its subsample. The Carr and Adams technique provided for rapid, accurate identification of food items from a large number of stomachs and has been used successfully by several investigators (Sheridan 1979; Stoner 1980; Livingston 1982; Lucas 1982).

Statistical Analysis

Dietary differences among various ontogenetic groups, between creeks, between stations within creeks, or for each month examined were compared using "normal" classification methods (Clifford and Stephenson 1975). Overlap of prey utilization was then determined using the complement of the Bray-Curtis dissimilarity measure:

$$\frac{\sum_{j=1}^n |x_{1j} - x_{2j}|}{\sum_{j=1}^n (x_{1j} + x_{2j})}$$

where n is the number of attributes (prey) and x_{1j}

and x_{2j} are the values of the j th attribute for any pair of entities (size, station, month).

Separate matrices were constructed for each comparison from untransformed, pooled monthly data using COMPAH (Boesch 1977). The data in each matrix were then clustered by the group-average method (Lance and Williams 1967). Diet information was based on dry weights of the 30 prey taxa categories, all of which were mutually exclusive except for the unidentified (UID) and miscellaneous (MISC) categories (Table 1). Prey items contributing <0.1 mg of total dry weight per size class were eliminated prior to the analysis. The miscellaneous category contains the total of all food items individually representing <2% of the final dry weight.

In addition to the clustering procedure, reciprocal averaging ordination (Guinochet 1973; Hill 1973) was used to provide independent verifica-

TABLE 1.—Prey categories used for tropic comparisons. All but unidentified (UID) and miscellaneous (MISC) are mutually exclusive feeding categories.

AMP	Amphipoda
BIV	Bivalves
BRA	Branchipoda
CAL	Calanoids
CAP	Caprellidae
CLS	Clam siphons
CHI	Chironomidae
CHL	Chlorophyta
COR	Corophiidae
Crs	<i>Crangon septemspinosa</i>
CRZ	Crab zoea
Cs	<i>Callinectes sapidus</i>
CYA	Cyathura
DET	Detritus
Eh	<i>Eteone heteropoda</i>
Et	<i>Edotea tribola</i>
FOR	Foraminifera
GAM	Gammaridae
HA ₁	Harpacticoid 1
HA ₂	Harpacticoid 2
La	<i>Leucon americanus</i>
Lp	<i>Leptocheirus plumulosus</i>
MAC	<i>Macoma</i> sp
MAL	Maldanidae
Me	<i>Monoculodes edwardsi</i>
MISC	Miscellaneous
Na	<i>Neomysis americana</i>
NEM	Nematoda
NER	Nereidae
OLI	Oligochaeta
OST	Ostracods
PAL	Palaemonidae
PI	<i>Polydora ligni</i>
PLA	Plant matter
POL	Polychaeta
SPI	Spionidae
TEL	Teleostei
UID	Unidentified remains
XAN	Xanthidae

tion of the dendrogram results. Reciprocal averaging is an eigenanalysis that ordinales both food type and habitat (or size class) variables simultaneously and defines axes such that the variance of the scores on each axis is maximized. The first axis, therefore, represents the path of maximum variance, the second axis the next greatest, and so forth. This analysis was performed with ORDIFLEX (Gauch 1977).

RESULTS

Physical Parameters

With the exception of April and May, temperatures were slightly cooler at Blevins Creek than at Goalders Creek (Table 2). Salinity within Goalders Creek was reasonably stable considering its meso-oligohaline location (Table 2). Except for a brief period in spring, Blevins Creek was polyhaline during the period of spot residence (salinity range 18-22‰). Salinity in Goalders Creek was always at least 4‰ lower than Blevins Creek and reached a maximum difference of 14‰ during April. Such variations in tidal creeks is typical of the estuarine salinity gradient with distance from the head of the estuary (Weinstein 1979; Weinstein et al. 1980). There were no distinct salinity differences observed between either creek and its adjacent shoal station.

Temporal Abundance and Distribution

Monthly abundance and distribution patterns for spot in each creek system and adjacent shoals

are shown in Figure 2. Overall, numbers of spot captured within the tidal creeks were similar, 2,355 versus 2,802 in Goalders and Blevins Creeks, respectively. Temporal distributions of spot within each locality were further compared by computing creek/shoal ratios.

Spot were not encountered during the first sampling trip during late March 1982, but postlarvae and juveniles appeared in small numbers in April. At that time, spot were more abundant at the shoal stations than in the creeks (creek/shoal ratio of 0.28 for Goalders and 0.16 at Blevins). Young-of-year spot reached their maximum abundance in May, with 1,047 specimens taken up-estuary at Goalders Creek and 2,110 individuals sampled from Blevins Creek. Spot at Goalders Creek were then more numerous at the stations within the creek (ratio 20.5), but still more prevalent on the shoal down-estuary at Blevins Creek (ratio 0.52). From June to September, however, spot were clearly more abundant in the creeks of both systems. By the end of the investigation (October 1982) spot once again dominated the shoal at Blevins Creek, but remained more abundant in the creek at Goalders.

Monthly size distributions of spot in the two tidal creeks and adjacent shoals were examined by dividing the samples taken at each station into 5 mm SL size classes and comparing their relative frequencies among stations and locations. With the exception of a short period during recruitment (May) when more small fish were collected in Goalders Creek than at the nearby shoal station, none of the size-frequency comparisons differed significantly (Friedman's ANOVA, $P < 0.05$; O'Neil 1983).

TABLE 2.—Monthly temperature (°C), salinity (‰), and values and sediment analysis (% total dry weight) by trawl station, York River estuary, 1982.

Month	Goalders Creek			Blevins Creek		
	Upstream	Downstream	Shoal	Upstream	Downstream	Shoal
Mar.	11.0 (2.0)	11.0 (2.0)	11.0 (2.0)	9.5 (16.0)	9.5 (16.0)	
Apr.	13.5 (5.0)	13.5 (5.0)	15.0 (7.5)	16.0 (18.0)	16.0 (18.0)	17.0 (19.0)
May	20.5 (10.0)	20.0 (10.0)	21.0 (11.0)	24.0 (18.0)	24.0 (20.0)	24.0 (18.0)
June	26.0 (7.0)	26.0 (7.0)	26.0 (8.0)	25.5 (20.0)	25.0 (19.0)	25.0 (18.0)
July	29.0 (10.0)	29.0 (13.0)	29.0 (13.0)	28.0 (22.0)	28.0 (20.0)	29.0 (22.0)
Aug.	28.0 (11.0)	28.0 (11.5)	28.5 (10.0)	27.0 (22.0)	27.0 (19.5)	27.0 (20.0)
Sept.	26.0 (13.0)	26.0 (14.5)	26.0 (16.0)	25.0 (21.0)	26.0 (21.0)	25.0 (20.0)
Oct.	16.5 (11.0)	17.0 (11.0)	17.0 (12.0)	14.0 (20.0)	14.5 (22.0)	15.0 (20.0)
Sediments (Sample cores taken in May)						
Sand and gravel	83.45	29.86	11.06	52.21	59.07	93.07
Silt	7.72	27.29	43.87	33.83	27.92	3.05
Clay	8.83	42.85	45.07	13.96	13.01	3.83
Organics	9.12	15.96	10.79	4.09	5.16	0.74

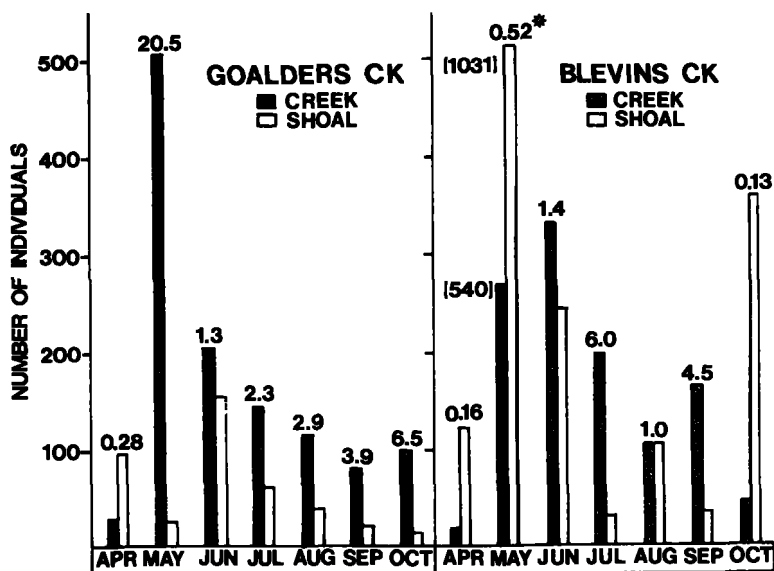


FIGURE 2.—Relative densities of spot at tidal creeks (values shown are monthly means of both creek stations) and shoal sampling localities. Asterisk indicates that May values for Blevins Creek are drawn to half scale. Values above histograms are ratios of creek to shoal densities.

Trophic Analysis

During this study, over 1,750 spot stomachs were removed and analyzed. In both creeks, spot underwent size-related, as well as temporal and spatial, changes in food utilization. Food utilization differences owing to size-related (ontogenetic) changes were examined by cluster analysis (Fig. 3). Calanoid copepods were the dominant prey of the smallest spot size classes (Fig. 4). The 26-30 mm size class had begun to consume more substrate-oriented prey (polychaetes and nematodes). All the spot examined between 40 and 100 mm SL had considerable overlap in a wide variety of food items. The great majority, however, were benthic organisms, e.g., maldanid and nereid polychaetes, *Leptocheirus* amphipods, free-living nematodes, and oligochaetes. Spot over 101 mm were clustered separately because of *Leucon americanus* in the diet. It thus appears that ontogenetic changes in spot diet shifted from a specialist mode when small to a more opportunistic strategy in larger size classes.

Size-class data were also subjected to reciprocal averaging ordination (Fig. 4). Results closely parallel those in the numerical classification. Axis 1, accounting for 49% of the variance, defined the small, planktonic size classes, which consumed

mostly calanoid copepods. The spot over 101 mm were separated along Axis 2, with *Leucon americanus* and *Monoculodes edwardsi* the dominant food items. The remaining size classes lay in the plane of Axes 2 and 3 in association with a large variety of benthic prey.

The dendrogram representing the differences between stations for all size classes of spot pooled (Fig. 5) indicated that there are two main clusters that correspond to the food distinctions between the two creeks. In addition, both shoal stations clustered as distinct outliers.

Dominant prey items at the Goalders Creek sites included nereid polychaetes, clam siphons, a gammarid amphipod (*Leptocheirus plumulosus*), and harpacticoid copepods. At Blevins Creek, spot utilized proportionately more nematodes, maldanid polychaetes, and oligochaetes. At both locations spot made significant use only of specific parts of some prey items, i.e., clam siphons and tails of maldanid polychaetes (Currin et al. 1984).

Prey utilization differences were also noted between the creek stations and the adjacent shoal. At Goalders Creek the amphipod *Monoculodes edwardsi*, which dominated feeding on the shoal, was partially responsible for the separation noted in the dendrogram (Fig. 5). In the polyhaline sys-

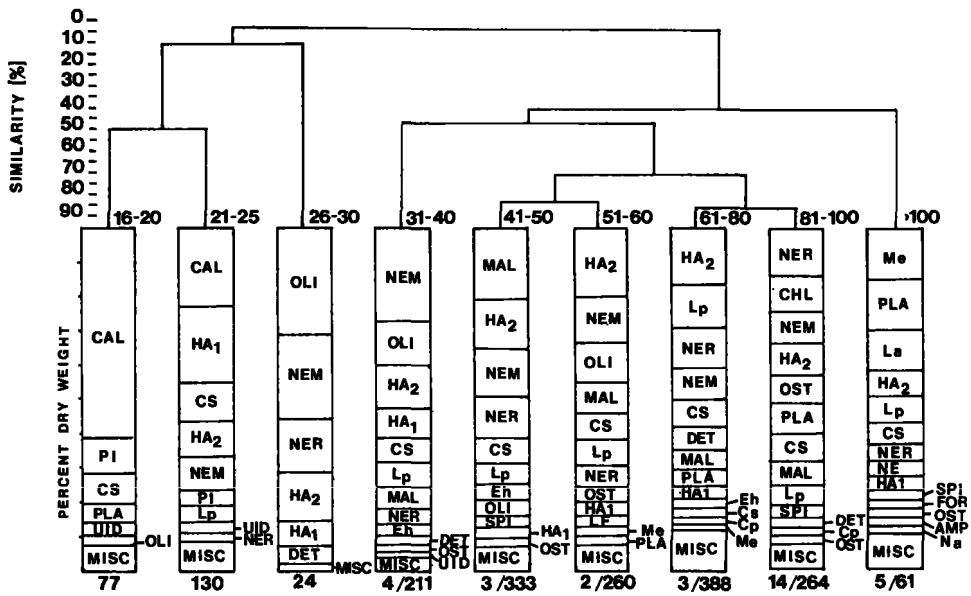


FIGURE 3.—Cluster analysis of prey similarity among *Leistostomus* size classes for the York River estuary, 1982. Prey abbreviations are listed in Table 1. Ratios at bottom of each column represent number of empty stomachs/total sample size.

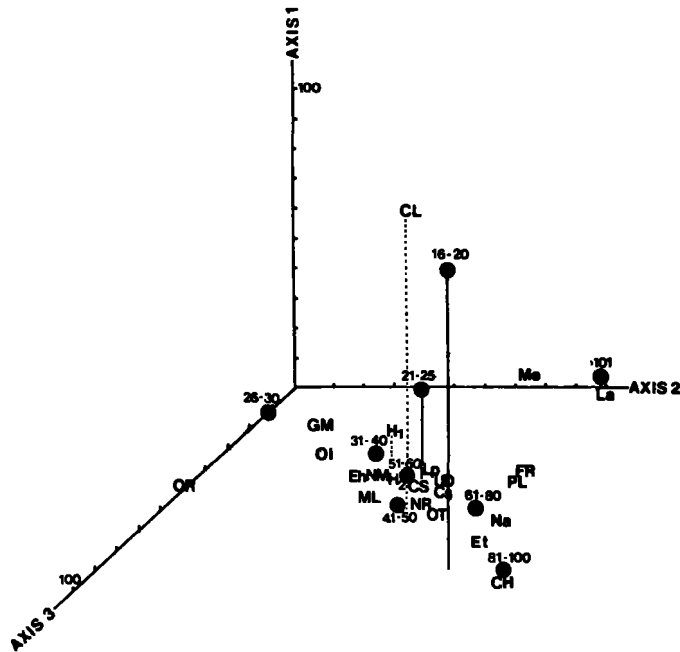


FIGURE 4.—Reciprocal averaging of prey and spot size class. Prey abbreviations: CH = Chlorophyta, CL = Calanoid copepods, Cs = *Crangon septemspinosa*, Eh = *Eteone heteropoda*, Et = *Edotea triloba*, FR = Foraminifera, GM = Gammaridae, H₁ = Small harpacticoid copepods, H₂ = Large harpacticoid copepods, La = *Leucon americanus*, Me = *Monoculodes edwardsi*, ML = Maldanidae, Na = *Neomysis americana*, OL = Oligochaeta, OR = Orbinidae, OT = Ostracods, PL = Plant matter.

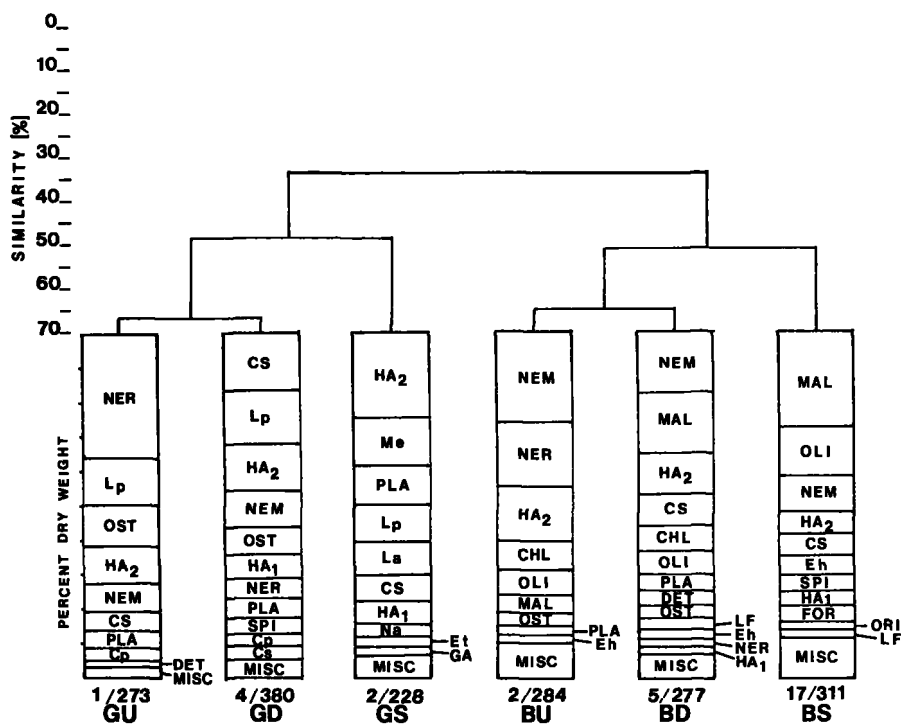


FIGURE 5.—Cluster analysis of prey similarity among habitats for spot from a polyhaline (BD = Blevins downstream, BU = creek, VA, 1982. Prey abbreviations are listed in Blevins upstream, BS = Blevins shoal) and a meso-oligohaline (GU = Goalders upstream, etc.) tidal Table 1. Ratios at the bottoms of each column represent number of empty stomachs/total sample.

tem, however, there were few clear differences caused by presence or absence of particular prey types. Instead, it was more a question of which food item was dominant. Spot appeared to eat more nematodes within the creek and more maldanid polychaetes on the shoal.

To confirm the results of the classification analysis, reciprocal averaging was used on the same food-habitat matrix (Fig. 6). Prey items located near a given station "lollipop" are the dominant food items utilized by spot at that station. Axis 1, accounting for 45% of the data variance, clearly separated the low and high salinity creek systems. Axis 2 (28% of the variance) isolated the shoal stations relative to the intracreek sites. Nematodes and maldanid polychaetes were again closely associated with the Blevins Creek sites. Nereids, *Leptocheirus*, and *Monoculodes* were dominant at the Goalders Creek habitats.

To compare seasonal patterns in food utilization between habitats, classification dendrograms were also constructed using monthly data for each creek (Figs. 7, 8). At Goalders Creek

there was little overlap of prey utilized in April compared to all other months (Fig. 7). The main reason for this appears to be the large proportion of calanoid copepods consumed in April. August and October were grouped together because of the amount of nereids eaten, and the remaining months were added to this cluster individually, depending on their overall dissimilarity.

April was also an outlier at Blevins Creek, because of the dominance of calanoids in the diet of young spot (Fig. 8). May and June were clustered together because of the similarity in the consumption of maldanid polychaetes and nematodes. August and September were similar in the proportions of four prey items utilized: maldanids, nematodes, nereids, and harpacticoid copepods. Although these food items were probably incidental in their diet, July was a separate group because of the large amount of Chlorophyta present in the stomachs examined from that month; October was isolated because Foraminifera became an important addition to the diet.

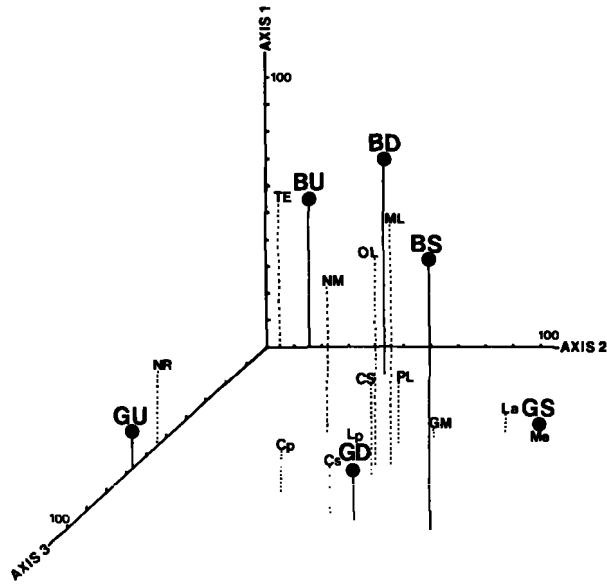


FIGURE 6.—Reciprocal averaging of prey and habitat for spot collected from tidal creeks and adjacent shoals of the York River, VA, 1982. Station abbreviations are the same as Figure 4. Prey abbreviations: Cp = *Cyathura polita*, CS = Clam Siphons, Ca = *Crangon septemspinosa*, GM = Gammaridae, Lp = *Leptocheirus plumulosus*, Me = *Monoculodes edwardsi*, ML = Maldanidae, NM = Nematoda, NR = Nereidae, OL = Oligochaeta, PL = Plant Matter, TE = Teleostei.

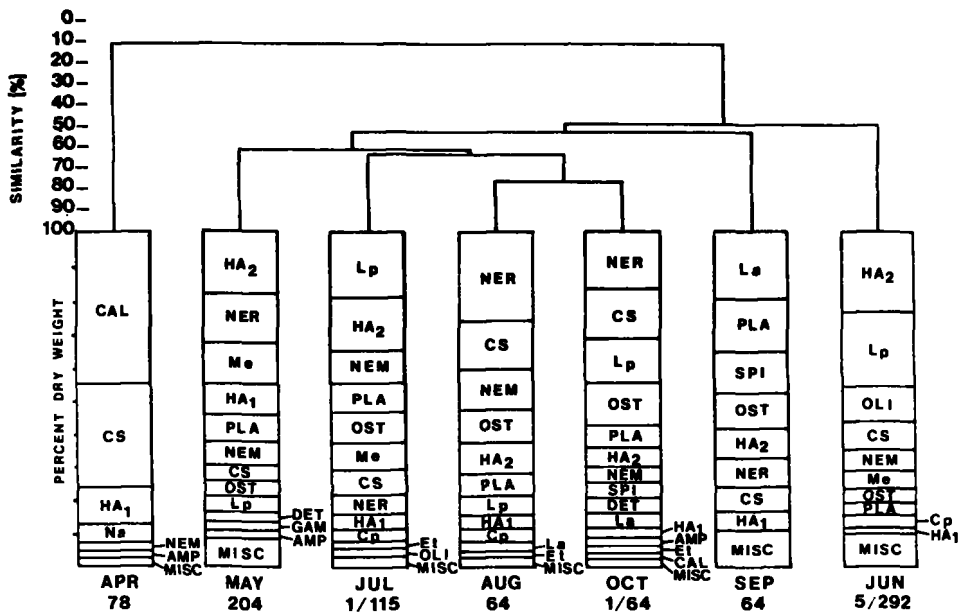


FIGURE 7.—Cluster analysis of monthly differences in prey utilization for young-of-year spot at Goalders Creek, VA, 1982. Prey abbreviations listed in Table 1. Ratios at the base of each column represent number of empty stomachs to total sample size.

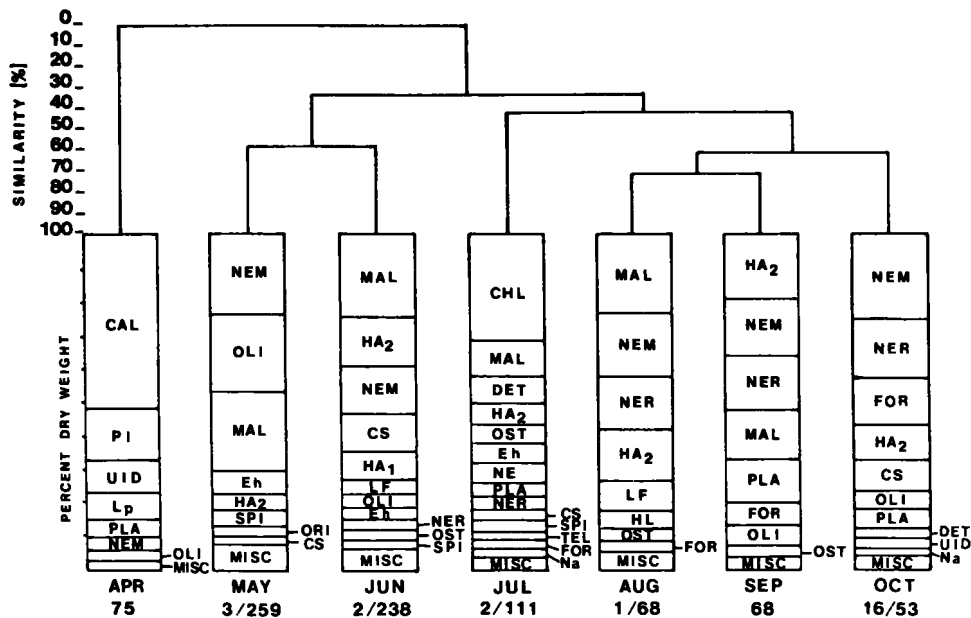


FIGURE 8.—Cluster analysis of monthly differences in prey utilization for young-of-year spot at Blevins Creek, VA, 1982. Prey abbreviations listed in Table 1. Ratios at base of each column represent number of empty stomachs/total sample.

DISCUSSION

As Livingston (1982) stated, "While food habits of fishes have been studied extensively, specific relationships of trophic interactions, habitat partitioning, and spatial/temporal variability of coastal fishes remain largely undetermined." While a more comprehensive understanding of these processes awaits properly designed experiments and hypothesis testing, several common patterns have begun to emerge. Despite the apparent abundant resources of the estuary as a whole, there seems to be a consistent "tracking" (among species) of these resources, reminiscent of resource partitioning in other aquatic systems (e.g., coral reefs). Individual species distributions are probably controlled by physiological constraints, predation pressure, and the availability of food (or a combination of these factors). That this tracking process, if real, may result from periodic scarcity of food in estuaries was tentatively stated by Thayer et al. (1974) and only recently reinforced by the studies of Weisburg and Lotrich (1986). The latter authors used experimental techniques to demonstrate food limitation occurring in the mummichog *Fundulus heteroclitus*, among fishes perhaps the most

"perfectly" adapted food generalist in the estuary.

We did not observe differences in relative fullness of spot stomachs between the two creek localities examined (O'Neil and Weinstein, unpubl. data). Therefore, suitable food appears to be readily available in both creeks. The types of prey utilized in each area, however, were different and generally followed the temporal and spatial distributions of the dominant macrobenthos in these creeks (Robert Diaz⁴). Spot apparently feed opportunistically on the available resources present in the tidal creeks and shoals at any one time and do well throughout the estuary. There were no differences in growth rates or condition of spot observed in the tidal creeks in our study (Weinstein and O'Neil⁵). Thus, from an energetics standpoint, spot seem able to achieve similar growth rates in different creeks (and corresponding salinity regimes).

Hodson et al. (1981) noted that individual stomachs of small spot captured in the Cape Fear estuary were typically dominated by a single food cat-

⁴Robert Diaz, Virginia Institute of Marine Science, Gloucester Point, VA 23062, pers. commun. July 1983.

⁵Weinstein, Michael P., and Steven P. O'Neil. manuscr. in prep. Virginia Institute of Marine Science, Gloucester Point, VA 23062.

egory. This was also observed in the present investigation. Individual stomachs from spot captured in the same sample were often found to contain thousands of harpacticoid copepods or were completely distended by half a dozen nereid polychaetes. Such observations reinforce the notion of opportunism and feeding activities related to the concentration and availability of prey.

Spot, as well as other estuarine sciaenids, undergo distinct ontogenetic changes in feeding mechanisms with increasing size (Chao 1976; Chao and Musick 1977; Govoni 1981). Postlarvae and small juveniles are characterized by large eyes and a terminal mouth. They prey on mainly pelagic calanoid copepods and other small plankton (Townsend 1956; Peters and Kjelson 1975; Kjelson et al. 1975; present study). April was an outlier in the seasonal dendrograms of Figures 6 and 7 because the majority of spot at that time were in the smallest size class in Figure 8 and fed on mainly calanoid copepods. Although Thayer et al. (1974) concluded that food for meroplanktonic life stages of estuarine fishes may be limiting, we observed no differences in feeding success between spot consuming plankton and those eating benthos.

At about 20 mm SL, spot become more benthic oriented, feeding on various epifauna and infauna (Livingston 1982; present study). Sheridan (1979) also noted a distinction in prey utilization of smaller spot (20-29 mm). In the habitats of Florida's Apalachicola Bay, however, he noted that individuals in this size class consumed more insect larvae and polychaetes than copepods. His larger size classes utilized more bivalves. The difference between his observations and those in our study may simply be due to the difference in prey availability at the various locations. It should also be noted that other studies on the food habits of spot failed to recognize any size-related differences (Roelofs 1954; Darnell 1958; Stickney et al. 1975; Chao and Musick 1977; Hodson et al. 1981). This is possibly due to the selective nature of the gear used. Large seines and trawls fail to sample small fish (Chao and Musick 1977), and block netting in the high marsh may select against large fish (Hodson et al. 1981).

The dominant prey items consumed by spot in each habitat, and the basis for intercreek and shoal versus creek differences observed during our study, are partly explained by distribution patterns of macrobenthic invertebrates reported by Boesch (1977) for the York River, VA. Although that study was conducted several years

before ours, and were restricted to the river shoals and channels, there is a close parallel between the patterns Boesch described and the diet of spot from similar localities within the York River. Boesch described a group of species that were "characteristically abundant in salinities of 10-20‰ throughout the Chesapeake Bay system but were not usually as abundant in higher salinities except in shallow water habitats or following disturbances." He referred to them as euryhaline opportunists that were important dietary constituents of spot at both creeks in our study.

Most of the identifiable polychaetes encountered in spot stomachs were from this group, e.g., *Nereis succinea*, *Eteone heteropoda*, and *Paraprionospio pinnata* (Spionidae). The cumacean *Leucon americanus* also belongs to this group and together with the amphipod *Monoculodes edwardsi* was consumed in large quantities by spot on Goaders shoal (Fig. 8). *Monoculodes* is a member of the group Boesch described as estuarine endemics, which are most frequent in meso-oligohaline areas. Down-estuary at Blevins Creek, the maldanid polychaetes, especially *Clymenella torquata*, figured prominently in spot diets and were determined to be most abundant in that vicinity by Boesch.

In another study, Boesch (1973) examined macrobenthic distributions as related to sediment composition and seasonality in Hampton Roads, VA. Those results give further insight to prey availability for the habitats and time periods described in the present study. Boesch (1973) found *Eteone heteropoda* more common in May and rare in August, but distributed over all sediment types in the areas of lower salinity. This species was commonly consumed by spot at Blevins Creek in May, June, and July (Fig. 7). Another polychaete, *Polydora ligni*, was common in stomachs from Blevins Creek only in April, and Boesch (1973) noted it was more abundant in the estuary between February and May. *Clymenella torquata*, also consumed at Blevins Creek, was less abundant seasonally but showed a preference for muddy-sand sites. This species was a dominant component in the diet of spot at the downstream and shoal stations, both of which had higher proportions of sand compared to the upstream station. Two polychaetes, *Nereis succinea* and *Paraprionospio pinnata* (Spionidae), were found by Boesch (1973) in sand-mud and mud-sand sediments, respectively, which generally characterized the Goaders upstream and downstream substrates, respectively (Table 2). Thus, it is likely

that spot feed on seasonally and spatially dominant prey types from the available array and that the observed differences between creeks and shoals simply reflect availability of dominant prey types. The diversity of food types in spot stomachs may also reflect the general strategy of the feeding opportunist, which is favored when 1) food densities are periodically low and there is a premium on the ability of the predator to take a range of prey, 2) the predator has a relatively long period to gain energy, and 3) prey densities fluctuate widely (Schoener 1969). These are characteristics of the marsh habitats that spot frequent as well as the general life history strategy of spot in terms of spawning season and residence period in the primary nurseries (Weinstein 1981; Weinstein and O'Neil 1986).

Finally, there is the question posed in the introduction to this paper, i.e., the relative role of these tidal creeks as feeding versus refuge zones. As suggested in the introduction and discussed above, there seemed to be adequate food for growth of spot in tidal creeks and shoal areas, at least during the year of this study. This observation was confirmed in a separate effort using increments of daily growth observed in the otoliths of spot collected in Goaders and Blevins Creeks in 1983, and in the same two creeks plus a mesohaline creek (Kings Creek, also located in the York River system) in the following year 1984 (Weinstein and O'Neil fn. 5). Unfortunately, comparative data on the mortality of spot in different tidal creeks and other habitats are not readily available. Weinstein and Walters (1981) reported evidence of differences in spot mortality among creeks in different marshes of the Cape Fear River estuary. Mortality was significantly higher in the polyhaline marshes of the Cape Fear system in 1977, and although the mean value was highest in the same marshes in 1978, the overall variability of the data resulted in a nonsignificant difference among marshes. Mortality rates calculated for spot in the studies of Weinstein (in press) and Weinstein et al. (1984) in Little Monday Creek and Blevins Creek (located about 1 km apart) differed from the values reported for polyhaline creeks in the Cape Fear estuary 0.029 and 0.015/day versus 0.061 and 0.052/day, respectively. The difference in mortality rates calculated for the two studies lies partly in the age distribution sampled from each population (youngest age cohorts were not sampled in the York River), but this factor alone is not believed to account for all of the difference in the rates.

The role of differential mortality in shaping the population dynamics of this species is clearly in need of further study.

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LITERATURE CITED

- BOESCH, D. F.
1973. Classification and community structure of macrobenthos in Hampton Roads area, Virginia. *Mar. Biol.* 21:226-244.
1977. A new look at the zonation of benthos along the estuarine gradient. In B. C. Coull (editor), *Ecology of marine benthos*, p. 245-266. Univ. South Carolina Press, Columbia.
- BOESCH, D. F., AND R. E. TURNER.
1984. Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries* 7(4A):460-468.
- CARR, W. E. S., AND C. A. ADAMS.
1972. Food habits of juvenile marine fishes: evidence of the cleaning habit in the leatherjacket, *Oligoplites saurus*, and the spottail pinfish, *Diplodus holbrooki*. *Fish. Bull.*, U.S. 70: 1111-1120.
- CHAO, L. N.
1976. Aspects of systematics, morphology, life history and feeding of western Atlantic Sciaenidae (Pisces: Perciformes). Ph.D. Thesis, College of William and Mary, Williamsburg, VA.
- CHAO, L. N., AND J. A. MUSICK.
1977. Life history, feeding habits and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. *Fish. Bull.*, U.S. 75:657-702.
- CLIFFORD, H. T., AND W. STEPHENSON.
1975. An introduction to numerical classification. *Acad. Press*, N.Y., 229 p.
- CURRIN, B. M., J. P. REED, AND J. M. MILLER.
1984. Growth, production, food consumption, and mortality of juvenile spot and croaker: A comparison of tidal and nontidal nursery areas. *Estuaries* 7(4A):451-459.
- DARNELL, R. M.
1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. *Publ. Inst. Mar. Sci. Univ. Texas* 5:353-416.
- GAUCH, H. G., JR.
1977. Ordiflex: a flexible computer program of four ordination techniques. Release B. *Ecol. System*, Cornell University, Ithaca, N.Y., 187 p.
- GOVONI, J. J.
1981. Alimentary canal development and its relation to the early life history of spot, *Leiostomus xanthurus* Lace-

- pede. In R. Lasker and K. Sherman (editors), The early life history of fish: Recent studies, p. 315. Cons. Int. Explor. Mer., Copenhagen, Denmark.
- GUINOCHE, M.
1973. Phytosociologie. Masson, Paris.
- HERKE, W. H.
1971. Use of natural and semi-impounded Louisiana tidal marshes as nurseries for fishes and crustaceans. Ph.D. Thesis, Louisiana State Univ., Baton Rouge.
- HILL, M. O.
1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61:237-249.
- HODSON, R. G., J. O. HACKMAN, AND C. R. BENNETT.
1981. Food habits of young spots of the Cape Fear River estuary, North Carolina. Trans. Am. Fish. Soc. 110:495-501.
- HURTUBIA, J.
1973. Trophic diversity measurement in sympatric predatory species. Ecology 54:885-890.
- KJELSON, M. A., D. S. PETERS, G. W. THAYER, AND G. N. JOHNSON.
1975. The general feeding ecology of postlarval fishes in Newport River estuary. Fish. Bull., U.S. 73:137-144.
- LANCE, G. N., AND W. T. WILLIAMS.
1967. A general theory of classification sorting analysis. I. Hierarchical systems. Comput. J. 9:373-380.
- LIVINGSTON, R. J.
1982. Trophic organization of fishes in a coastal seagrass system. Mar. Ecol. Prog. Ser. 7:1-12.
- LUCAS, J. R.
1982. Feeding ecology of the gulf silverside, *Menidia peninsulae*, near Crystal River, Florida, with notes on its life history. Estuaries 5:138-144.
- O'NEIL, S. P.
1983. The distribution and trophic ecology of young-of-year spot (*Leiostomus xanthurus*; Lacepede) in polyhaline versus meso-oligohaline tidal creeks and adjacent shoals of the York River, Virginia. M.S. Thesis, Virginia Commonwealth Univ., Richmond.
- PARKER, J. C.
1971. The biology of the spot, *Leiostomus xanthurus* Lacepede, and Atlantic croaker, *Micropogon undulatus* (Linnaeus) in two Gulf of Mexico nursery areas. Ph.D. Thesis, Texas A & M Univ., College Station.
- PETERS, D. S., AND M. A. KJELSON.
1975. Consumption and utilization of food by various postlarval and juvenile fishes of North Carolina estuaries. In E. L. Cronin (editor), Estuarine research, Vol. 1, Chemistry, biology and the estuarine system, p. 448-472. Acad. Press, N.Y.
- REMANE, A.
1934. Die Brackwasser fauna. Zool. Anz. (Suppl.) 7:34-74.
- ROELOFS, E. W.
1954. Food studies of young sciaenid fishes, *Micropogon* and *Leiostomus*, from North Carolina. Copeia 1954: 151-153.
- SCHOENER, T. W.
1969. Optimal size and specialization in constant and fluctuating environments: an energy-time approach. Brookhaven Symp. Biol. 22:103-114.
- SHERIDAN, P. F.
1979. Trophic resource utilization by three species of sciaenid fishes in a northwest Florida estuary. Northeast Gulf Sci. 3:1-15.
- SMITH, S. M., J. G. HOFF, S. P. O'NEIL, AND M. P. WEINSTEIN.
1984. Community and trophic organization of nekton utilizing shallow marsh habitats, York River, Virginia. Fish. Bull., U.S. 82:433-467.
- 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.
- STONER, A. W.
1980. The feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): variation and functional responses. Fish. Bull., U.S. 78:337-352.
- THAYER, G. W., D. E. HOSS, M. A. KJELSON, W. F. HETTLER, JR., AND M. W. LACROIX.
1974. Biomass of zooplankton in the Newport River in relation to prey size and habitat structure: Consequences for prey distribution and abundance. J. Exp. Mar. Biol. Ecol. 23:255-266.
- TOWNSEND, L.
1956. A study of the spot, *Leiostomus xanthurus*, in Alligator Harbor, Florida. M.S. Thesis, Florida State Univ., Tallahassee, 43 p.
- VINCE, S. I., VALIELA, AND N. BACKUS.
1976. Predation by salt marsh killifish, *Pundulus heteroclitus* (L.) in relation to prey size and habitat structure: consequences for prey distribution and abundance. J. Exp. Mar. Bio. Eco. 23:255-266.
- WEINSTEIN, M. P.
1979. Shallow marsh habitats as primary nurseries for fishes and shellfish, Cape Fear River, North Carolina. Fish. Bull., U.S. 77:339-357.
1981. Plankton productivity and the distribution of fishes on the southeastern U.S. continental shelf. Science 214:351-352.
1983. Population dynamics of an estuarine-dependent finfish along a tidal creek-seagrass meadow coenocline. Can. J. Fish. Aquat. Sci. 40:1633-1638.
- WEINSTEIN, M. P., AND H. A. BROOKS.
1983. Comparative ecology of nekton residing in a tidal creek and adjacent seagrass meadow: community composition and structure. Mar. Ecol. Prog. Ser. 12:15-27.
- WEINSTEIN, M. P., AND S. P. O'NEIL.
1986. Exchange of marked juvenile spots between adjacent tidal creeks in the York River estuary, Virginia. Trans. Am. Fish. Soc. 115:93-97.
- WEINSTEIN, M. P., AND M. F. WALTERS.
1981. Growth, survival, and production in young-of-year spot *Leiostomus xanthurus* Lacepede, residing in tidal creeks. Estuaries 4:185-197.
- WEINSTEIN, M. P., S. L. WEISS, AND M. F. WALTERS.
1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear Estuary, North Carolina. Mar. Biol. 58:227-243.
- WEINSTEIN, MICHAEL P., LARRY SCOTT, STEVEN P. O'NEIL, ROBERT C. SIEGFRIED, AND STEPHEN T. SZEDLMAYER.
1984. Population dynamics of spot, *Leiostomus xanthurus*, in polyhaline tidal creeks of the York River Estuary, Virginia. Estuaries 7:444-450.
- WEISBERG, S. B., AND V. A. LOTRICH.
1982. The importance of an infrequently flooded intertidal marsh surface as an energy source for the mummichog *Fundulus heteroclitus*: An experimental approach. Mar. Biol. 66:307-310.
1986. Food limitation of a Delaware salt marsh population of the mummichog, *Fundulus heteroclitus* (L.). Oecologia 68:168-173.